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

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1 **Title: A temperature-driven model of phenological mismatch**

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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.

38   **Keywords:**

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

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41   **1. Introduction**

42   Anthropogenic climate change has increasingly disrupted ecological interactions for the past

43   century (Pachauri et al., 2014). This trend is expected to continue and amplify as interacting

44   species are likely to respond differently to similar environmental changes and selective pressures

45   (Parmesan, 2006). Trophic interactions between consumers and resources, which are

46   fundamental to the functioning of ecosystems, may be affected by climate change through: (1)

47   direct changes in life history traits (e.g., fecundity, mortality) of consumer and/or resource (Bale

48   et al., 2002), (2) changes in abundance of consumer and/or resource due to cascading effects

49   from other trophic levels (e.g., changes in the consumer's predators) (Both, et al., 2009), and (3)

50   differential shifts in the phenology of consumer and/or resource leading to phenological

51   mismatch (Kharouba et al., 2018).

52   The concept of phenological mismatch has evolved since its inception in the early 1990s

53   and is still debated today (e.g., Singer & Parmesan, 2020's response to Kharouba & Wolkovich,

54   2020). In its stricter, original form, it states that the recruitment of a consumer is highest if the

55   most energy expensive part of its life cycle is in synchrony with the peak availability of its

56   resource (Cushing, 1990). The concept was later extended to the case where the phenologies of

57   consumer and resource varied (Visser & Holleman, 2001), but still assumed that maximum

58   fitness of the consumer is achieved at phenological synchrony. However, recent observations

59   suggest that, in some systems, phenological mismatch is the historical baseline (Singer &

60   Parmesan, 2010). Historical mismatch can result from trade-offs between fecundity and mortality

61   (Singer & Parmesan, 2010), mutualistic interactions (Forrest & Thomson, 2012) or intraspecific

62   competition (Iwasa et al., 1983). Relaxing the assumption of baseline synchrony complicates

63   predictions of potential climate change impacts. Indeed, if synchrony is the baseline, any

64   differential change will be detrimental to the consumer's fitness. If the baseline is a mismatch, a

65   change that decreases asynchrony will likely be beneficial to the consumer (but see Régnière &

66   Nealis, 2018) while the opposite might exacerbate the detrimental effect of asynchrony to the

67   point of extinction of the consumer (Singer & Parmesan, 2010).

68   Many organisms have advanced their phenology in recent decades (Post et al., 2001;

69   Parmesan & Yohe, 2003), particularly the timing of spring events at mid-high latitudes

70   (Parmesan, 2006; Cohen et al., 2018). In a meta-analysis of 27 pairs of interacting species,

71   Kharouba et al. (2018) found that phenology advanced by an average of 4 days/decade across

72   species since the early 1980s. Interacting species have advanced their phenology by similar

73   magnitudes, resulting in relatively small (6.1 days/decade) but significant increases in mismatch.

74   The observed mismatch had no consistent direction as 31 interactions shifted closer while 23

75   shifted further apart. The clearest examples of climate-driven mismatch have been reported for

76   insect herbivores at high altitudes or latitudes (Renner & Zohner, 2018), where many organisms

77   rely on a seasonal resting period because temperatures affecting physiological processes tend to

78   be below species optima for most of the year. After a seasonal arrest in development that can last

79   for several months, synchrony between the emergence of phytophagous insects from diapause

80   and the end of their host plants dormancy, is critical to the consumer's fitness (Van Asch &

81   Visser, 2007). Spring defoliators have evolved to exploit foliage at its annual optimal nutritional

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82   qualities, i.e., high concentration in nutrient and water and low concentrations in fibre and

83   secondary metabolites (Mattson & Scriber, 1987). This strategy requires a precise phenological

84   match between the consumer and its resource because the quality of foliage declines quickly with

85   foliar expansion. If the consumer emerges too early, it may encounter a long initial period with

86   no food or poor food quality. If it emerges too late, the speed at which the nutritional quality of

87   the foliage degrades may outpace the consumer's capacity to adjust physiologically, thus

88   negatively impacting its fitness.

89   The seasonal resting phase of many organisms is divided into two successive stages called

90   endodormancy and ecodormancy in perennial woody plants, and diapause and quiescence in

91   insects (Chuine & Régnière, 2017). Development and metabolism are generally inhibited by

92   internal factors (e.g., depletion of energy reserves, hormones) in the first stage and by external

93   factors (e.g., temperature, photoperiod) in the second. In our study system, the consumer and its

94   resource show a seasonal resting period during part of the year (e.g., during winter). For both, we

95   assume that the first stage is accomplished early in the winter before the return of favourable

96   conditions, a common case in temperate and colder climates, and that temperature is the main

97   driver that triggers the end of the second stage and therefore the resting period. We will refer to

98   the second stage of the seasonal resting period simply as the "resting period".

99   Science is currently unable to predict the direction or the magnitude of phenological

100   mismatch between consumer and resource induced by climate change and the associated risks

101   that it poses to species (Samplonius et al., 2021). While patterns of change in phenological

102   synchrony are observed at an increasing rate because of climate change (Kharouba et al. 2018),

103   they have been difficult to explain mechanistically. Different mechanisms can lead to a

104   phenological mismatch between a consumer and its resource. Different species can respond to

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105   different climatic factors or to the same factor but in a different way.   Species can also face

106   different constraints in phenological plasticity (Both & Visser, 2001) or have different costs

107   associated with phenological response (Gienapp & Visser, 2006).

108   The aim of this study is to investigate potential effects of climate change on the

109   phenological synchrony between a consumer and its resource when both species respond to the

110   same climatic factor (i.e., temperature). The interaction occurs at the end of both species' resting

111   periods, which is often the case for insect herbivores in mid-high latitudes. We begin with the

112   general theoretical aspects that determine the duration of the resting period according to

113   temperature, and their effects on synchrony / mismatch between phenological stages of the two

114   species. Then we use a major insect pest of the Canadian boreal forest, the spruce budworm

115   (SBW), and its main host, balsam fir, as a case study. We investigate the phenological synchrony

116   between budworm's emergence from winter diapause and balsam fir's budburst across a gradient

117   of latitudes and a number of different future climates.

118   2. The general model

119   We begin with a unified description of the mechanisms that determine the duration of the resting

120   period of a consumer and its resource in terms of accumulation of ambient temperature. Then, we

121   develop the main theoretical results at the single species level and for two interacting species.

122   2.1 Theoretical development

123   Throughout the resting period, an organism accumulates units of some quantity. The

124   instantaneous rate of accumulation depends on ambient temperature. The resting period ends

125   when a certain level of the quantity has accumulated. For trees, this quantity can be heat, for

126   example in degree-day models (Colombo, 1998) or more recent nonlinear models (Chuine, 2000;

127   Desbiens, 2007). For insects, the quantity can be the proportion of the corresponding life-cycle

128   stage that they have completed (also referred to as physiological stage) (Cobbold & Powell, 2011;

129   Régnière, et al., 2012). Since the development rate is temperature dependent, this quantity

130   ultimately measures accumulated heat. This concept of an accumulating quantity is "still the most

131   important assumption in plant and animal phenology modelling" (Chuine & Régnière, 2017).

132   We denote time by t in days and temperature by $x = x(t)$ in degrees Celsius. The

133   instantaneous rate of accumulation is some nonnegative, increasing function of temperature,

134   denoted by $R = R(x)$. While developmental rates may decrease when temperatures exceed an

135   upper threshold (Amarasekare & Coutinho, 2014), such temperatures do not generally arise

136   during the winter resting period in mid-high latitudes. The resting period begins at time t_0 and

137   ends at time t^* when the accumulated quantity reaches the threshold level F. The fundamental

138   equation that connects all these quantities and determines the end of the resting period is

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

139   A typical example for the accumulation rate function is

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

140   with parameters $b < 0$ and c (Chuine, 2000; Rebaudo & Rabhi, 2018). We illustrate the rate

141   function in Eq. 2 as well as the condition in Eq. 1 for two different species and two simplistic

142   temperature time series in Figure 1. As temperature patterns during the resting period change

143   because of climate change, the end time of the resting period of a species may shift. When

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144   temperatures increase, accumulation occurs faster and the phenology advances, i.e., the end time

145   is earlier (Fig. 1D).

146   We are particularly interested in the case where the two species are a consumer and its

147   resource. Their rate accumulation functions generally differ even in the same temperature regime

148   (compare solid and dashed curves in Fig. 1C), which typically leads to different end times of the

149   resting period (Fig. 1D). In view of our intended application, we also refer to the consumer as the

150   insect and to the resource as the tree. We denote the corresponding end times by t_e^* (emergence

151   time) for the consumer (insect) and by t_b^* (budburst time) for the resource (its host tree). We call

152   the difference in end times the *mismatch* between the two species (i.e., *mismatch* = t_e^*-t_b^*). When

153   the end times of the resting period of two species respond differently to climate change, then the

154   mismatch between the two species will change. This is the fundamental quantity that we study

155   here (Fig. 1D).

2.2 Theoretical results

157   Model equation (Eq. 1) can in general not be solved explicitly for the end time, t^*, at least not for

158   realistic temperature time series $x(t)$. Instead, we derive a general approximation formula for how

159   t^* changes when future temperature time series ($x_2(t)$) deviate from historical expectation ($x_1(t)$)

160   by a small amount (see Supplementary Material). We use this formula to evaluate and discuss the

161   impact of climate change on the phenology of a single species and the phenological mismatch

162   between two species in two particular cases: a constant temperature difference throughout the

163   resting period or a warm or cold spell during a short time period. Our results here apply to any

164   general rate accumulation function.

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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

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

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

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

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

178 slope. For the rate function in Eq. 2, this occurs at temperature $x=c$.

179   **2.2.2 Effects on the mismatch between two species**

180   When heat accumulation occurs independently in each species, the mismatch between the two

181   changes if they respond differently to changes in temperature. The mismatch increases if the

182   phenology of the earlier emerging species advances more quickly and decreases if it advances

183   more slowly. Equations 3 and 4 require information about the current phenology $(R(x_1(t_1^*)))$ and

184   the sensitivity $(R'(x_1(t_1)))$ to quantify the change in phenology in each species and therefore the

185   change in mismatch.

186   For a theoretical example, we consider the scenario that the resource emerges before the

187   consumer and is more sensitive at lower temperatures. Then, if temperatures are higher than

188   historical averages early in the season, the phenology of the resource is likely to advance more

189   than that of the consumer, so that the mismatch increases. Vice versa, if temperatures exceed

190   historical averages only late in the season, when the consumer is more sensitive, the phenology of

191   the consumer is expected to advance more, so that the mismatch decreases. Hence, a change in

192   mismatch is most likely if the two species are most sensitive at different temperatures, i.e., when

193   the maximal slopes of their respective rate accumulation functions occur at very different

194   temperatures.

195   In reality, the periods of high sensitivity of the two species may overlap more or less, and

196   the rate functions at emergence time (the terms in the denominators in Eqs 3 and 4) could differ

197   significantly. As a result, the effect of temperature increases depends on details of each scenario.

198   We illustrate this dependence using a simplified time series of daily mean temperatures as

199   modelled by

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

200   where the mean, amplitude and offset have been chosen to match historical averages in

201   Fredericton (NB, Canada). We denote the end times of the consumer for the time series $x_i(t)$ by

202    $t_{e,i}{}^*$ (emergence time) and of the resource by $t_{b,i}{}^*$ (budburst time).

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

204   Eq. 3 to each species (R_e is for the insect, and R_b is for the tree). The resulting mismatch changes

205   according to

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

206   The resulting linear approximation captures the actual end of the resting period very well (see

207   supplementary Fig. S1). The derivative has to be integrated over the whole development period.

208   Thus, it is difficult to estimate the resulting trend at first glance because it mostly depends on the

209   amount of time that temperatures stay in the sensitive range of each species (that drives the

210   numerator values), but it also depends on the value of the function at emergence time

211   (denominator).

212   When future time series differ from historical expectation by a short spell of duration Δt

213   and temperature difference Δx, we apply the corresponding formula (Eq. 4) to each species. Then

214   the mismatch changes according to

$$t_{e,2}^* - t_{b,2}^* = t_{e,1}^* - t_{b,1}^* - \Delta x \Delta t \left(\frac{R_e'(x_1(t_s))}{R_e(x_1(t_{e,1}^*))} - \frac{R_b'(x_1(t_s))}{R_b(x_1(t_{b,1}^*))} \right). \qquad \text{Eq. 7}$$

$$\underbrace{t_{e,2}^* - t_{b,2}^*}_{mismatch2} = \underbrace{t_{e,1}^* - t_{b,1}^*}_{mismatch1}$$

215   In case of non-overlapping sensitivity periods, each species exhibits a sensitivity that is a

216 relatively narrow peak around a maximum at $x=c_i$, and they peak at different temperatures. The

217 phenology of one species will advance noticeably only when the spell occurs near its peak

218 temperature. The other species is not affected (Fig. 2A).

219   In the case of two overlapping sensitivity periods, one species (e.g., the consumer) may

220 exhibit a broader sensitivity that peaks at a different temperature than the other species (e.g., the

221 resource). Hence, in this example, the phenology of the consumer will advance noticeably no

222 matter when a warm spell occurs, whereas the phenology of the resource will advance noticeably

223 only when it occurs near the temperature $x=c_1$ (Fig. 2B).

224   However, among all scenarios, the rate function at emergence (the denominators in Eq. 7)

225 may differ vastly between the two species. Consequently, even if the resource is more sensitive

226 than the consumer at the time of the spell ($R_e' > R_b'$), the difference in parentheses in Eq. 7 can

227 still be negative if the denominator in the first term is much larger than in the second.

228   Despite their simplicity, these scenarios give us some important insights into the evolution

229 of the mismatch. The advance of the phenology of each species is a nonlinear function of

230 temperature increase and each species has a temperature regime during which its phenology is

231 most sensitive to change, namely when the slope of the rate function is large. In this section, we

232 used Eq. 1 to develop general theoretical insights. The model is agnostic about the specific R

233 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

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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.

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, et al., 2014).

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

256   trees (Régnière & Nealis, 2008). Consequences for late-emerging SBW are severe: larval

257 survival is depressed (from about 60% normal survival down to 10%), development is delayed,

258 and average pupal mass decreases by about 50% (Lawrence et al., 1997). In the boreal forests of

259 eastern Canada, the higher vulnerability of balsam fir to SBW defoliation compared to other host

260 species has been attributed to its early budburst (Blais, 1957). The emergence of SBW generally

261 precedes balsam fir budburst by several days. Balsam fir phenology appears to be related to

262 forcing temperatures but not photoperiod (Osawa et al., 1983).

263 We assessed historical patterns and climate change predictions of synchrony between

264 SBW's emergence from diapause and balsam fir's budburst using an existing model of budworm

265 phenology and a general budburst model fitted to observations of budburst phenology in Canada.

266 Each species has its own accumulation function which we used to illustrate the general

267 theoretical case (see section 2.2.2 and Fig. 2).

268 3.2 Phenological models

269 3.2.1 Phenological model of spruce budworm's spring emergence

270 The first stage of SBW diapause is assumed to end in late winter, but the physiological processes

271 and environmental factors that control this are still unknown (Bean, 1961). For modelling

272 purposes, March 1st is generally taken as the start of the quiescent stage (Régnière, et al., 2012).

273 Taking an earlier starting date would not affect the predicted date of emergence since

274 temperatures are generally well below the 2.5ºC development threshold prior to March 1st across

275 the vast majority of SBW's geographical range. The heat accumulation rate of the overwintering

276 stage (L_{2o}) of SBW is defined as (Régnière, et al., 2012)

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$$R(x(t)) = \begin{cases} \beta_1\left[\dfrac{1}{1 + exp\,(\beta_2 - \beta_3^\tau)} - exp\,((\tau - 1)/\beta_4)\right], if\, x_b \leq x(t) \leq x_m \\ 0, otherwise \end{cases}$$

Eq. 8

277   where

$$\tau = \frac{x(t) - x_b}{x_m - x_b}$$

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 $F=1$.

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   et al., 2014). BioSIM interpolates weather station historical data and climate change scenarios

308   across North America. We used data from 1996 to 2016 to explore latitudinal trends of past insect

309   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.

315   Both models used temperature data with a four-hour time interval, which allows for the

316   capture of warm events within a day.

3.4. Mismatch in the spruce budworm - balsam fir system

3.4.1 Fitting and sensitivity

319   Fitting the *Uniforc* model to phenological data from Quebec and New Brunswick resulted in the

320   parameter values: b = -1.32, c = 7.14 °C, t_0 = 87 (March 28th), and F^* = 18.6 (RMSE = 12.6).

321   The residuals of this fitting follow a Normal distribution centred on 0 (Fig. 5A). There is no

322   obvious pattern for the residuals across latitude in the range of our study (Fig. 5B).

323   In order to test the accuracy of both insect and tree models, we compared predicted budburst

324   and emergence date with available data for two years (2013, 2014) in two sites in Quebec

325   (Pureswaran, et al., 2019). Measured budburst occurred between May 16th and June 17th, in

326   2013, and between May 29th and June 15th, in 2014. The model predicts a median budburst on

327   May 27th in 2013, and May 28th in 2014. For the insect, the emergence peak occurred on May

328   9th in 2013, and on May 23th in 2014. The model predicts a median emergence on May 20th in

329   2013, and May 21th in 2014. Hence, the model gives satisfactory results.

330   The budworm model is sensitive to most parameters (Fig. 5C). The only exception is x_m (the

331   maximal temperature) since very high temperatures are rare during late winter and spring, and to

332   a certain extent β_1. Increasing parameters β_2, β_4, and x_b (minimal temperature) delays

333   emergence, while increasing β_3 strongly advances phenology. The tree model is most sensitive to

334   parameters t_0 (when the tree starts accumulating heat) and b (which drives the speed of

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

336   5D).

3.4.2 Spruce budworm – balsam fir system across latitude

338   The model predicts median dates of emergence and budburst for each year. Results for past and future

339   data were analyzed using a one-way analysis of variance (see supplementary material for full results).

340   Both emergence (Fig. 6A) and budburst (Fig. 6B) occur later at higher latitudes: $p < 0.05$ between sites 1,

341   2, 3 (South) and 4, 5, 6 (North), although some discrepancies may occur due to altitude (sites 2 and 4).

342   However, insects and trees are not affected by temperatures in the same way. Hence, the mismatch

343   between both species varies across latitude ($p < 0.05$ between sites 1, 3 and 5, 6) (Fig. 6C). At lower

344   latitudes, emergence is expected to occur 5 to 10 days before budburst. Hence, the majority of the larval

345   population may have time to emerge before budburst occurs, which allows larvae to benefit from an

346   important source of nutrients. Fuentealba, et al. (2017) evaluated SBW performance on balsam fir

347   according to their phenological mismatch. According to their study, we can infer SBW survival to

348   be around 45% and reproductive output (fecundity * survival) to be 45%. At higher latitudes, emergence

349   may sometimes occur before budburst and sometimes after, which would lead to 30% survival and 20%

350   reproductive output. In brief, insects seem more adapted to their host phenology at lower than at higher

351   latitudes.

3.4.3 Predicted trends according to warming scenarios

353   Across all scenarios, emergence and budburst are expected to occur earlier when temperatures

354   increase. The differences in emergence, budburst and mismatch across latitude is highly

355   significant ($p < 10^{-16}$ for almost all sites and for all scenarios). Warmer scenarios lead to an

356   increase of variance, more than a real shift in date compared to less warm scenarios. Insects and

357   trees react differently to temperature increase. Balsam fir shows an historical (1996-2016)

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358   difference between northern and southern sites of 10 days on average. This difference stays

359   approximately the same in case of warmer temperatures (i.e., budburst date is shifted similarly

360   across latitude, see Fig. 6B). By contrast, emergence of SBW is expected to shift differently

361   across latitude (about 15 days difference compared to 10 historically, see Fig. 6A).

362   Therefore, the mismatch is affected. Southern sites are expected to show emergence occurring

363   before budburst most of the time. In case of a moderate warming scenario (RCP2.6), the waiting

364   time is expected to be short, which would allow the larvae to have access to a rich source of

365   nutrients. Thus, a moderate warming could be beneficial for the insect at low latitudes. In case of

366   greater warming (RCP4.5, RCP8.5), variance may lead to emergence occurring too early some

367   years, leading to larvae dying from starvation. Thus, a greater temperature increase may lead to

368   stronger population variances among years.

369   In northern sites, all warming scenarios lead to an increased synchrony between the insect and

370   its host. The overall pattern appears similar to what is currently expected in southern sites.

371   However, the variance is expected to be greater with warmer scenarios, which may increase

372   insect mortality from time to time, when emergence occurs too late.

373   ## 4. Discussion

374   We propose a temperature-driven mechanistic model to determine the end of the seasonal resting

375   period of species. We investigate the effects of temperature on species phenology, and its

376   consequences on consumer-resource synchrony, across latitude and under future climate

377   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

400   increase of the phenological mismatch may limit the consumer's food intake, which affects its

401   biomass, its life cycle, and potentially even its ability to persist in the considered geographic zone

402   (Simmonds et al., 2020). If a subsidiary resource is available, the consumer may switch resources

403   (Stålhandske et al., 2016). A decrease of the phenological mismatch may lead to a stronger

404   depletion of the resource. Both of these outcomes may cause ripple effects through the food web.

405   Thus, a shift in relative phenology between the consumer and its resource can affect species

406   demography in many ways (Miller-Rushing et al., 2010), as well as their geographic distribution.

407   Our work, which is based on heat accumulation, improves our ability to predict the direction and

408   the magnitude of the change in phenological synchrony, a research challenge identified by earlier

409   studies (Kharouba et al. 2018).

410   4.2 The spruce budworm - balsam fir system and its general implications

411   We apply our general theory to predict the future mismatch between spruce budworm and

412   balsam fir across latitude under different warming scenarios. According to the general theory, a

413   warm spell occurring at any time during the heat accumulation period is likely to affect the insect

414   because its $R'(\cdot)$ has a wide profile (see Fig. 2B, and section 2.2.2). The tree will react only if

415   the warm spell occurs within its narrow sensitivity period. Therefore, under a change in

416   temperature regime that would lead to several warm spells, the insect will advance its phenology

417   more than the tree. Simulations with realistic temperature time series (showing several warm

418   spells) confirm the theoretical results. Under an increase of temperatures, insect phenology would

419   advance by 15 days on average, while the tree phenology would advance by 7 days on average.

420   The expected overall mismatch increases by approximately 7 days on average (see Fig. 6 and

421   section 3.4.2).

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422   Budworms have to emerge within two weeks of budburst to have access to a rich source

423   of nutrients. A shift in phenology increasing the likelihood of this pattern would in turn increase

424   larval survival and population persistence in previously non-favourable regions. Under historical

425   temperature regimes, budworm emergence date in northern sites is close to budburst date, which

426   causes the budworm to emerge too late in some years, while emergence in southern sites occurs

427   within 15 days before budburst. An increase of the mismatch benefits the insect in northern sites

428   since it would emerge before budburst most of the time, while in southern sites, the budworm

429   would emerge too early some years. A shift in phenology that leads to emergence occurring too

430   early (or too late) would cause severe budworm mortality and prevent its persistence in some

431   parts of its current distribution. Conversely, an increase in the persistence of the insect in other

432   regions will increase damages to host trees. Since insect pests (especially SBW) are one of the

433   main drivers of forest composition in the black spruce, white spruce and balsam fir zones (Harper

434   et al., 2003), a change in phenological synchrony between these species may affect their future

435   geographic distributions.

436   A change in mismatch between budworm and balsam fir would also affect other potential

437   host species. It is known that black spruce is a suitable host, but its phenological mismatch with

438   budworm protects the tree from a long-term budworm establishment (Pureswaran, et al., 2015).

439   Moreover, in northern sites, black spruce seems to be somehow protected because the budworm

440   cannot establish for a long period due to a high frequency of cold years (Pureswaran, et al.,

441   2015). However, our model predicts that warming should lead to a better synchrony between the

442   insect and balsam fir in these sites, therefore the budworm might be able to establish and generate

443   outbreaks, which in turn would affect black spruce populations. To test this hypothesis, we

22

444   require *in situ* phenological data for a parameterization of the tree model (Eq. 2) for black

445   spruce.

446   Our model assumes that neither the consumer nor the resource affects the phenology of

447   the other species. Only temperature drives phenology. Recent observations of interactions

448   between defoliation and host phenology suggest that severe defoliation by budworm may

449   advance budburst phenology (Deslauriers et al., 2019). According to our model, an increase in

450   temperature should increase the mismatch by advancing the budworm phenology more than that

451   of the tree. If defoliation leads to an advance in phenology for the tree, then the resulting

452   mismatch would stay close to the historical mismatch, which would reduce the benefit of this

453   physiological response for the tree.

454   ## 4.3 Future extensions

455   The present study provides novel insights towards a better understanding of the effects of

456   an increase of temperatures on species phenology. Further studies may consider specific features

457   that we do not include in the model. First, our study is limited to cases where the phenology is

458   directly constrained by environmental variables (more specifically temperature). Organisms can

459   also use temperature (or any other environmental variables) indirectly as cues for predicting an

460   optimal time window to have access to resources or convenient environmental conditions (e.g.,

461   photoperiod, rainfall) (McNamara et al., 2011).

462   Second, we measure mismatch as the time lag between peaks of consumer demand and

463   resource availability. Some authors have argued that more precise measurements should take into

464   account the shape and location of the phenological distributions around these peaks (e.g., Lindén,

465   2018) while others showed that, in some cases, time lag between phenological peak dates was a

23

466   better predictor of resource availability than the overlap between phenological distributions

467   (Ramakers et al., 2020).

468   Third, a change in phenological synchrony will have an effect on the whole life cycle,

469   which would be beyond the scope of the present study. Rising temperatures are likely to affect

470   physiological processes at later life stages, by affecting metabolism for example (Brown, et al.,

471   2004). It is also clear that a change in the mismatch is likely to affect the ecological and

472   evolutionary dynamics of the consumer-resource system. These aspects provide avenue for

473   further studies.

474   The theoretical framework presented here can be applied to other consumer-resource

475   systems. The concrete example of the spruce budworm - balsam fir system informs the required

476   methodology. To estimate the mismatch, the two rate accumulation functions must be calibrated

477   accurately. It appears that the model is sensitive to the temporal resolution of the temperature

478   time series. There are two timescales at which temperatures affect the outcome of the model. The

479   first one occurs at the daily scale. Average daily temperatures lead to different results than a four-

480   hour time interval for temperatures (used throughout the present study) since variations within a

481   day may allow for development during a few hours, even when the average temperature over the

482   whole day may not.

483   The second one occurs at a broader timescale (e.g., weekly). For the study system,

484   temperature data modelled by BioSim (Régnière, et al., 2014) lead to realistic emergence and

485   budburst dates when compared to real data (see section 3.2) and to a phenological mismatch, i.e.,

486   budworm usually emerging before budburst, similar to field observations (Pureswaran, et al.,

487   2019). More simplistic distributions that do not contain any warm spell can lead to the opposite

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488   pattern (i.e., budburst occurs first). Realistic temperatures show warm periods during days with

489   low average temperatures (i.e., late winter - early spring), which advance the insect phenology

490   compared to simplified (cosine) distributions. The tree is less sensitive to these short warm

491   events.

492   The modelling approach presented here allows for investigation of potential effects of

493   climate change on consumer-resource systems. Synchrony / mismatch between a consumer and

494   its resource is fundamental to predict future species distribution. Future studies may go further by

495   including more complex mechanistic approaches (e.g., energy budget models) in order to model

496   the whole life cycle of the consumer, which could lead to new insights on the dynamics of the

497   systems. Our model could be linked to models that explore the consequences of phenological

498   mismatch on the population dynamics of consumer – resource systems (e.g., Bewick et al., 2016).

499

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Authors' contribution

505   All authors conceptualized the study. FL and SP built the theoretical model. SP calibrated the tree

506   model, gathered the temperature data, and performed the simulations. SP, JNC and FL analyzed

507   the results, wrote and edited the manuscript.

Data Availability

509   Code will be stored on Zenodo public depository. Data on balsam fir phenology can be made available on

510   demand to Dr. J. Régnière (Natural Resources Canada).

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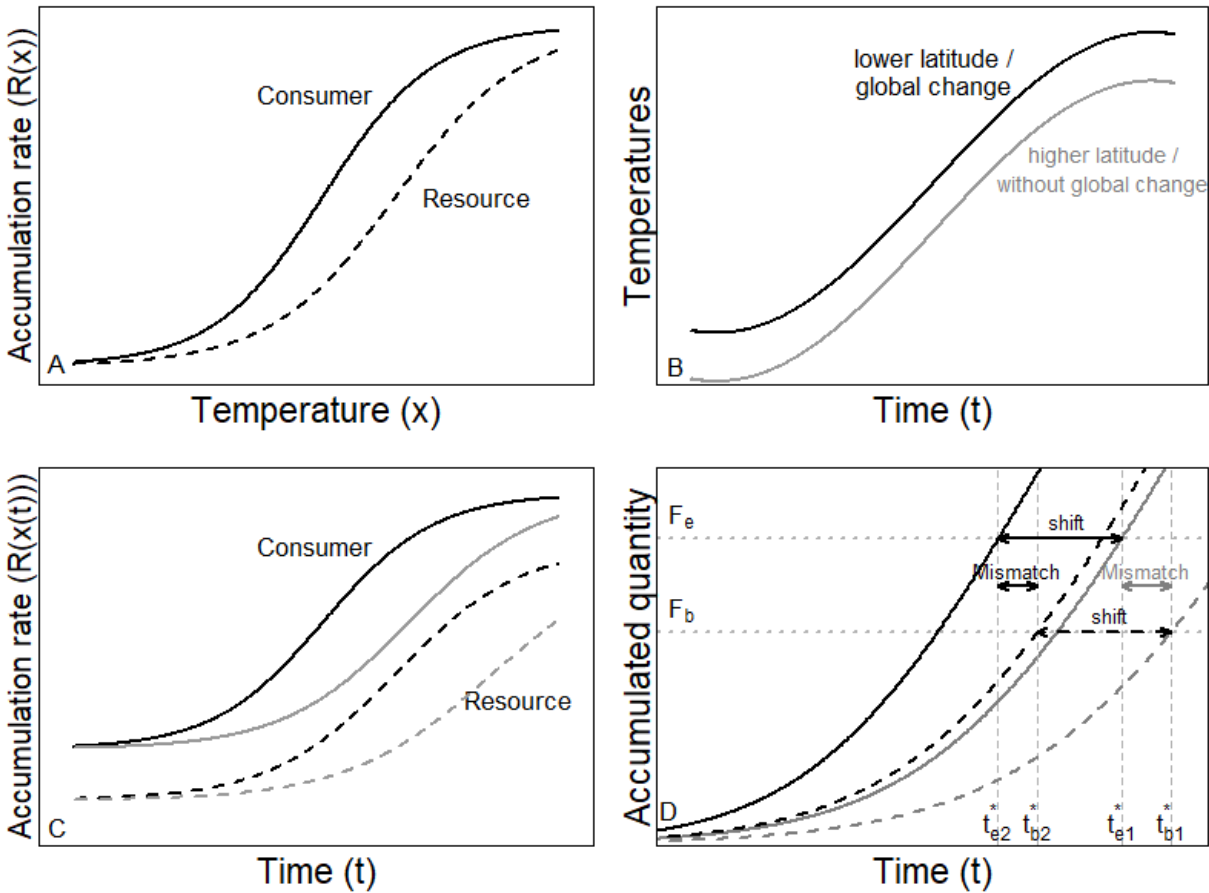680   *Interface*, *10*(86), 20121018. doi: 10.1098/rsif.2012.1018

681

682

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
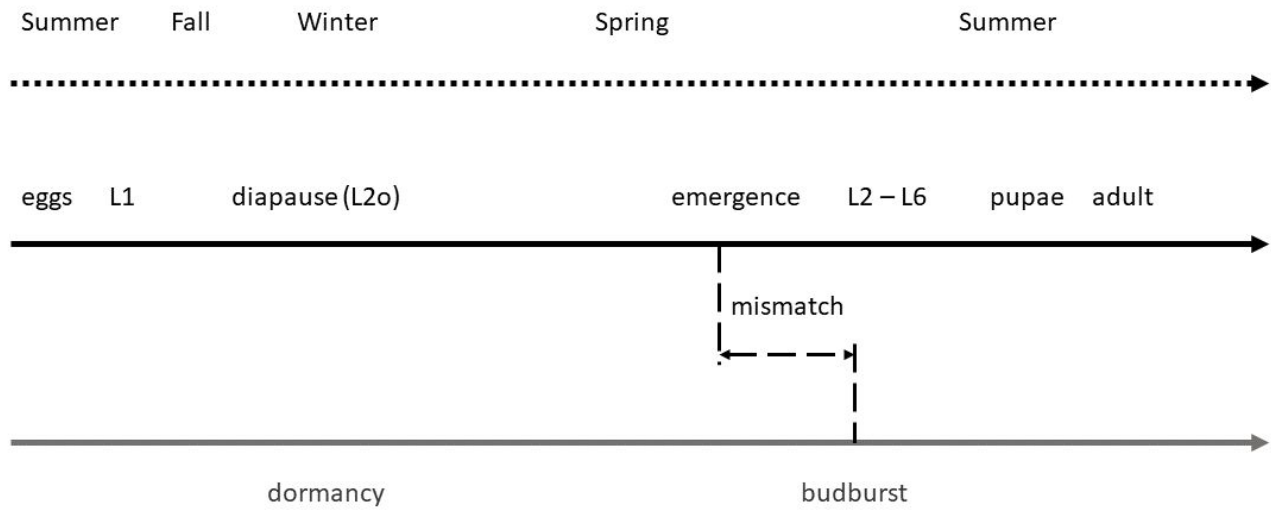
692　　(same location and same time). Accumulation functions for both the consumer and the resource

693　　use Eq. 2 with the following parameter values: $b_c = -1.32$, $c_c = 7.14$, $b_r = -1.16$, $c_r = 8.14$.

694
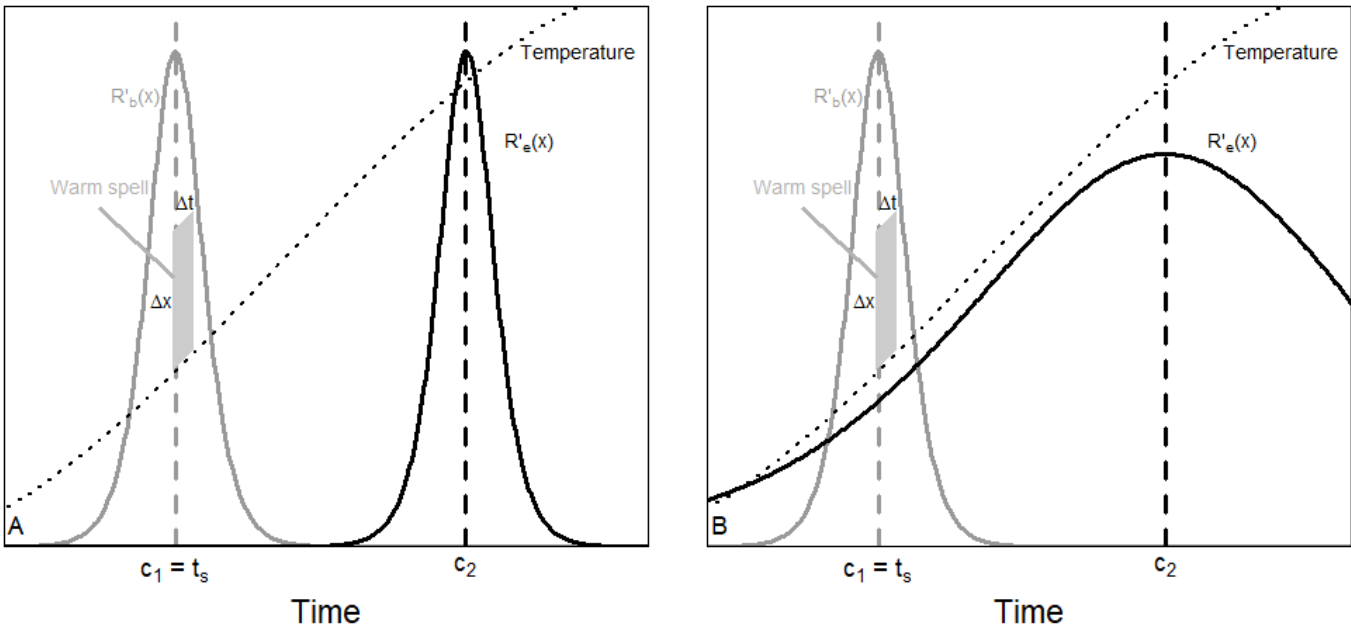
Figure 2: Sensitivity of resource accumulation functions, *R'(x(t))*, for two species when there is

no (A) or some (B) overlap. In (A), the warm spell indicated will advance the phenology of

species 1 (grey curve) but not alter that of species 2 (black curve). In (B), the same warm spell

will advance both phenologies. For this illustration, we used the accumulation function in Eq 2

for species 1 with parameter values for balsam fir (see section 3.4.1). We used the same function

for species 2 in (A), but with $c = 15.2$. In (B), we used the accumulation function for spruce

budworm in Eq. 8 with corresponding parameter values (see section 3.2.1). The temperature is

chosen according to Eq. 5 (from January to June).

703

Summer   Fall   Winter   Spring   Summer

eggs   L1   diapause (L2o)   emergence   L2 – L6   pupae   adult

mismatch
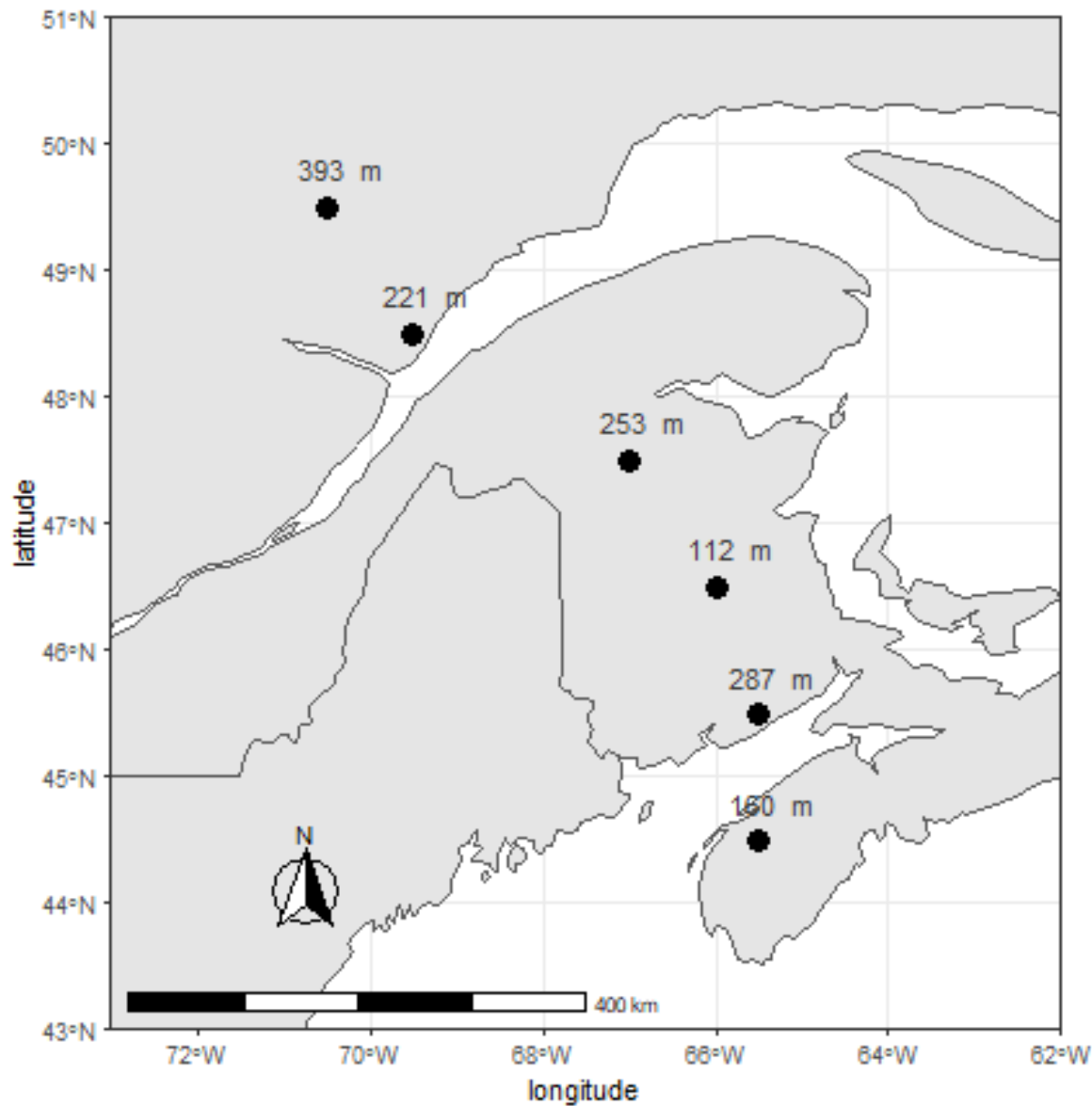
dormancy   budburst

704

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

706   line is balsam fir life cycle.

707

708   **Figure 4**: Location of the sample sites where temperature data were collected for past and future

709   trends. Points are located across a gradient of latitude in Nova-Scotia, New Brunswick, and

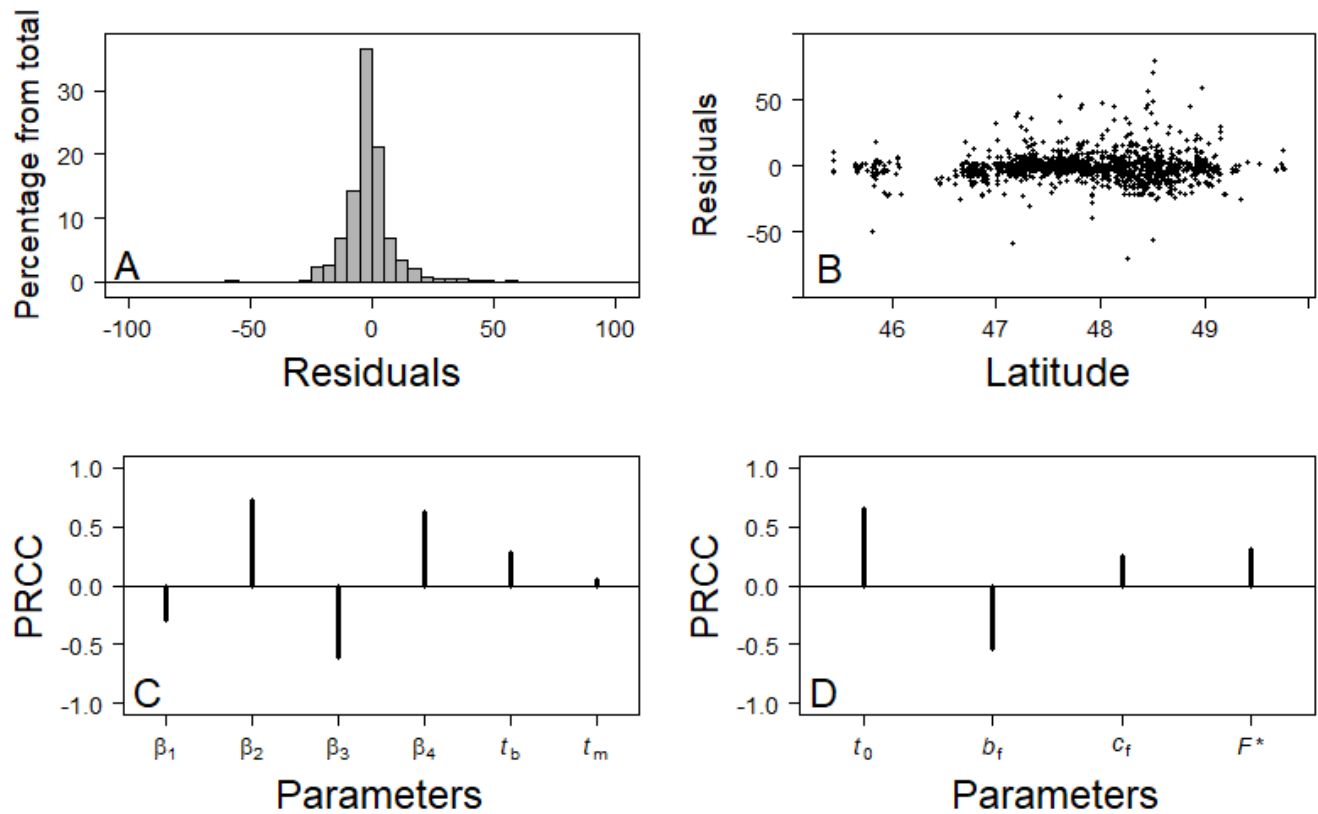710   Quebec. Altitude is indicated above each point.

711

Figure 5: Fitting residuals of the balsam fir model and sensitivity analysis. (A) Residuals follow

a Normal distribution centered on 0. (B) No obvious latitudinal patterns can be found on the

residuals within the range of latitudes that is used throughout the rest of the study. (C) Partial

Rank Correlation Coefficient (PRCC) shows that the SBW model is sensitive to most parameters

especially β_2, β_4 and x_b that delay emergence, and β_3 that advances phenology. (D) The tree

model is mostly sensitive to b_f that hastens budburst, and t_0 that delays budburst.

718
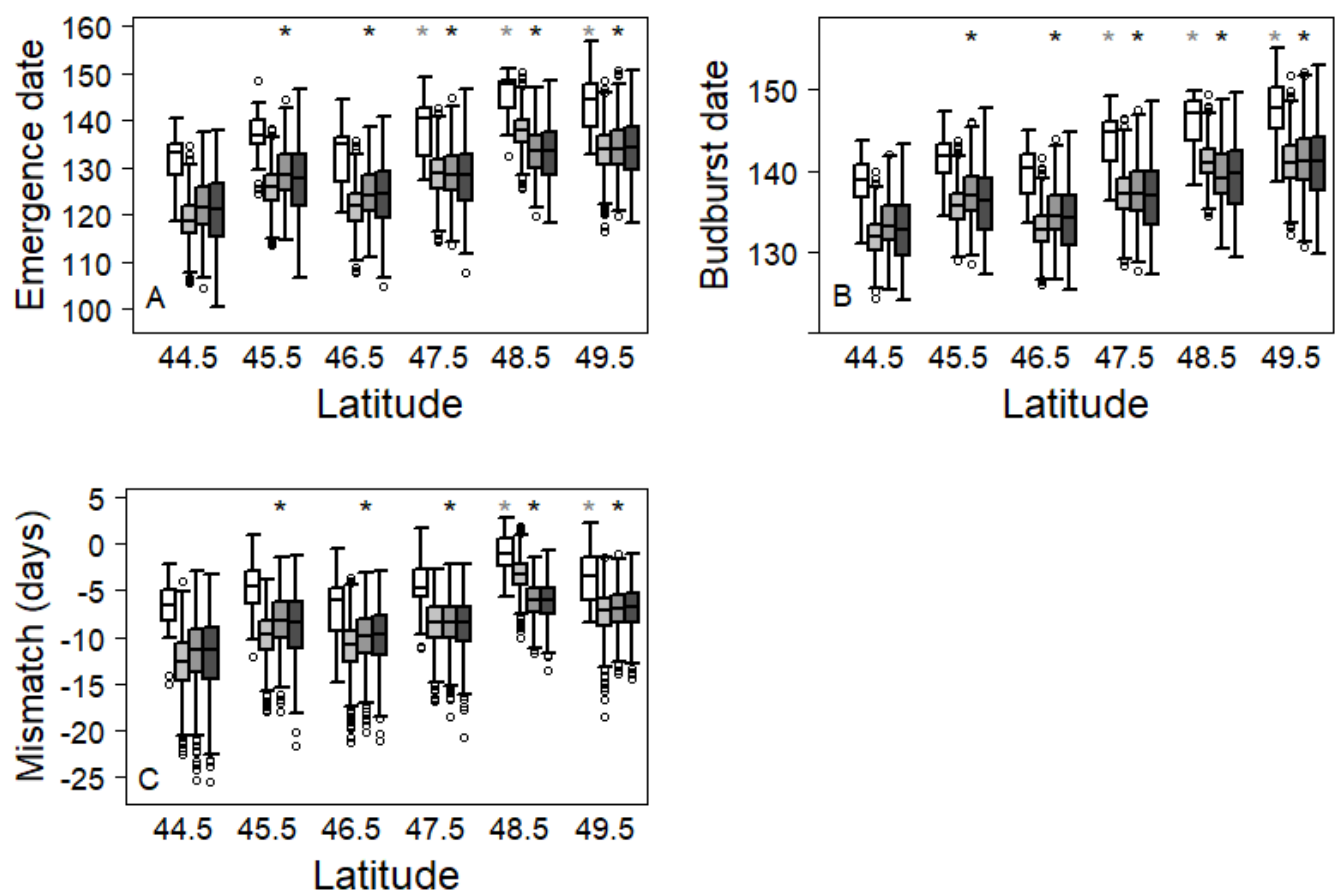
Figure 6: Latitudinal distribution of (A) median emergence date of SBW (Julian days), (B)

median budburst date, and (C) mismatch between emergence and budburst date. For each

latitude, the white box (left one) represents the 1996-2016 period. Grey boxes represent expected

outcomes according to RCP 2.6 (light grey), RCP 4.5 (dark grey), and RCP 8.5 (black) scenarios

over 2021 to 2100. A black (grey) star means that the corresponding site shows a significant

difference with the most southern site for present (future) predicted trait. Both emergence and

budburst are expected to occur later at higher latitudes. Overall warming scenarios, both events

are expected to occur earlier in the year. Nowadays, emergence is expected to occur 5 to 10 days

before budburst at low latitudes, while at higher latitudes, emergence may sometimes occur

before budburst and sometimes after. For all warming scenarios, an increase in mismatch is

729   expected. At low latitudes, emergence may occur too early some years, which may lead to low

730   survival of SBW. At higher latitudes, emergence is expected to systematically occur a few days

731   before budburst, which would increase survival of SBW.

42

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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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1 Theoretical developments

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

$$\int_{t_0}^{t^*} R(x(t))\,\mathrm{d}t = F. \qquad \text{Eq. S1}$$

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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

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

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

$$\frac{\mathrm{d}t^*}{\mathrm{d}\epsilon} \text{ for } \epsilon = 0. \qquad \text{Eq. S3}$$

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

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

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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

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

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

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

Hence, the end time has the linear approximation

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

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

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

$$t^*(\epsilon) \approx t^*(0) - \Delta x \frac{\int_{t_0}^{t^*} R'(x(t))\mathrm{d}t}{R(x(t^*))}.$$

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

$$\epsilon \int_{t_0}^{t^*} R'(x(t))z(t)\mathrm{d}t = \Delta x \int_{t_s}^{t_s+\Delta t} R'(x(t))\mathrm{d}t \approx \Delta x \Delta t R'(x(t_s))$$

Eq. S9

Hence, the expression for the end time is approximately

$$t^*(\epsilon) \approx t^*(0) - \Delta x \frac{\Delta t R'(x(t_s))}{R(x(t^*))}$$

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.

The two formulas (Eq. S8 and Eq. S10) may seem different, but they express the same idea. One has to integrate R' for all times where the two time series differ. When the two time series differ by a constant for all times, the one has to integrate over the entire time series. When the two

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time series differ only on an interval of length Δt, then one has to integrate over only that interval.

If the interval is short, then the value of $R(x(t))$ does not change much and therefore the integral

is approximated by the product of the length of the interval (Δt) and the value of the integrand

$(R(x(t_s)))$.

Derivative of the rate function

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

we can explicitly calculate the derivative as

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

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

and find

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

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

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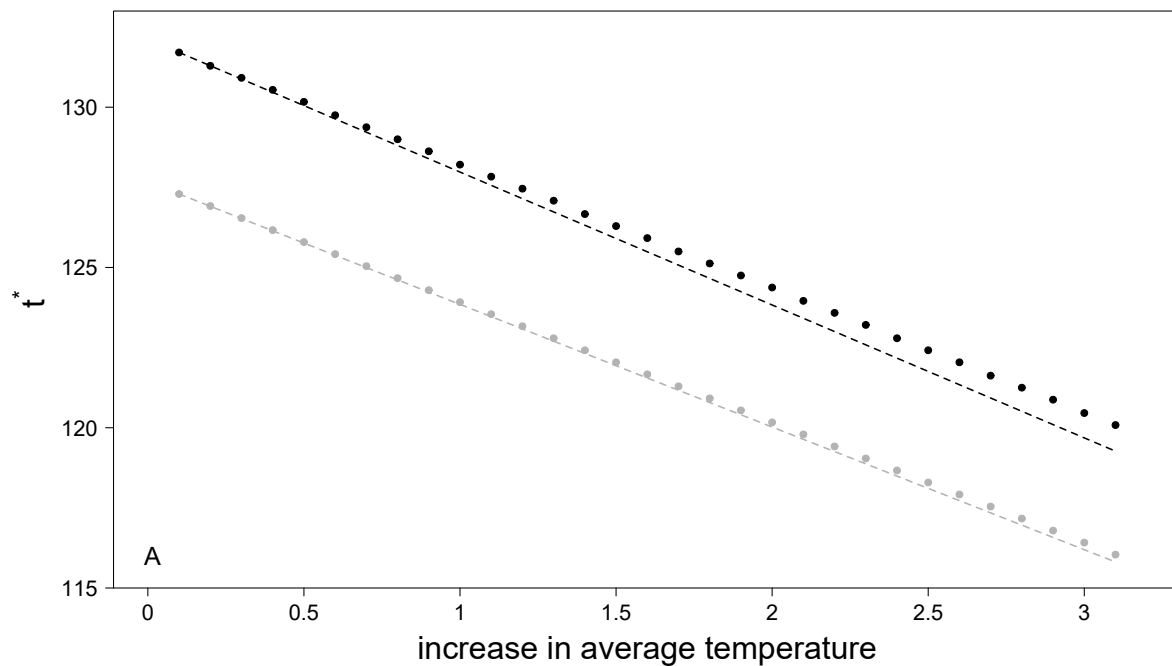Portalier, Candau & Lutscher

Figure S1: Effects of a constant temperature difference on species phenology. Black is the consumer (SBW), and grey is the resource (balsam fir). A constant temperature difference advances species phenology. Dotted is the predicted value (Eq. 3 used with the R functions of SBW and balsam fir), dashed is the linear approximation from the model with simple time series.

2 Analysis of variance

Here, we present the full results of the analysis of variance done on emergence date, budburst date and mismatch across latitude, for past/present temperatures, and for the three RCP scenarios. There are 6 sites ranged from site 1 (southern site: 44.5° N) to site 6 (northern site: 49.5° N) (see Fig. 4 and 6, and main text for details). The analysis was performed with R.

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2.1 Historical data

Emergence date

```
##                Df Sum Sq Mean Sq F value  Pr(>F)

## Site            5    3374   674.8    17.89 3.2e-13 ***

## Residuals    120    4527    37.7

##

## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

##

##   Pairwise comparisons using t tests with pooled SD

##

##          Site1    Site2    Site3    Site4    Site5

## Site2 0.20440    -        -        -        -

## Site3 1.00000 0.64190    -        -        -

## Site4 0.00574 1.00000 0.02647    -        -

## Site5 2.0e-09 0.00021 2.0e-08 0.01493    -

## Site6 1.5e-08 0.00102 1.4e-07 0.05283 1.00000

##

## P value adjustment method: bonferroni
```

Budburst date

```
##                Df Sum Sq Mean Sq F value   Pr(>F)

## Site            5    1332  266.43    21.72 1.94e-15 ***
```

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```
## Residuals    120    1472    12.26

##

## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

##

##  Pairwise comparisons using t tests with pooled SD

##

##        Site1   Site2   Site3   Site4   Site5

## Site2 0.21247   -       -       -       -

## Site3 1.00000 1.00000   -       -       -

## Site4 0.00062 1.00000 0.01185   -       -

## Site5 6.5e-09 0.00050 3.5e-07 0.18502   -

## Site6 3.1e-12 8.8e-07 2.2e-10 0.00155 1.00000

##

## P value adjustment method: bonferroni
```

Mismatch

```
##             Df Sum Sq Mean Sq F value  Pr(>F)

## Site         5  545.7  109.13    11.08 8.7e-09 ***

## Residuals  120 1182.1    9.85

##

## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

##
```

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```
##  Pairwise comparisons using t tests with pooled SD

##

##        Site1    Site2   Site3    Site4   Site5

## Site2 0.5382     -        -        -        -

## Site3 1.0000   0.5175     -        -        -

## Site4 0.2684   1.0000  0.2572     -        -

## Site5 1.4e-07  0.0014  1.3e-07 0.0038      -

## Site6 0.0042   1.0000  0.0039   1.0000 0.2517

##

## P value adjustment method: bonferroni
```

2.2   RCP 2.6 data

Emergence date

```
##              Df Sum Sq Mean Sq F value Pr(>F)

## Site      5 305237    61047     3334 <2e-16 ***

## Residuals   7194 131707       18

##

## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

##

##  Pairwise comparisons using t tests with pooled SD

##

##        Site1    Site2   Site3    Site4   Site5
```

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```
## Site2 <2e-16    -       -       -       -

## Site3 <2e-16 <2e-16    -       -       -

## Site4 <2e-16 <2e-16 <2e-16    -       -

## Site5 <2e-16 <2e-16 <2e-16 <2e-16    -

## Site6 <2e-16 <2e-16 <2e-16 <2e-16 <2e-16

##

## P value adjustment method: bonferroni
```

Budburst date

```
##               Df Sum Sq Mean Sq F value Pr(>F)

## Site      5  94260   18852    2896 <2e-16 ***

## Residuals   7194  46827       7

##

## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1


##

##  Pairwise comparisons using t tests with pooled SD

##

##        Site1  Site2  Site3  Site4  Site5

## Site2 <2e-16    -       -       -       -

## Site3 <2e-16 <2e-16    -       -       -

## Site4 <2e-16 <2e-16 <2e-16    -       -

## Site5 <2e-16 <2e-16 <2e-16 <2e-16    -
```

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```
## Site6 <2e-16 <2e-16 <2e-16 <2e-16 1

##

## P value adjustment method: bonferroni
```

Mismatch

```
##                 Df Sum Sq Mean Sq F value Pr(>F)
## Site      5  66174   13235    2316 <2e-16 ***
## Residuals  7194  41116       6

##

## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1


##

##  Pairwise comparisons using t tests with pooled SD

##

##        Site1  Site2  Site3  Site4  Site5

## Site2 <2e-16   -      -      -      -

## Site3 <2e-16 <2e-16   -      -      -

## Site4 <2e-16 <2e-16 <2e-16   -      -

## Site5 <2e-16 <2e-16 <2e-16 <2e-16   -

## Site6 <2e-16 <2e-16 <2e-16 <2e-16 <2e-16

##

## P value adjustment method: bonferroni
```

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2.3 RCP 4.5 data

Emergence date

```
##                Df Sum Sq Mean Sq F value Pr(>F)

## Site       5 139304   27861    1045 <2e-16 ***

## Residuals   7194 191768      27

##

## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

##

##  Pairwise comparisons using t tests with pooled SD

##

##        Site1  Site2  Site3  Site4  Site5

## Site2 <2e-16    -      -      -      -

## Site3 <2e-16 <2e-16    -      -      -

## Site4 <2e-16 1.000  <2e-16    -      -

## Site5 <2e-16 <2e-16 <2e-16 <2e-16    -

## Site6 <2e-16 <2e-16 <2e-16 <2e-16 0.006

##

## P value adjustment method: bonferroni
```

Budburst date

```
##                Df Sum Sq Mean Sq F value Pr(>F)

## Site       5  51477   10295    1046 <2e-16 ***
```

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```
## Residuals   7194  70813        10
##
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
##  Pairwise comparisons using t tests with pooled SD
##
##        Site1  Site2  Site3  Site4  Site5
## Site2 <2e-16   -      -      -      -
## Site3 <2e-16 <2e-16   -      -      -
## Site4 <2e-16 0.62   <2e-16   -      -
## Site5 <2e-16 <2e-16 <2e-16 <2e-16   -
## Site6 <2e-16 <2e-16 <2e-16 <2e-16 <2e-16
##
## P value adjustment method: bonferroni
```

Mismatch

```
##             Df Sum Sq Mean Sq F value Pr(>F)
## Site     5  23457    4691   651.4 <2e-16 ***
## Residuals   7194  51815       7
##
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
```

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Pairwise comparisons using t tests with pooled SD

##

Site1 Site2 Site3 Site4 Site5

Site2 <2e-16   -   -   -   -

Site3 <2e-16 <2e-16   -   -   -

Site4 <2e-16 0.22   <2e-16   -   -

Site5 <2e-16 <2e-16 <2e-16 <2e-16   -

Site6 <2e-16 <2e-16 <2e-16 <2e-16 <2e-16

##

P value adjustment method: bonferroni

2.4 RCP 8.5 data

Emergence date

Df Sum Sq Mean Sq F value Pr(>F)

Site   5 155376   31075   727.7 <2e-16 ***

Residuals   7194 307197   43

##

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

##

Pairwise comparisons using t tests with pooled SD

##

Site1 Site2 Site3 Site4 Site5

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```
## Site2 <2e-16    -        -         -         -

## Site3 <2e-16 <2e-16    -         -         -

## Site4 <2e-16 0.202  <2e-16     -         -

## Site5 <2e-16 <2e-16 <2e-16 <2e-16     -

## Site6 <2e-16 <2e-16 <2e-16 <2e-16 0.014

##

## P value adjustment method: bonferroni
```

Budburst date

```
##                 Df Sum Sq Mean Sq F value Pr(>F)

## Site      5  58046   11609    690.5 <2e-16 ***

## Residuals   7194 120951        17

##

## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1


##

##  Pairwise comparisons using t tests with pooled SD

##

##        Site1    Site2    Site3    Site4    Site5

## Site2 < 2e-16    -        -         -         -

## Site3 8.2e-16 < 2e-16    -         -         -

## Site4 < 2e-16 0.0097  < 2e-16    -         -

## Site5 < 2e-16 < 2e-16 < 2e-16 < 2e-16    -
```

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```
## Site6 < 2e-16 < 2e-16 < 2e-16 < 2e-16 < 2e-16

##

## P value adjustment method: bonferroni
```

Mismatch

```
##                Df Sum Sq Mean Sq F value Pr(>F)

## Site      5  25363    5073   572.3 <2e-16 ***

## Residuals   7194  63763       9

##

## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1


##

##  Pairwise comparisons using t tests with pooled SD

##

##        Site1   Site2   Site3   Site4   Site5

## Site2 < 2e-16   -       -       -       -

## Site3 < 2e-16 < 2e-16   -       -       -

## Site4 < 2e-16 1        < 2e-16   -       -

## Site5 < 2e-16 < 2e-16 < 2e-16 < 2e-16   -

## Site6 < 2e-16 < 2e-16 < 2e-16 < 2e-16 1.1e-11

##

## P value adjustment method: bonferroni
```
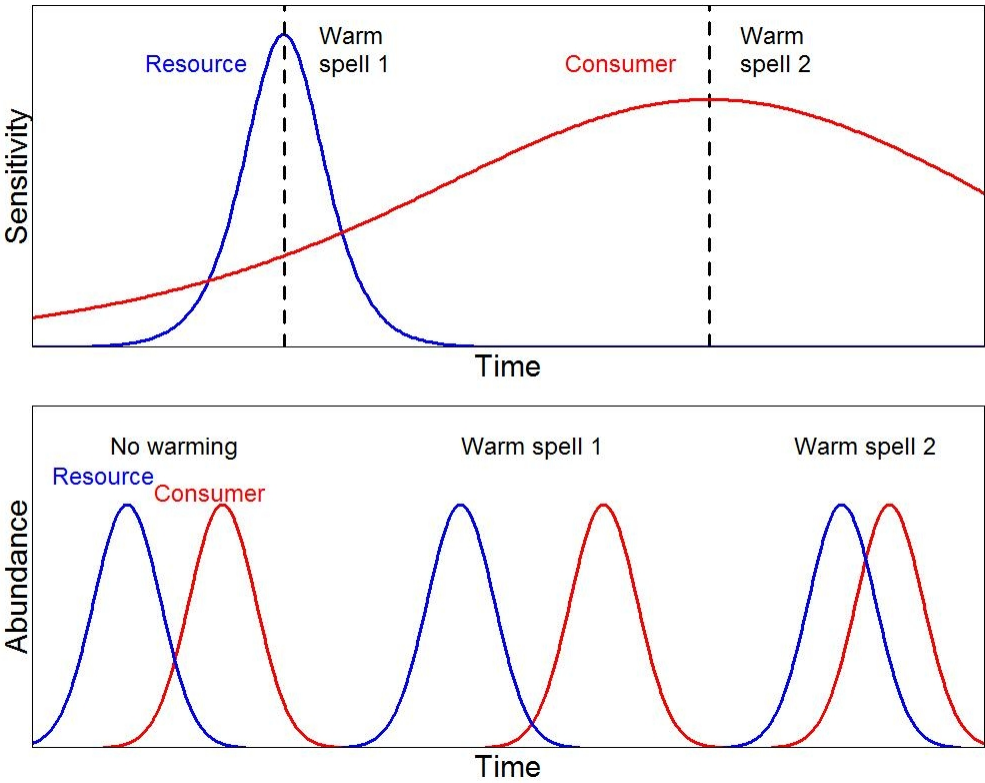
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352x282mm (72 x 72 DPI)