

# Warming counteracts defoliation-induced mismatch by increasing herbivore-plant phenological synchrony

Ping Ren<sup>1,2,3</sup>  | Valérie Néron<sup>2</sup> | Sergio Rossi<sup>2,4</sup> | Eryuan Liang<sup>1,5</sup>  | Mathieu Bouchard<sup>6</sup> | Annie Deslauriers<sup>2</sup>

<sup>1</sup>Key Laboratory of Alpine Ecology and Biodiversity, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing, China

<sup>2</sup>Département des Sciences Fondamentales, Université du Québec à Chicoutimi, Chicoutimi, QC, Canada

<sup>3</sup>College of Life Sciences, Anhui Normal University, Wuhu, China

<sup>4</sup>Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems, Guangdong Provincial Key Laboratory of Applied Botany, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou, China

<sup>5</sup>CAS Centre for Excellence in Tibetan Plateau Earth Sciences, Beijing, China

<sup>6</sup>Direction de la Recherche Forestière, Ministère des Forêts, de la Faune et des Parcs du Québec, Québec, QC, Canada

## Correspondence

Ping Ren, Key Laboratory of Alpine Ecology and Biodiversity, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing 100101, China.  
Email: renping@itpcas.ac.cn

## Funding information

Ministry of Forests, Wildlife and Parks in Québec (MFFP); Natural Sciences and Engineering Research Council of Canada; National Natural Science Foundation of China, Grant/Award Number: 41525001 and 41807443; China Scholarship Council, Grant/Award Number: 201804910179

## Abstract

Climate change is altering phenology; however, the magnitude of this change varies among taxa. Compared with phenological mismatch between plants and herbivores, synchronization due to climate has been less explored, despite its potential implications for trophic interactions. The earlier budburst induced by defoliation is a phenological strategy for plants against herbivores. Here, we tested whether warming can counteract defoliation-induced mismatch by increasing herbivore-plant phenological synchrony. We compared the larval phenology of spruce budworm and budburst in balsam fir, black spruce, and white spruce saplings subjected to defoliation in a controlled environment at temperatures of 12, 17, and 22°C. Budburst in defoliated saplings occurred 6–24 days earlier than in the controls, thus mismatching needle development from larval feeding. This mismatch decreased to only 3–7 days, however, when temperatures warmed by 5 and 10°C, leading to a resynchronization of the host with spruce budworm larvae. The increasing synchrony under warming counteracts the defoliation-induced mismatch, disrupting trophic interactions and energy flow between forest ecosystem and insect populations. Our results suggest that the predicted warming may improve food quality and provide better growth conditions for larval development, thus promoting longer or more intense insect outbreaks in the future.

## KEYWORDS

boreal forest, budburst, *Choristoneura fumiferana*, global warming, outbreak, phenology

## 1 | INTRODUCTION

Phenology, the seasonal timing of life events such as growth, reproduction, and migration, is one of the key mechanisms for organisms to adapt to and survive in their environment (Badeck et al., 2004; Chuine & Régnière, 2017; Piao et al., 2019). Phenological synchrony refers to the temporal convergence of the phenology of interacting species. In mutualistic interactions between plants and pollinators,

for example, the timing of pollinator feeding must coincide with plant flowering to ensure both the acquiring of food and pollination; this temporal convergence allows the populations of the two species to persist (Hegland, Nielsen, Lazaro, Bjerknes, & Totland, 2009). In antagonistic interactions between a plant host and parasite, host feeding must correspond to a specific stage of plant development to ensure a sufficient quality of the food resource (Singer & Parmesan, 2010) and thus the survival and growth of the

parasite (Regniere & Nealis, 2018). These synchronies between species ensure that resource demand matches availability, a critical aspect that underlies trophic interactions and energy-flows across ecosystems (Miller-Rushing, Hoyer, Inouye, & Post, 2010).

Anthropogenic climate change is altering the phenology of plant and animal species; however, the magnitude of this change in seasonal timing varies among taxa (Penuelas & Filella, 2001; Thackeray et al., 2016). This non-uniform shift leads to a divergence in the timing of life events of interacting species (Thackeray et al., 2010) and alters the strength of the interaction (Both, van Asch, Bijlsma, van den Burg, & Visser, 2009). A meta-analysis of 54 pairs of interacting species showed that phenological synchrony began to change at a rapid and accelerating rate after 1981, with an average of 6.1 days/decade of increased or decreased synchrony between species (Kharouba et al., 2018). The phenological mismatch between species related to the warming climate is well known and widely described (Durant, Hjernann, Ottersen, & Stenseth, 2007; Edwards & Richardson, 2004; Stenseth & Mysterud, 2002). For example, birds that have a phenological timing that no longer coincides with that of the caterpillars upon which they feed are susceptible to population decline (Moller, Rubolini, & Lehikoinen, 2008; Saino et al., 2011). Similarly, Memmott, Craze, Waser, and Price (2007) simulated the effects of global warming on a plant-pollinator network and found that 17%–50% of all pollinator species suffer from a disruption of their food supply due to mismatch.

In contrast, phenological shifts can also remove temporal barriers, synchronizing activities that were previously separated in time, and thereby establishing climate-induced interactions (Kharouba et al., 2018). For example, during years of anomalously warm springs, brown bears switch their food preferences from salmon to elderberries, which usually mature several weeks earlier (Deacy et al., 2017). Such a shift in feeding alters the trophic network that is based on the ecological interaction between salmon and their predators (Helfield & Naiman, 2006). Relative to examples of climate-related mismatch between species, climate-related increase in phenological synchronization has been described only at plant species and regional level (Liu et al., 2019; Vitasse, Signarbieux, & Fu, 2018) despite the potentially big implications for trophic interactions.

Phenological synchrony between herbivores and their hosts is particularly important for pests (Renner & Zohner, 2018). Years of high synchrony between an insect and an optimal food source may promote insect outbreaks (van Asch & Visser, 2007); these events have adverse effects on nutrient cycling, carbon sequestration, and biodiversity (Ayres & Lombardero, 2000). Compared to plants, insects exhibit a greater sensitivity to interannual variations in temperature (Parmesan, 2007). Climate warming is expected to advance insect phenology more rapidly than plant phenology. Nonetheless, an earlier budburst has also been observed in trees previously defoliated by insects, resulting in a phenological mismatch between host and herbivore (Carroll & Quiring, 2003; Deslauriers, Fournier, Carteni, & Mackay, 2019; Quiring & McKinnon, 1999). To the best of our knowledge, no studies have assessed whether warming will affect the defoliation-induced mismatch between budburst and insect.

Here, we compare the development of spruce budworm (*Choristoneura fumiferana* Clemens), an important defoliator of the boreal forest, with budburst and shoot development in saplings of its host species growing under different thermal conditions in a controlled environment. We selected three species—balsam fir (*Abies balsamea* L. Mill.), white spruce (*Picea glauca* Moench, Voss), and black spruce (*Picea mariana* B.P.S. [Mill.]). Balsam fir is the main host of spruce budworm due to the tight synchrony with larval development via food quality, that is, needle characteristics (Despland et al., 2011; Fuentealba, Sagne, Pureswaran, Bauce, & Despland, 2018; Maclean, 1984). The timing of budburst is critical for young larvae because the suitability of foliage as food declines quickly after budburst (Quiring & McKinnon, 1999). We aimed to compare budburst on both defoliated and non-defoliated saplings with the timing of insect phenology under different thermal conditions. We hypothesized that warming counteracts the defoliation-induced mismatch by increasing the herbivore-plant phenological synchrony.

## 2 | MATERIALS AND METHODS

### 2.1 | Plant preparation and defoliation treatment

We used three conifer species to represent the main spruce budworm hosts: balsam fir, white spruce, and black spruce. In spring 2015, we placed 72 5 year old saplings (24 plants × 3 species) in a greenhouse in Chicoutimi, QC, Canada (48°25'N, 71°04'W, 150 m a.s.l.). We planted the saplings in 4.5 L plastic reverse-conical pots filled with peat moss, perlite, and vermiculite. Each pot received a dose of 1 g/L of NPK (20–20–20) fertilizer dissolved in 500 ml of water. The plants were split into 36 control and 36 defoliated saplings, each host having 12 control (non-defoliated) and 12 defoliated saplings. To simulate a natural defoliation, we placed 60 second-stage (L2) larvae of *C. fumiferana* (standard code Gfrc:IPQL:Cfum01 to Cfum16; Roe, Demidovich, & Dedes, 2018) in groups of 15 individuals near the terminal buds of branches in the upper half of the saplings in the spring of the previous growing season. No larvae were placed on the control saplings for non-defoliation (Deslauriers et al., 2019). In mid-September, following defoliation and after the adult budworms had mated and females laid their eggs on the remaining foliage, the saplings were moved into an open field and exposed to natural winter conditions. Defoliation in 2015 was similar among species with observed levels ranging from 80% to 95% of defoliation (Deslauriers et al., 2019). In spring 2016, the second instar larvae emerged naturally on the defoliated saplings.

### 2.2 | Experimental design

In spring 2016, the saplings were placed in three growth chambers (Conviron), and submitted to temperatures of 12, 17, and 22°C,

which were kept constant during day and night. Photoperiod was maintained at 18 hr during the experiment. A 12°C temperature with a photoperiod of 18 hr is representative of conditions during the budbreak phase in the southern limit of the boreal forest in Quebec (Antonucci et al., 2015; De Barba, Rossi, Deslauriers, & Morin, 2016). We installed a white net (Proteknet 60 g, 1.9 mm × 0.95 mm) in the middle of each chamber. The net allowed 93% of the light to pass through but isolated the defoliated saplings to prevent the dispersal of larvae toward the controls.

## 2.3 | Phenological and growth measurements

For each sapling, we made observations and measurements every 2 days on the three lateral shoots of the first verticil. We classified the budburst phases according to Dhont, Sylvestre, Gros-Louis, and Isabel (2010): (a) open bud, with a pale spot at the tip of the bud; (b) elongated bud, with lengthening brown scales; (c) swollen bud, with smooth and pale-colored scales but no visible needles; (d) translucent bud, with needles visible through the scales; (e) split bud, with open scales but needles still clustered; and (f) exposed shoot, with needles completely emerged from the surrounding scales and spreading outward. We used an electronic caliper to measure shoot growth at an accuracy of 0.001 cm.

We determined the larval stages of spruce budworm based on the size of the head capsule following McGugan (2012). For determining larval stage, we randomly selected three larvae per sapling. After observation, we placed the larvae back on the shoots. The percentage of defoliation was visually assessed on the three lateral shoots, using the shoot-count method based on six defoliation classes corresponding to a median percentage of defoliation of shoot (Maclean & Lidstone, 1982; Piene, MacLean, & Wall, 1981), and recorded as a percentage from 0 (absence of defoliation) to 100% (complete defoliation).

## 2.4 | Statistical analysis

We described the temporal dynamics of shoot growth and defoliation using a modified von Bertalanffy growth equation according to the formula:

$$y = a \times (1 - e^{-k(x-b)}),$$

where  $y$  is shoot growth or defoliation,  $x$  represents the day from the beginning of the experiment,  $a$  represents the asymptote,  $k$  is the growth rate, and  $b$  is the horizontal intercept representing the starting date of shoot growth and defoliation (Butto, Rossi, Deslauriers, & Morin, 2019). The nonlinear analysis regresses the residuals onto the model's partial derivatives and evaluates combinations of initial values that produce the smallest residual sums of squares until the estimates converge. We analyzed standard errors and distribution of the residuals to evaluate the goodness of fit of each regression.

We estimated the probability of co-occurrence of intensively feeding larvae (fourth to sixth instars) and buds susceptible to defoliation (phases 3–6) for each tree species and temperature combination as well as for defoliated and non-defoliated (control) saplings. The classification method adopted a parametric approach based on multivariate normal distributions within each group to derive discriminant quadratic functions. We assumed unequal variances between groups using the observed within-group covariance matrices. All statistics were performed using SAS 9.4 (SAS Institute Inc.).

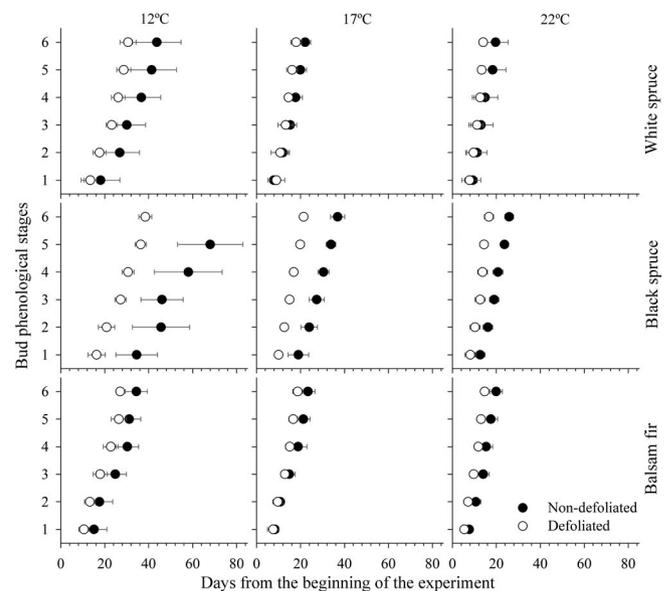
## 3 | RESULTS

### 3.1 | Budburst

On average, the first phase of budburst occurred 5–35 days after the beginning of the experiment (Figure 1). We observed the last phase of budburst 14–68 days after the beginning of the experiment; this resulted in the budburst process lasting 6–33 days.

In the control saplings, budburst for balsam fir and white spruce began almost at the same time, after 8 days from the beginning of the experiment at 17 and 22°C and about 1 week later at 12°C. The duration of budburst decreased with increasing temperature, lasting 19–12 days in balsam fir, and 26–10 days in white spruce. The budburst in black spruce began 13 days after the beginning of the experiment at 22°C, and after 19 and 35 days at 17 and 12°C, respectively. The duration of budburst was similar between species at 17 and 22°C but lasted 1–2 weeks longer for black spruce saplings at 12°C.

Defoliated saplings had an earlier and shorter budburst compared with the controls (Figure 1). At 12°C, budburst on the defoliated



**FIGURE 1** Budburst phases (mean and SD) detected on balsam fir, black spruce, and white spruce at 12, 17, and 22°C. The six budburst phases correspond to open bud (1), elongated bud (2), swollen bud (3), translucent bud (4), split bud (5), and exposed shoot (6)

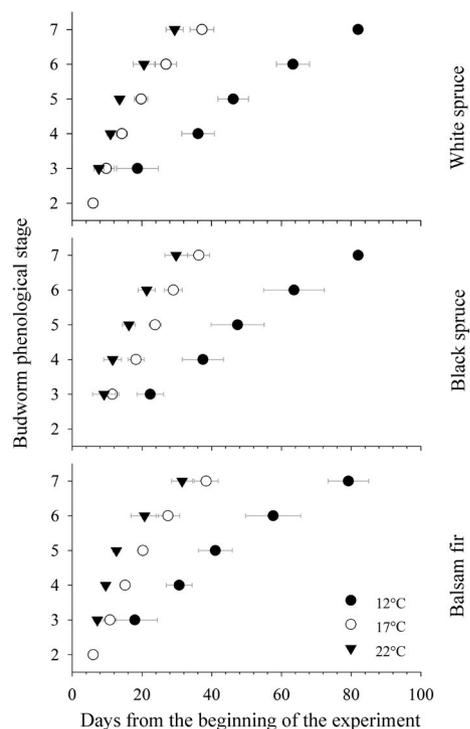
saplings in balsam fir and white spruce was 6 and 9 days earlier than the controls, respectively; this difference was 3 days at 17 and 22°C. For defoliated black spruce saplings, budburst began 24 days earlier than the controls at 12°C; this difference reduced to 13 and 7 days at 17 and 22°C, respectively.

### 3.2 | Larval phenology

We observed third instar larvae on average 8–22 days after the beginning of the experiment, and pupae (seventh instar) emerged 29–82 days after the beginning of the experiment (Figure 2). Thus, we observed a larval development process that lasted 21–63 days. Temperature explained much of this variability in the timing of larval development with host species accounting for another portion of the variability. Larval phenology at 17°C started 7–10 days earlier than at 12°C; at 22°C, larval phenology started only 2–4 days earlier than at 17°C. The duration of larval phenology at 17°C was about 27 days for all species, much shorter than that at 12°C but similar to that at 22°C. At the same temperature, larval development was very similar on the different host species, differing by 3 days or less.

### 3.3 | Shoot growth

Shoot growth was quicker at the beginning of the season (Figure 3; Table S1). Although we observed some trends in the models' residuals,



**FIGURE 2** Larval phases of spruce budworm (mean and SD) feeding on the balsam fir, black spruce, and white spruce at 12, 17, and 22°C

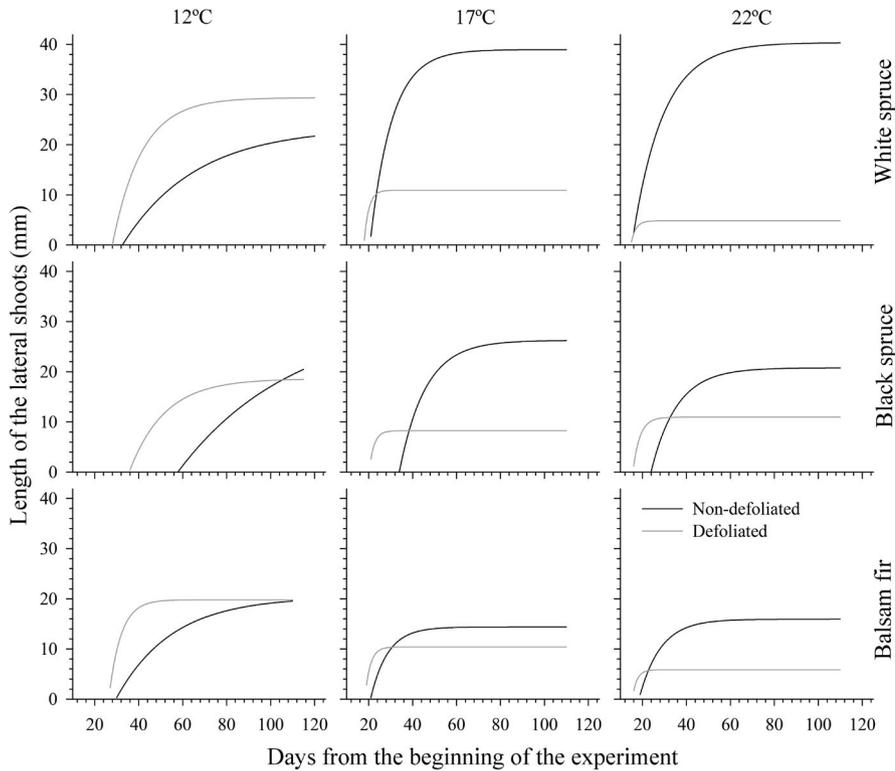
the studentized residuals were distributed around zero and ranged mostly between  $-2$  and  $2$ , that is, the 95% confidence interval. We therefore considered these analyses to be reliable (Figure S1). We observed a similar growth trend for all species and temperatures; however, final shoot lengths differed between species. Growth began 15–58 days after the beginning of the experiment at a growth rate of 0.03–0.47 mm/day. Final shoot lengths ranged between 5 and 40 mm.

In the non-defoliated saplings, the earliest shoot growth of balsam fir was observed at 18 days after the beginning of the experiment at 22°C, then 3 and 12 days later at 17°C and 12°C, respectively. The fastest and slowest growth rates for balsam fir were 0.13 and 0.04 mm/day at 17 and 12°C, respectively. Average final shoot length decreased with temperature from 20 to 14 mm. The timing and growth rates for white spruce matched those for balsam fir, although final shoot length increased with temperature from 23 to 40 mm. Black spruce shoot development occurred later than for balsam fir and white spruce. For the 22°C treatment, we observed the earliest growth in black spruce 23 days after the beginning of the experiment; shoot growth began 11 and 35 days later for saplings at 17 and 12°C, respectively. The growth rate of black spruce was 0.08 mm/day at both 17 and 22°C, a rate that was four times higher than that at 12°C.

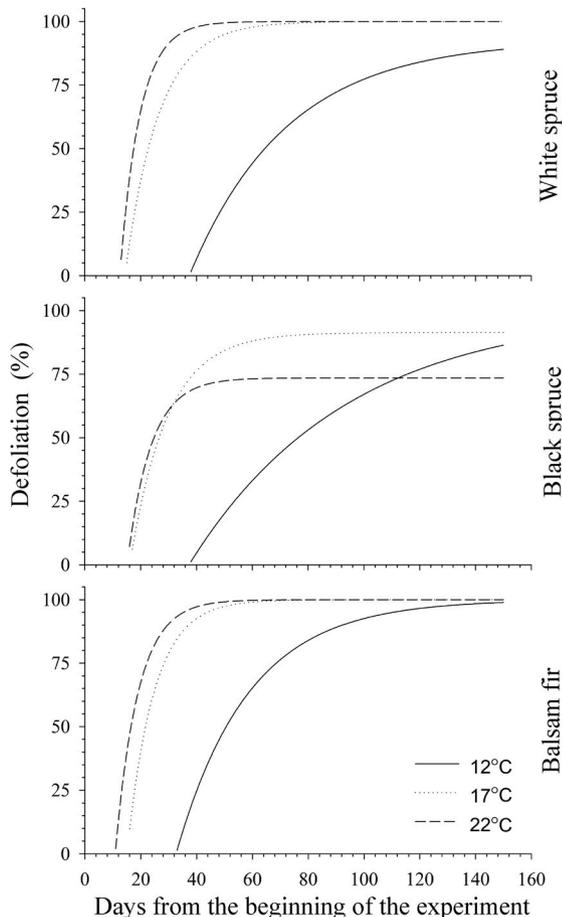
Relative to the controls, defoliated saplings grew earlier and faster at 12°C, and produced a shorter final shoot length at 17 and 22°C (Figure 3; Table S1). For balsam fir, lateral growth in the defoliated saplings began only 3 days earlier than in the non-defoliated saplings at all temperatures. Under warming conditions, the growth rate increased from 0.18 to 0.47 mm/day, but final shoot length decreased by 14 mm. The growth patterns of white spruce generally matched those of balsam fir, although warming affected final shoot length more strongly in the defoliated saplings. In black spruce, the temporal difference in the initiation of shoot growth between the defoliated and control saplings decreased from 22 to 8 days as temperature increased from 12 to 22°C. The highest growth rate and shortest final shoot length were observed at 17°C.

### 3.4 | Defoliation

Defoliation trends mirrored those of shoot growth, with a rapid increase observed at the beginning of the experiment, followed by a decreasing trend (Figure 4; Table S2). The studentized residuals were uniformly distributed within the 95% confidence interval, although they clearly underestimated defoliation during its earlier stages, 30–40 days after the beginning of the experiment (Figure S2). However, the error was small in terms of absolute value and was systematic across the different groups. Defoliation at 17 and 22°C was synchronous in the period ranging between 10 and 30 days after the beginning of the experiment. Defoliation occurred later at 12°C, 30–80 days after the beginning of the experiment. The defoliation rate at 17 and 22°C was higher than that at 12°C. The percentage of total defoliation varied with species and temperature. Balsam fir was completely defoliated at all three temperatures. In the two spruce species, the percentage of defoliation ranged between 73% and 100%.



**FIGURE 3** Growth trends of lateral shoots on balsam fir, black spruce, and white spruce at 12, 17, and 22°C



**FIGURE 4** Defoliation (%) for balsam fir, black spruce, and white spruce at 12, 17, and 22°C

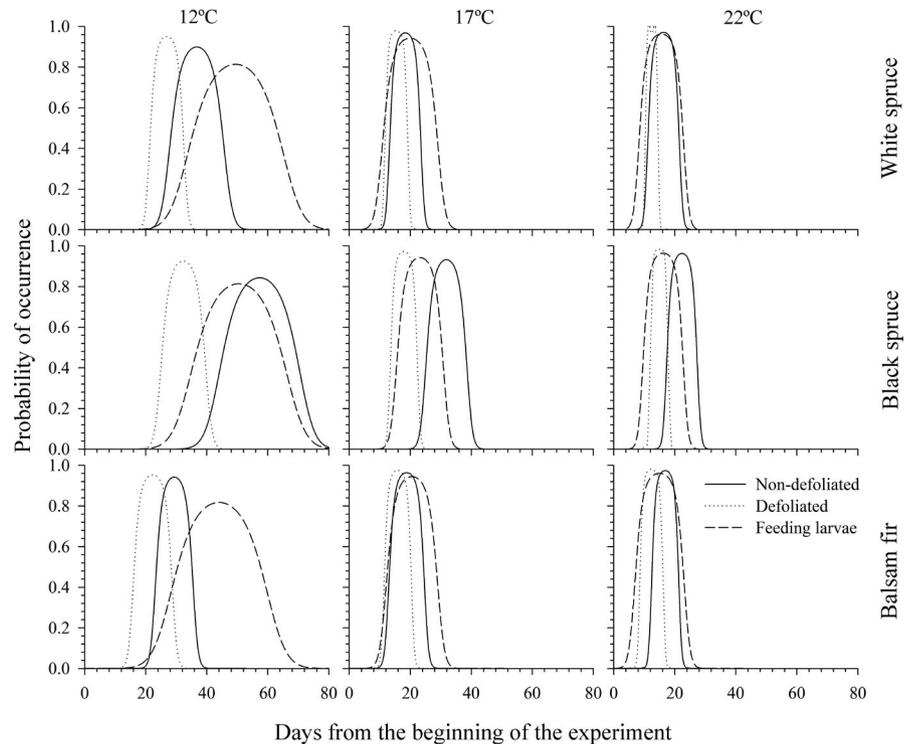
### 3.5 | Phenological synchrony of plant-insect interactions

The gap between the optimal larval feeding stage and optimal foliage availability varied between 0 and 22 days, depending on treatment, species, and temperature (Figure 5). In general, larval phenology was better synchronized with the non-defoliated controls than defoliated saplings. At 12°C, larvae were observed 15, 12, and 7 days after budburst on the non-defoliated (control) saplings of balsam fir, white spruce, and black spruce, respectively. At 12°C, we observed a longer gap of 18–22 days between the optimal larval feeding window and foliage availability in the defoliated saplings of all species. This gap decreased to only 2–9 days at 17°C and 0–6 days at 22°C.

## 4 | DISCUSSION

In this study, we compared the timing of larval development of spruce budworm with budburst on defoliated and non-defoliated saplings under three thermal conditions (12, 17, and 22°C). On defoliated saplings, budburst occurred 6–24 days earlier than on non-defoliated saplings; therefore, defoliation increased the mismatch with larval development. This mismatch, however, decreased to only 3–7 days when growth chamber temperatures increased by 5 or 10°C. The phenological convergence between plants and herbivore observed at higher temperatures supports our initial hypothesis and demonstrates the complex mechanisms that underlie species interactions under warming conditions.

**FIGURE 5** Probability of co-occurrence of intensively feeding larvae (fourth to sixth instars) and buds susceptible to defoliation (phases 3–6) on defoliated and non-defoliated (control) saplings for balsam fir, black spruce, and white spruce at 12, 17, and 22°C



#### 4.1 | Species interaction and phenological synchrony

The interaction between a pair of species can affect the phenological timing of either one or both taxa. Juenger and Bergelson (1998) observed that herbivore damage delays the date of first flowering in scarlet gilia by 7–14 days. When infected by anther smut, members of the white campion family exhibit a larger proportion of later flowering individuals (Biere & Antonovics, 1996; Elzinga et al., 2007). These phenological shifts in flowering can therefore generate a mismatch between species. In our study, budburst on defoliated saplings advanced by 6–24 days. Similarly, buds on white spruce flushed 2 days earlier on shoots damaged by spruce bud moth (*Zeiraphera canadensis*) compared to the flushing on undamaged branches (Carroll & Quiring, 2003). These earlier phenological events in defoliated conifers can be explained by a sugar-mediated response, via an earlier starch breakdown and higher sugar availability supplied for budburst (Deslauriers et al., 2019). Barbier, Lunn, and Beveridge (2015) demonstrated that high sucrose levels promote bud release and growth by repressing the expression of the key transcriptional regulator responsible for maintaining bud dormancy (Mason, Ross, Babst, Wienclaw, & Beveridge, 2014), a response mediated by trehalose-6-phosphate (Fichtner et al., 2017).

A phenological mismatch between antagonistic species can negatively affect herbivore feeding. A lower quality of food increases the risk of starvation for herbivores, thus decreasing their survival and reproduction (Fuentealba, Pureswaran, Bause, & Despland, 2017). As a consequence of the phenological mismatch, the young larvae try to disperse to prospect for food elsewhere. During this process,

the movement, particularly ballooning, can increase larval exposition to different mortality factors (Regniere & Nealis, 2018). Moreover, due to the mismatch, shoot growth exceeded 50% of its final length before the maturity of spruce budworm larvae (Deslauriers et al., 2019).

#### 4.2 | Climate change and phenological synchrony

Climate change is expected to affect phenological synchrony by altering the timing of life-cycle events of interacting species. Diverging phenological events result from differential responses to increased temperatures among species (Thackeray et al., 2016). For example, climate warming steadily increased the mismatch between the phenology of the great tit and its caterpillar prey (Reed, Grotan, Jenouvrier, Saether, & Visser, 2013); the timing of peak caterpillar development in the spring advanced at a rate of more than twice that of great tit egg-laying. Butterfly emergence or migratory arrival advanced at a rate three times faster than that of the first flowering of herbs, portending an increased asynchrony in insect–plant interactions (Parmesan, 2007).

In our study, spruce budworm exhibited a greater sensitivity to temperature than its host species. Under conditions of 5 and 10°C of warming, larval phenology advanced by 26 and 32 days on average, respectively, whereas bud phenology advanced by only 18 and 22 days, respectively, in non-defoliated saplings; this advance was 10 and 13 days for defoliated saplings for 5 and 10°C of warming, respectively. The relationship between temperature and phenology tends to be stronger for species such as spruce budworm that undergo an earlier spring reactivation (Forrest, 2016); this early

reactivation could explain the faster larval development at higher temperatures. As such, the phenological mismatch between larvae and saplings narrowed from 21 to 4 days as temperatures warmed from 12 to 17°C, leading to a resynchronization of the host with the herbivore. Similar results are the consequence of the variable responses to temperature between species; for example, the mean interval between the forest tent caterpillar (*Malacosoma disstria*) and its host trees, that is, aspen and birch, decreased by 3 days with a warming by 3.4°C, thus, increasing the synchrony between trees and insects (Schwartzberg et al., 2014).

Black spruce exhibits a greater sensitivity to temperature than balsam fir and white spruce. When temperatures increased by 5 and 10°C, budburst on the black spruce control saplings advanced by 16 and 22 days; this advance was less than 10 days for the other two host species. Similarly, Pureswaran, Neau, Marchand, De Grandpre, and Kneeshaw (2019) found that budburst in black spruce occurred 2.8 days earlier under a warming of 1°C. For spruce budworm, the optimal phenological matching occurs when larval emergence precedes balsam fir and white spruce budburst by about 2 weeks (Lawrence, Mattson, & Haack, 2012). In general, bud phenology in black spruce occurs 2 weeks after that of balsam fir (Antonucci et al., 2015); this delay is a major factor explaining the lower damage of black spruce relative to balsam fir. However, this 2 week delay in black spruce budburst decreased with warming. As such, this species could become more suitable as a food source for spruce budworm as warming proceeds in the boreal zone (Pureswaran et al., 2019).

Additive or antagonistic effects of warming and defoliation on tree physiology must also be taken into account (DeLucia, Nability, Zavala, & Berenbaum, 2012). An earlier or higher sugar availability can advance budburst on defoliated trees (Deslauriers et al., 2019); however, warming also decreases soluble sugars, especially glucose and fructose (Deslauriers et al., 2014; Way & Sage, 2008). Black spruce growing under warming conditions assimilate less carbon due to a limited photosynthetic acclimation (Way & Sage, 2008), thereby limiting the advance of budbreak. Therefore, a lower availability in soluble sugars could also explain the reduced differences between budburst occurrence on the control and defoliated saplings and favor improved synchrony between host and herbivore under warmer conditions. These multiple interactive physiological and warming effects must thus be considered in cases of herbivore host (Forrest, 2016).

## 5 | CONCLUSION

Phenological shifts related to ongoing climate warming are receiving increased attention given the consequences of altered phenological timing between interacting species (Fuentealba et al., 2017; Pureswaran et al., 2019). Although phenological mismatches under warming have been widely explored, few studies have documented greater synchronization among species subjected to warmer climatic conditions. Here, we compared larval development of spruce budworm and the budburst of its host species at different temperatures

within a controlled environment. We observed an earlier budburst on saplings defoliated by spruce budworm to produce a phenological mismatch of 18–22 days at 12°C. However, warmer temperatures (17 and 22°C) increased the synchrony between larval development and plant budburst. The phenological timing of a plant host is critical for the young larvae as the food quality of foliage drops quickly after budburst. Our results suggest that increased synchrony with warming can counteract the defoliation-induced mismatch and provide better growth conditions for larval development. The enhanced food quality that is available for spruce budworm larvae under warming conditions could affect the growth of spruce budworm populations and result in longer or more intense insect outbreaks. Thus, accurately predicting insect outbreaks with future warming requires a consideration of how temperature affects the phenological timing of both the insect and its host species.

## ACKNOWLEDGEMENTS

The work was supported by the Natural Sciences and Engineering Research Council of Canada (Discovery Grant) and the Ministry of Forests, Wildlife and Parks in Québec (MFFP). P. Ren received a State Scholarship Fund (201804910179) provided by the China Scholarship Council to conduct this research. E. Liang and P. Ren were supported by the National Natural Science Foundation of China (41525001, 41807443). The authors thank M. Hay and A. Garside for checking the English text.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

## ORCID

Ping Ren  <https://orcid.org/0000-0001-7647-8666>

Eryuan Liang  <https://orcid.org/0000-0002-8003-4264>

## REFERENCES

- Antonucci, S., Rossi, S., Deslauriers, A., Lombardi, F., Marchetti, M., & Tognetti, R. (2015). Synchronisms and correlations of spring phenology between apical and lateral meristems in two boreal conifers. *Tree Physiology*, 35(10), 1086–1094. <https://doi.org/10.1093/treephys/tpv077>
- Ayres, M. P., & Lombardero, M. J. (2000). Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *The Science of the Total Environment*, 262(3), 263–286. [https://doi.org/10.1016/S0048-9697\(00\)00528-3](https://doi.org/10.1016/S0048-9697(00)00528-3)
- Badeck, F.-W., Bondeau, A., Bottcher, K., Doktor, D., Lucht, W., Schaber, J., & Sitch, S. (2004). Responses of spring phenology to climate change. *New Phytologist*, 162(2), 295–309. <https://doi.org/10.1111/j.1469-8137.2004.01059.x>
- Barbier, F. F., Lunn, J. E., & Beveridge, C. A. (2015). Ready, steady, go! A sugar hit starts the race to shoot branching. *Current Opinion in Plant Biology*, 25, 39–45. <https://doi.org/10.1016/j.pbi.2015.04.004>
- Biere, A., & Antonovics, J. (1996). Sex-specific costs of resistance to the fungal pathogen *Ustilago violacea* (*Microbotryum violaceum*) in *Silene alba*. *Evolution*, 50(3), 1098–1110. <https://doi.org/10.1111/j.1558-5646.1996.tb02350.x>

- Both, C., van Asch, M., Bijlsma, R. G., van den Burg, A. B., & Visser, M. E. (2009). Climate change and unequal phenological changes across four trophic levels: Constraints or adaptations? *Journal of Animal Ecology*, 78(1), 73–83. <https://doi.org/10.1111/j.1365-2656.2008.01458.x>
- Butto, V., Rossi, S., Deslauriers, A., & Morin, H. (2019). Is size an issue of time? Relationship between the duration of xylem development and cell traits. *Annals of Botany*, 123(7), 1257–1265. <https://doi.org/10.1093/aob/mcz032>
- Carroll, A. L., & Quiring, D. T. (2003). Herbivory modifies conifer phenology: Induced amelioration by a specialist folivore. *Oecologia*, 136(1), 88–95. <https://doi.org/10.1007/s00442-003-1240-5>
- Chuine, I., & Régnière, J. (2017). Process-based models of phenology for plants and animals. *Annual Review of Ecology, Evolution, and Systematics*, 48(1), 159–182. <https://doi.org/10.1146/annurev-ecolsys-110316-022706>
- De Barba, D., Rossi, S., Deslauriers, A., & Morin, H. (2016). Effects of soil warming and nitrogen foliar applications on bud burst of black spruce. *Trees-Structure and Function*, 30(1), 87–97. <https://doi.org/10.1007/s00468-015-1152-0>
- Deacy, W. W., Armstrong, J. B., Leacock, W. B., Robbins, C. T., Gustine, D. D., Ward, E. J., ... Stanford, J. A. (2017). Phenological synchronization disrupts trophic interactions between Kodiak brown bears and salmon. *Proceedings of the National Academy of Sciences of the United States of America*, 114(39), 10432–10437. <https://doi.org/10.1073/pnas.1705248114>
- DeLucia, E. H., Nabity, P. D., Zavala, J. A., & Berenbaum, M. R. (2012). Climate change: Resetting plant-insect interactions. *Plant Physiology*, 160(4), 1677–1685. <https://doi.org/10.1104/pp.112.204750>
- Deslauriers, A., Beaulieu, M., Balducci, L., Giovannelli, A., Gagnon, M. J., & Rossi, S. (2014). Impact of warming and drought on carbon balance related to wood formation in black spruce. *Annals of Botany*, 114(2), 335–345. <https://doi.org/10.1093/aob/mcu111>
- Deslauriers, A., Fournier, M. P., Carteni, F., & Mackay, J. (2019). Phenological shifts in conifer species stressed by spruce budworm defoliation. *Tree Physiology*, 39(4), 590–605. <https://doi.org/10.1093/treephys/tpy135>
- Despland, E., Gundersen, M., Daoust, S. P., Mader, B. J., Delvas, N., Albert, P. J., & Bause, E. (2011). Taste receptor activity and feeding behaviour reveal mechanisms of white spruce natural resistance to Eastern spruce budworm *Choristoneura fumiferana*. *Physiological Entomology*, 36(1), 39–46. <https://doi.org/10.1111/j.1365-3032.2010.00760.x>
- Dhont, C., Sylvestre, P., Gros-Louis, M., & Isabel, N. (2010). *Field guide for identifying apical bud break and bud formation stages in white spruce*. Ottawa, ON, Canada: Natural Resources Canada, Quebec.
- Durant, J. M., Hjermann, D., Ottersen, G., & Stenseth, N. C. (2007). Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*, 33, 271–283. <https://doi.org/10.3354/cr033271>
- Edwards, M., & Richardson, A. J. (2004). Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*, 430(7002), 881–884. <https://doi.org/10.1038/nature02808>
- Elzinga, J. A., Atlan, A., Biere, A., Gigord, L., Weis, A. E., & Bernasconi, G. (2007). Time after time: Flowering phenology and biotic interactions. *Trends in Ecology & Evolution*, 22(8), 432–439. <https://doi.org/10.1016/j.tree.2007.05.006>
- Fichtner, F., Barbier, F. F., Feil, R., Watanabe, M., Annunziata, M. G., Chabikwa, T. G., ... Lunn, J. E. (2017). Trehalose 6-phosphate is involved in triggering axillary bud outgrowth in garden pea (*Pisum sativum* L.). *The Plant Journal*, 92(4), 611–623. <https://doi.org/10.1111/tpj.13705>
- Forrest, J. R. (2016). Complex responses of insect phenology to climate change. *Current Opinion in Insect Science*, 17, 49–54. <https://doi.org/10.1016/j.cois.2016.07.002>
- Fuentealba, A., Pureswaran, D., Bause, E., & Despland, E. (2017). How does synchrony with host plant affect the performance of an outbreaking insect defoliator? *Oecologia*, 184(4), 847–857. <https://doi.org/10.1007/s00442-017-3914-4>
- Fuentealba, A., Sagne, S., Pureswaran, D., Bause, E., & Despland, E. (2018). Defining the window of opportunity for feeding initiation by second-instar spruce budworm larvae. *Canadian Journal of Forest Research*, 48(3), 285–291. <https://doi.org/10.1139/cjfr-2017-0133>
- Hegland, S. J., Nielsen, A., Lazaro, A., Bjercknes, A. L., & Totland, O. (2009). How does climate warming affect plant-pollinator interactions? *Ecology Letters*, 12(2), 184–195. <https://doi.org/10.1111/j.1461-0248.2008.01269.x>
- Helfield, J. M., & Naiman, R. J. (2006). Keystone interactions: Salmon and bear in riparian forests of Alaska. *Ecosystems*, 9(2), 167–180. <https://doi.org/10.1007/s10021-004-0063-5>
- Juenger, T., & Bergelson, J. (1998). Pairwise versus diffuse natural selection and the multiple herbivores of scarlet gilia, *Ipomopsis aggregata*. *Evolution*, 52(6), 1583–1592. <https://doi.org/10.1111/j.1558-5646.1998.tb02239.x>
- Kharouba, H. M., Ehrlén, J., Gelman, A., Bolmgren, K., Allen, J. M., Travers, S. E., & Wolkovich, E. M. (2018). Global shifts in the phenological synchrony of species interactions over recent decades. *Proceedings of the National Academy of Sciences of the United States of America*, 115(20), 5211–5216. <https://doi.org/10.1073/pnas.1714511115>
- Lawrence, R. K., Mattson, W. J., & Haack, R. A. (2012). White spruce and the spruce budworm: Defining the phenological window of susceptibility. *The Canadian Entomologist*, 129(2), 291–318. <https://doi.org/10.4039/Ent129291-2>
- Liu, Q., Piao, S., Fu, Y. H., Gao, M., Peñuelas, J., & Janssens, I. A. (2019). Climatic warming increases spatial synchrony in spring vegetation phenology across the Northern Hemisphere. *Geophysical Research Letters*, 46(3), 1641–1650. <https://doi.org/10.1029/2018gl081370>
- Macleán, D. A. (1984). Effects of spruce budworm outbreaks on the productivity and stability of balsam fir forests. *The Forestry Chronicle*, 60(5), 273–279. <https://doi.org/10.5558/tfc60273-5>
- Macleán, D. A., & Lidstone, R. G. (1982). Defoliation by spruce budworm: Estimation by ocular and shoot-count methods and variability among branches, trees, and stands. *Canadian Journal of Forest Research*, 12(3), 582–594. <https://doi.org/10.1139/x82-090>
- Mason, M. G., Ross, J. J., Babst, B. A., Wienclaw, B. N., & Beveridge, C. A. (2014). Sugar demand, not auxin, is the initial regulator of apical dominance. *Proceedings of the National Academy of Sciences of the United States of America*, 111(16), 6092–6097. <https://doi.org/10.1073/pnas.1322045111>
- McGugan, B. M. (2012). Needle-mining habits and larval instars of the spruce budworm. *The Canadian Entomologist*, 86(10), 439–454. <https://doi.org/10.4039/Ent86439-10>
- Memmott, J., Craze, P. G., Waser, N. M., & Price, M. V. (2007). Global warming and the disruption of plant-pollinator interactions. *Ecology Letters*, 10(8), 710–717. <https://doi.org/10.1111/j.1461-0248.2007.01061.x>
- Miller-Rushing, A. J., Hoyer, T. T., Inouye, D. W., & Post, E. (2010). The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 365(1555), 3177–3186. <https://doi.org/10.1098/rstb.2010.0148>
- Moller, A. P., Rubolini, D., & Lehikoinen, E. (2008). Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proceedings of the National Academy of Sciences of the United States of America*, 105(42), 16195–16200. <https://doi.org/10.1073/pnas.0803825105>
- Parnesan, C. (2007). Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology*, 13(9), 1860–1872. <https://doi.org/10.1111/j.1365-2486.2007.01404.x>
- Peñuelas, J., & Filella, I. (2001). Responses to a warming world. *Science*, 294(5543), 793–795. <https://doi.org/10.1126/science.1066860>
- Piao, S., Liu, Q., Chen, A., Janssens, I. A., Fu, Y., Dai, J., ... Zhu, X. (2019). Plant phenology and global climate change: Current progresses and

- challenges. *Global Change Biology*, 25(6), 1922–1940. <https://doi.org/10.1111/gcb.14619>
- Piñe, H., MacLean, D. A., & Wall, R. E. (1981). *Effects of spruce budworm-caused defoliation on the growth of balsam fir: Experimental design and methodology*. Fredericton, NB: Maritimes Forest Research Centre, Canadian Forestry Service.
- Pureswaran, D. S., Neau, M., Marchand, M., De Grandpre, L., & Kneeshaw, D. (2019). Phenological synchrony between eastern spruce budworm and its host trees increases with warmer temperatures in the boreal forest. *Ecology and Evolution*, 9(1), 576–586. <https://doi.org/10.1002/ece3.4779>
- Quiring, D. T., & McKinnon, M. L. (1999). Why does early-season herbivory affect subsequent budburst? *Ecology*, 80(5), 1724–1735. [https://doi.org/10.1890/0012-9658\(1999\)080\[1724:wdesha\]2.0.co;2](https://doi.org/10.1890/0012-9658(1999)080[1724:wdesha]2.0.co;2)
- Reed, T. E., Grotan, V., Jenouvrier, S., Saether, B. E., & Visser, M. E. (2013). Population growth in a wild bird is buffered against phenological mismatch. *Science*, 340(6131), 488–491. <https://doi.org/10.1126/science.1232870>
- Regniere, J., & Nealis, V. G. (2018). Two sides of a coin: Host-plant synchrony fitness trade-offs in the population dynamics of the western spruce budworm. *Insect Science*, 25(1), 117–126. <https://doi.org/10.1111/1744-7917.12407>
- Renner, S. S., & Zohner, C. M. (2018). Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. *Annual Review of Ecology, Evolution, and Systematics*, 49(1), 165–182. <https://doi.org/10.1146/annurev-ecolsys-110617-062535>
- Roe, A. D., Demidovich, M., & Dedes, J. (2018). Origins and history of laboratory insect stocks in a multispecies insect production facility, with the proposal of standardized nomenclature and designation of formal standard names. *Journal of Insect Science*, 18(3), 1–9. <https://doi.org/10.1093/jisesa/iey037>
- Saino, N., Ambrosini, R., Rubolini, D., von Hardenberg, J., Provenzale, A., Hüppop, K., ... Sokolov, L. (2011). Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proceedings of the Royal Society B: Biological Sciences*, 278(1707), 835–842. <https://doi.org/10.1098/rspb.2010.1778>
- Schwartzberg, E. G., Jamieson, M. A., Raffa, K. F., Reich, P. B., Montgomery, R. A., & Lindroth, R. L. (2014). Simulated climate warming alters phenological synchrony between an outbreak insect herbivore and host trees. *Oecologia*, 175(3), 1041–1049. <https://doi.org/10.1007/s00442-014-2960-4>
- Singer, M. C., & Parmesan, C. (2010). Phenological asynchrony between herbivorous insects and their hosts: Signal of climate change or pre-existing adaptive strategy? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1555), 3161–3176. <https://doi.org/10.1098/rstb.2010.0144>
- Stenseth, N. C., & Mysterud, A. (2002). Climate, changing phenology, and other life history traits: Nonlinearity and match-mismatch to the environment. *Proceedings of the National Academy of Sciences of the United States of America*, 99(21), 13379–13381. <https://doi.org/10.1073/pnas.212519399>
- Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., ... Wanless, S. (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, 535(7611), 241–245. <https://doi.org/10.1038/nature18608>
- Thackeray, S. J., Sparks, T. H., Frederiksen, M., Burthe, S., Bacon, P. J., Bell, J. R., ... Wanless, S. (2010). Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology*, 16(12), 3304–3313. <https://doi.org/10.1111/j.1365-2486.2010.02165.x>
- van Asch, M., & Visser, M. E. (2007). Phenology of forest caterpillars and their host trees: The importance of synchrony. *Annual Review of Entomology*, 52, 37–55. <https://doi.org/10.1146/annurev.ento.52.110405.091418>
- Vitasse, Y., Signarbieux, C., & Fu, Y. H. (2018). Global warming leads to more uniform spring phenology across elevations. *Proceedings of the National Academy of Sciences of the United States of America*, 115(5), 1004–1008. <https://doi.org/10.1073/pnas.1717342115>
- Way, D. A., & Sage, R. F. (2008). Elevated growth temperatures reduce the carbon gain of black spruce [*Picea mariana* (Mill.) B.S.P.]. *Global Change Biology*, 14(3), 624–636. <https://doi.org/10.1111/j.1365-2486.2007.01513.x>

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** Ren P, Néron V, Rossi S, Liang E, Bouchard M, Deslauriers A. Warming counteracts defoliation-induced mismatch by increasing herbivore-plant phenological synchrony. *Glob Change Biol*. 2020;26:2072–2080. <https://doi.org/10.1111/gcb.14991>