INTRODUCTION

In temperate climates, the degree of synchrony between herbivorous insects and their host plants is crucial to the completion of insect life cycles (Van Asch & Visser, 2007). Recent studies on forest responses to warming predict extension of the growing season with earlier springs and delayed winters (Gunderson et al., 2012). Northern range limits of temperate and boreal species are determined by the duration of the growing season and winter temperature (Bale et al., 2002). Therefore, plants and defoliating insects are highly sensitive to changes in temperature that trigger, respectively, budburst and emergence from diapause (Beck, 1983; Logan, Régnière, & Powell, 2003). Climate change has also been implicated in altering the seasonal phenology of trees, herbivores, and natural enemies at different rates (Singer & Parmesan, 2010; Stireman et al., 2005; Voigt et al., 2003), thereby changing species distributions (Chuine, 2010; Hill,
Griffiths, & Thomas, 2011) as well as interspecific interactions. As a result, changes have recently been observed in the distribution of plants and their insect herbivores including shifts to new hosts and consequently, in the disturbance regimes of pest species (Haynes, Allstadt, & Kilmetzek, 2014; Jepsen, Hagen, Ims, & Yoccoz, 2008; Jepsen et al., 2011).

The recognition of phenology as an important adaptive trait shaping species distributions requires examination of responses to temperature by both plants and their insect herbivores. Among North American and European pest species that cause outbreaks, landscape-level consequences of phenological changes are becoming more pronounced. In European Lepidoptera, examination of variation in phenological change of 566 species over a 150-year period suggests that shifts in phenology related to climate change are correlated with traits involving interactions with host plants (Altermatt, 2010 and references therein). Among forest defoliators, recent changes in distribution patterns of the winter moth, Operophtera brumata (Hagen, Jepsen, Ims, & Yoccoz, 2007) and the autumnal moth, Epirrita autumnata (Jepsen et al., 2008) have been reported.

In North America, flexible voltinism (from semivoltine to univoltine) in response to temperature has been recorded in the spruce beetle, Dendroctonus rufipennis (Hansen & Bentz, 2003; Hansen, Bentz, Powell, Gray, & Vandygriff, 2011), particularly in the northern part of its range, increasing severity of outbreaks in recent years (Berg, Henry, Fastie, Volder, & Matsuoka, 2006; Werner & Holsten, 1985a, 1985b; Werner, Holsten, Matsuoka, & Burnside, 2006). As predicted by Williams and Liebold (2002), there are now instances of outbreaks of the southern pine beetle, Dendroctonus frontalis, in more northern pine forests in the United States that they attribute to an increase in minimum winter temperatures (Tran, Ylioja, Billings, Régnière, & Ayres, 2007; Weed, Ayres, & Hicke, 2013).

Similarly, the current outbreak of an important defoliator in the eastern North American boreal forest, the eastern spruce budworm, Choristoneura fumiferana, is occurring farther north than in the past, and in areas that were not previously affected by outbreaks (Pureswaran et al., 2015). Spruce budworm is a univoltine moth whose larvae feed on current year buds of balsam fir (Abies balsamea (L.) Mill.) and black spruce (Picea mariana (Mill.).) Larvae emerge from diapause in the spring and disperse on silk to settle on new buds. Budburst of balsam fir, the preferred host, may occur up to two weeks following larval emergence, in which case, larvae may mine old foliage while waiting for budburst. A lag that is too long between larval emergence and budburst results in high rates of larval mortality (Blais, 1957; Nealis & Régnière, 2004; Trier & Mattson, 1997). Synchrony with budburst and its consequences on survival were recorded to be optimal when larval emergence preceded budburst by about 2 weeks on white spruce (Lawrence, Mattson, & Haack, 1997), whose budburst occurs at the same time as balsam fir (Greenbank, 1963). Emerging too late in relation to budburst also reduces fitness as lignified foliage is difficult for young larvae to feed on (Lawrence et al., 1997). Recent studies that manipulated the availability of new buds to second instar larvae showed that phenological asynchrony with both balsam fir and black spruce has a negative impact on spruce budworm performance (Fuentealba, Pureswaran, Bauce, & Despland, 2017; Fuentealba, Sagne, Pureswaran, Bauce, & Despland, 2018).

The northern boreal forest is composed of balsam fir as well as a high proportion of black spruce. White spruce is a minor component in this region and is grouped with balsam fir in forest inventories. Black spruce is usually a secondary host species, that in the past suffered little mortality from defoliation for two reasons: (a) the cool, short summers that characterize this northern ecosystem limited completion of spruce budworm’s life cycle; (b) budburst of black spruce occurs two weeks later than that of balsam fir (Nealis & Régnière, 2004). The 3–4 week lag between budburst of black spruce and larval emergence from diapause has historically been sufficient to allow black spruce to phenologically escape from severe herbivory during outbreaks. However, during the current outbreak, we documented significant defoliation of black spruce (Bognounou, Grandpré, Pureswaran, & Kneeshaw, 2017), raising concerns about an increase in the severity of outbreaks if an advance in budburst due to climate warming were to render black spruce phenologically better suited to spruce budworm.

Several studies in Europe and North America have examined the role of climate change in relation to tree phenology (Menzel et al., 2006; Wolkovich et al., 2012). Other studies have looked at the role of temperature in relation to insect developmental rates (Régnière, Powell, Bentz, & Nealis, 2012). Fewer studies have examined the impact of temperature on both plant and insect phenology, including changes in phenological synchrony and mismatches due to simulated climate warming (Buse & Good, 1996; Schwartzberg et al., 2014). Still fewer studies have been conducted in nature to evaluate in situ variation in phenology between forest insects and their host trees and their response in the long-term to warmer ambient temperatures. In the midst of a burgeoning spruce budworm outbreak (Ministère des Forêts & de la Faune des Parcs, 2016), we used naturally occurring microclimates in mixed stands of black spruce and balsam fir to test the following predictions: (a) warm microclimates will advance budburst of balsam fir and black spruce, (b) warm microclimates will also advance the emergence of spruce budworm larvae from diapause, and (c) if there are advances in budburst and larval emergence, they will occur at different rates, potentially increasing phenological synchrony between spruce budworm and both or one of its host species.

2 | METHODS

2.1 | Study sites and sampling design

The study area is located in the transition between meridional balsam fir-dominated boreal forests to more northern black spruce-dominated forests in eastern Quebec, Canada (Saucier, Robitaille, Grondin, Bergeron, & Gosselin, 2011). A cold maritime climate characterizes this region, where mean annual temperature varies from -2.0 to 1.5°C and mean annual precipitation ranges from 950 to
1,350 mm, of which about 40% falls as snow. The growing period lasts 120 to 150 days (Saucier et al., 2009).

We established two sites in the midst of an ongoing spruce budworm outbreak, 50 km north of the town of Baie-Comeau, one in 2013 (49°43′46.84″N, −68°10′8.76″W) and the other in 2014 (49°42′59.00″N, −68°8′26.30″W) in mixed black spruce/balsam fir stands older than 90 years. Balsam fir and black spruce about three meters in height were selected at each site with 20 trees of each species in 2013 and 30 in 2014. Trees were chosen to represent a gradient of microclimates. Average defoliation in the region of our study was 50% in 2012, 64% in 2013, and 75.8% in 2014. The average defoliation of balsam fir and black spruce trees reached 86.3% and 46.7%, respectively, in the summer of 2013 inhibiting bud production by balsam fir trees the following year. We had to change study plots in 2014 because severe defoliation by the spruce budworm made it impossible to collect data from the same trees for more than one summer.

2.2 Phenology measurements

We monitored the onset of budburst and emergence of second instar larvae (L2) from diapause on all trees. Every 2–3 days, 30 or 50 buds, in 2014 and 2013 respectively, were randomly selected on branches located around each tree to observe budburst. Buds were classified as “open,” when bud scales started to separate and the tips of needles were visible (Dorais & Kettela, 1982; Numainville & Desponts, 2004), or “closed” otherwise. Yellow “dry-touch” sticky traps (Solida, Saint-Ferréol-les-Neiges, QC, Canada) were installed 2–3 cm below selected branches (Figure 1) to capture larvae as they emerged from diapause and before they dispersed in search of food. Because of the proximity of the sticky traps to the selected branches, it was highly likely that the larvae we captured emerged from the branch directly above the trap (Figure 1). Traps were monitored every 2–3 days until no more larvae were collected. The onset of budburst was defined as the date when at least one bud was open on the tree, and larval emergence was estimated at peak emergence, when the maximum number of larvae was observed on each tree. Synchrony was calculated as the time difference (lag, in days) between these two phenological events.

2.3 Climate data

Temperature data were recorded hourly between May and July each year. HOBO Pendant® (UA-002-64, Onset Computer Corporation, Bourne, MA, USA) or Thermochron iButton® (DS1921G, Maxim Integrated Products, Inc., San Jose, CA, USA) temperature data loggers were installed on each tree from which phenology data were collected. Sensors were placed on a south facing branch at a height of about 1.30 m. Based on data availability, a common reference period was designated (Julian days 155–173) and hourly measurements taken during that period were averaged for each tree. This average temperature was used to define microclimates and compare trees within the same site (year).

In order to estimate spring temperatures before the beginning of our sampling, daily air temperature was interpolated for our sites with BioSIM 10 software (Régnière, 1996; Régnière & St-Amant, 2007; Régnière, St-Amant, & Bechard, 2014), using the daily climatic model (Régnière & Bolstad, 1994). BioSIM interpolates daily minimum and maximum temperatures (°C), precipitation (mm), relative humidity, and wind speed by matching georeferenced sources of weather data (eight nearest weather stations) to spatially georeferenced points (study sites), adjusting for differences in latitude, longitude, and elevation between the source of weather data and each site location using spatial regressions (Régnière et al., 2014).

2.4 Statistical analysis

The influence of temperature on budburst onset and phenological synchrony was assessed using linear regression models. Regression analysis was also initially used to evaluate the relationship between peak larval emergence and temperature. However, peak larval emergence was synchronous, that is, on the same day in a given year on most trees, regardless of temperature (Figures 2 and 3a,b; i.e., day 129 in 2013 and day 143 in 2014). Therefore, we did not perform regression analysis on larval emergence data.

A single model containing microclimates, species, site, and their interactions was adjusted to both dependent variables, that is, budburst onset and phenological synchrony. Models were parametrized to provide slope estimates for each group (species x site) and their appropriate standard errors (Schielzeth, 2010). Temperature was mean-centered before analyses to facilitate interpretation of intercept terms, and residuals were plotted to verify model assumptions. The glht function of the multcomp package (Hothorn, Bretz, & Westfall, 2008) was then used to simultaneously perform slope comparison tests between species and sites (years). Two trees were removed before analyses, one black spruce tree in 2013 was too...
severely defoliated to follow budburst, and another black spruce in 2014 had too few larvae on it to estimate peak emergence.

Preliminary ordinary least squares regressions showed unequal variance in the residuals between groups, violating the assumption of homoscedasticity. Generalized least squares (GLS) regressions were performed, using the gls function of the nlme package (Pinheiro, Bates, DebRoy, Sarkar, & Team, 2016) in R (R Core Team, 2016). This procedure allows for heteroscedastic within-group errors by directly modeling the variance-covariance structure of the response (Pinheiro & Bates, 2000). Different variance structures were tested and compared using AICc (Akaike’s information criterion) corrected for small sample sizes (Burnham & Anderson, 2002) using the AICc function in the AICcmodavg package (Mazerolle, 2016). Models with the varIdent variance function (Pinheiro & Bates, 2000), allowing for different variances for each group, provided the best fit. Examination of standardized residuals further showed that heteroscedasticity was properly accounted for.

3 | RESULTS

3.1 | Microclimates and air temperature

We found a maximum temperature difference of 3.82°C between the coldest and warmest microclimates, sampled across sites (years) and species (Figure 4). The range was greater in 2013 (2.83°C for balsam fir and 3.82°C for black spruce) than in 2014 (2.4°C for balsam fir and 2.01°C for black spruce). Climate records from the province of Quebec indicate an increase of 1–3°C of mean annual temperatures over a period of between 1950–2011. This trend is expected to continue so that annual temperatures rise by approximately 2–4°C for the 2041–2070 period (Ouranos, 2015). The temperature range in our study therefore reflects predicted warming scenarios. Average air temperatures interpolated for each site were consistent with average observed microclimate temperatures and show that the period preceding the phenological events was colder in 2014 than in 2013 (Figure 2).

3.2 | Larval emergence from diapause

A total of 3,394 second instar larvae (L2) were sampled during the study; 300 on black spruce and 377 on balsam fir in 2013, and 893 on black spruce and 1,824 on balsam fir in 2014. Peak emergence of L2s was neither influenced by microclimate nor host species (Table 1, Figure 3a,b). Larval emergence peaked on the same date for all but one tree in both years (Figure 3a,b). In 2013, peak emergence occurred on day 129 except for one balsam fir (day 134); in 2014, larvae emerged on day 143 (two weeks later) except for one black spruce (day 149). A few larvae had emerged before we started collecting our samples in 2013, but it is highly likely that our sampling period captured peak larval emergence. According to interpolated air temperatures before larval sampling began, a mean temperature of 10°C was not attained before day 127 when our sticky traps were
FIGURE 3  Relationships between onset of second instar larval (L2) emergence (a, b), onset of budburst (c, d), and synchrony (e, f) with mean-centered microclimate temperatures, for 2013 (left column; n = 39) and 2014 (right column; n = 59). Solid lines show model predictions in the observed range of temperatures. Dotted lines are 95% confidence intervals. No model was fitted to L2 emergence data but observed values are plotted to show the relationship between the two phenological events and synchrony.
installed (Figure 2). Based on the 2014 results, larval emergence appears to occur once average air temperatures reach 10°C. On day 136, when temperatures reached 10°C, a few larvae began to emerge (Figure 2). Three days later, temperatures dropped below this threshold and the number of sampled larvae dropped correspondingly. When temperatures reached 10°C again around day 142, peak emergence occurred.

3.3 | Budburst phenology

In 2013, the onset of budburst started on day 136 (May 16th) and ended on day 168 (June 17th), the onset period lasting 15 days for balsam fir and 21 days for black spruce. In 2014, the budburst period started almost two weeks later (day 149—May 29th) but was shorter (17 days overall, 8 days for balsam fir and 7 days for black spruce) and ended earlier, on day 166 (June 15th). The timing of budburst advanced with increasing temperature for both species and in both years (Figure 3c,d, Table 2). The effect was strongest for balsam fir in 2013: budburst occurred on average 4.62 days earlier for an increase in temperature of 1°C. This represents a difference of almost two weeks (13 days) between the warmest and coolest microclimates observed for that group (with a temperature range of 2.83°C). In the same year, black spruce budburst onset advanced by 11 days (slope: −2.79, temperature range of 3.82°C). The influence of microclimate temperature was lower in 2014, with budburst advancing by only three days for between the warmest and coolest microclimates for both species (slopes: −1.39 and −1.53, ranges: 2.40 and 2.01°C, for balsam fir and black spruce, respectively). The GLS model provided a good fit to the data (Figure 5). Slope comparisons among groups were not statistically significant, except for balsam fir when compared between years (Table 3). This is due to large confidence intervals around estimates. In 2013, the onset of budburst occurred 16 days earlier, at mean microsite temperature, for balsam fir compared to black spruce (Table 2). The difference between species was half this value in 2014 (8 days), with balsam fir budburst occurring almost 10 days later than in 2013.

3.4 | Synchrony between budburst onset and peak larval emergence

In 2013, the number of days between the onset of budburst and peak larval emergence ranged from 7 to 22 days for balsam fir and 18 to 39 days for black spruce. The phenological events were more synchronous in 2014 when the number of days between budburst and larval emergence varied from 6 to 14 days on balsam fir and 16 to 23 days for black spruce.

Peak larval emergence is practically the same for all trees sampled in the same year and thus differences in synchrony are due primarily to the onset of budburst (Figures 2 and 3; Tables 2 and 3). Comparing microclimates, synchrony was 13 and 11 days closer in 2013, for balsam fir and black spruce, respectively in the warmest versus the coolest microclimates. The difference between species was not statistically significant (Table 3). In 2014, synchrony increased by only three days for both species between the minimum and maximum observed temperatures, but the length of the budburst period was also shorter.

4 | DISCUSSION

Our study has shown that under natural conditions, while larval emergence responds to a rise in average daily air temperature above 10°C (Figure 2), budburst in both host species advances significantly for every degree rise in microsite temperature (Figure 3c,d, Table 2). An advance in budburst, and as a consequence, tighter phenological synchrony between spruce budworm and its hosts (Figure 3, Table 2), can potentially decrease larval mortality due to predation or starvation that occurs during the waiting period, particularly on balsam fir, the primary host of spruce budworm. Black spruce, that is currently less accessible as a host (Nealis & Régnière, 2004), would become more suitable to emerging second instar larvae. Lawrence et al. (1997) noted that spruce budworm larval survival on white spruce, Picea glauca, was greatest when larval development began about two weeks before budburst, presumably because early budburst and foliage maturation may impede feeding, whereas, late budburst would lead to starvation of young larvae. We expect that the “phenological window” of host suitability could potentially increase for both balsam fir and black spruce as phenological synchrony becomes tighter.

The effects of temperature on advance in budburst (Figure 3c,d) and correspondingly on synchrony (Figure 3e,f) were
more pronounced in 2013 than in 2014 because of the wider range of temperatures that prevailed in the microclimates of our sampled trees in 2013 (Figure 4). In spite of this difference in variation in temperature between years, budburst and synchrony advanced with temperature in both years (Figure 3, Table 2). Similar changes in budburst phenology were recently observed by Rossi (2015) who showed in greenhouse experiments that one-year-old black spruce seedlings from cold sites that were subjected to warm temperatures had earlier budburst. In the southern part of its range, black spruce budburst occurs when temperatures are between 9 and 13°C (Huang, Deslauriers, & Rossi, 2014). Within this range of temperatures, a slight warming could significantly advance budburst and create changes in the phenological synchrony between interacting species. The phenological delay between black spruce and spruce budworm, and as a consequence, the diminished performance and

| 2013 | 2014 |
|------|------|
| Sample size | 20 | 30 |
| L2 emergence onset date | 129.3 (1.1) | 143 (0) |
| Budburst onset date | 145.1 (4.1) | 152.9 (1.9) |
| Lag (no. of days) | 15.9 (4.0) | 9.9 (1.9) |

**TABLE 2** Parameter estimates from generalized least squared (GLS) regression models

| GLS models | Budburst onset | Synchrony |
|------------|---------------|-----------|
| Mean for balsam fir 2013 | 143.6*** (142.5, 144.7) | 14.4*** (13.3, 15.4) |
| Difference in means (days) | | |
| Balsam fir 2014 | 9.6*** (8.3, 10.8) | −4.2*** (−5.5, −3.0) |
| Black spruce 2013 | 16.3*** (14.0, 18.6) | 16.5*** (14.3, 18.8) |
| Black spruce 2014 | 17.9*** (16.6, 19.1) | 3.9*** (2.7, 5.1) |
| Effect of temperature | | |
| Balsam fir 2013 | −4.6*** (−5.9, −3.3) | −4.5*** (−5.8, −3.2) |
| Balsam fir 2014 | −1.4* (−2.6, −0.2) | −1.4* (−2.6, −0.2) |
| Black spruce 2013 | −2.8*** (−4.4, −1.1) | −2.8*** (−4.4, −1.1) |
| Black spruce 2014 | −1.5* (−2.9, −0.2) | −1.4* (−2.6, −0.1) |
| Residual standard error | 4.4 | 4.4 |
| Corr² | 0.88 | 0.91 |
| Number of observations | 98 | 98 |

Note. Values in parentheses are 95% confidence intervals. Corr² indicates the squared correlation between predicted and observed values. Since temperature was mean-centered before analyses, intercept terms represent mean at average microsite temperature and comparisons with the reference group (balsam fir 2013). Model was parametrized to provide group slope estimates, that is, a temperature slope for each species and site (year). Onset of budburst and synchrony are measured in number of days.

Asterisks indicate statistical significance:

* p < 0.05  ** p < 0.01  *** p < 0.001

**FIGURE 5** Relationship between predicted and observed values, for the budburst onset and synchrony generalized least squared (GLS) regression models. The straight line represents perfect agreement, and Corr² indicates the squared correlation between the two
low population densities on this host species, were first reported by Swaine and Craighead (1924). Blais (1957) further documented that black spruce as a food resource had no adverse effect on the rate of larval development nor survival of spruce budworm larvae and concluded that phenological delay in budburst was the main factor that rendered black spruce relatively resistant to defoliation. More recent work has shown that while survival of early stages of spruce budworm may be low on black spruce due to its delayed budburst, survival of late instar larvae was relatively high as phenological differences among hosts decreased as the summer season progressed and foliage on all hosts became equally suitable (Nealis & Régnière, 2004).

Our prediction that emergence of second instar larvae from diapause would also advance under warmer temperatures did not hold true over the temperature gradient we observed. Larval emergence did not exhibit any discernable relationship with neither temperature nor host species (Figure 3a,b, Table 1). Instead, maximum larval emergence occurred once air temperature exceeded 10°C (Figure 2). Diapause in spruce budworm is completed by the end of February after which larvae remain quiescent, waiting for suitable environmental cues such as temperature and photoperiod before they emerge to continue development (Bean, 1961). Development rates during the post-diapause period were found to increase at temperatures above 11°C (Régnière, 1990). Similarly, in a study of the response of the western spruce budworm, Choristoneura occidentalis, to temperature, Reichenbach and Stairs (1984) noted that development of all life stages was minimal below 10°C. Régnière (1987) also found that low temperatures delayed larval emergence.

The prolonged post-diapause development period of overwintering larvae (Bean, 1961) usually makes it difficult to predict timing of larval emergence in the spring based on developmental physiology (Régnière, 1990). Emergence under field conditions can peak, with larvae emerging more simultaneously than was accounted for by variability in developmental rates and often occurred earlier than models predicted (Lysyk, 1989). Fluctuating temperatures can also synchronize post-diapause development in the population (Régnière, 1987) and lead to simultaneous emergence of larvae as we observed in our study. There are several benefits to simultaneous emergence in overwintering larvae, particularly in northern latitudes with relatively short summers, because they need to take advantage of environmental conditions as soon as they become favorable.

Emerging from diapause or hatching too far in advance of budburst incurs several costs, and global warming is likely to disrupt existing phenological relationships. When subjected to warm spring temperatures, egg hatch of the winter moth was predicted to occur up to three weeks before budburst of pedunculate oak, Quercus robur, becoming poorly synchronized as a result (Visser & Holleman, 2001). In general, tighter phenological synchrony with host plants has a positive impact on the population dynamics of defoliating Lepidoptera and can potentially increase outbreak severity (Van Asch & Visser, 2007). Trends similar to those observed in our study in which host tree phenology advanced more than insect phenology in response to temperature, thereby decreasing the lag between egg hatch and budburst of hosts and improving synchrony, have also been observed for the forest tent caterpillar, Malacosoma disstria (Schwartzberg et al, 2014).

Demonstrating the precise impacts of climate change on natural ecosystems, particularly across trophic levels is a challenging task (Mjaaseth, Hagen, Yoccoz, & Ims, 2005; Parmesan & Yohe, 2003). Most current information on relative changes between host budburst and insect emergence is from experimental manipulation or predictive models (Harrington, Woiwood, & Sparks, 1999). Our study is the first to measure emergence from diapause in the field for the spruce budworm in association with budburst phenology and temperature. From a practical standpoint, one of the challenges we encountered was that emergence from diapause often occurred earlier than models predicted (Lysyk, 1989) while there was still over a meter of snow on the forest floor. Phenological traits are also reported to be highly heritable (Chuine, 2010) and are subject to rapid selection in insects. However, there are not many empirical studies evaluating natural selection on phenological traits over several generations. So far, the winter moth–pedunculate oak system is the only forest insect for which the potential to adapt rapidly to changing host phenology, restoring synchrony of egg hatch with host budburst has been demonstrated (Van Asch, Tienderen, Holleman, & Visser, 2007). To predict the impacts of climate change in forest pest systems, it will be crucial to determine the relative speed of adaptation at different trophic levels and the consequences for population dynamics (Forrest & Miller-Rushing, 2010; Harrington et al., 1999).

The spruce budworm system, an increase in synchrony between both host species and spruce budworm may increase the severity of outbreaks, particularly in mixed stands of black spruce and balsam fir (Bognounou et al., 2017). The "phenological window of host suitability" in this case, would widen by sustaining populations on black spruce later in the season, as well as during the course of the outbreak cycle after balsam fir is defoliated and larvae spill over to feed on black spruce. Long-term studies over several generations are therefore required to determine whether the peak emergence dates

### Table 3
Simultaneous tests for general linear hypotheses (slope comparisons). Values in parentheses are 95% confidence intervals. Onset of budburst and synchrony are measured in number of days.

| Slope comparisons                        | Budburst onset | Synchrony   |
|-----------------------------------------|----------------|-------------|
| Balsam fir 2013 versus Balsam fir 2014 | 3.2** (1.0, 5.4) | 3.1** (0.9, 5.3) |
| Black spruce 2013 versus Black spruce 2014 | 1.3 (-1.4, 3.9) | 1.4 (-1.1, 4.0) |
| Balsam fir 2013 versus Black spruce 2013 | 1.8 (-0.8, 4.5) | 1.7 (-0.9, 4.3) |
| Balsam fir 2014 versus Black spruce 2014 | -0.1 (-2.4, 2.1) | 0.04 (-2.1, 2.2) |

Note. Asterisks indicate statistical significance: * p < 0.05 ** p < 0.01 *** p < 0.001
of overwintering larvae might shift in adaptation to the budburst phenotype of black spruce.

ACKNOWLEDGMENTS

We thank S. Bourassa, D. Gervais and D. Boucher for technical assistance; D. Gray, J. Régnière, V. Nealis and E. Despland for discussions during this study. Y. Boulanger and two anonymous reviewers provided comments on a draft that improved the clarity of the paper. This project was funded by the Quebec Ministry of Forests (Fonds Vert), the Canadian Forest Service and an NSERC Discovery Grant to DSP

AUTHOR CONTRIBUTIONS

DSP originally formulated the idea. DSP and LDG conceived and designed the study. MN performed the experiments and collected data. MM analyzed the data. DSP, MM, LDG, and DK wrote and edited the manuscript.

DATA ACCESSIBILITY

Data and R-scripts will be deposited upon acceptance of manuscript for publication in a publicly accessible repository such as Dryad or FigShare.

ORCID

Deepa S. Pureswaran [https://orcid.org/0000-0002-4040-7708]

REFERENCES

Altermatt, F. (2010). Tell me what you eat and I’ll tell you when you fly: Diet can predict phenological changes in response to climate change. Ecology Letters, 13, 1475–1484.

Bale, J. S., Masters, G. J., Hodkinson, I. D., Awmack, C., Bezemer, T. M., Brown, V. K., … Whittaker, J. B. (2002). Herbivory in global climate change research: Direct effects of rising temperatures on insect herbivores. Global Change Biology, 8, 1–16. https://doi.org/10.1046/j.1365-2486.2002.00451.x

Bean, J. L. (1961). Predicting emergence of second instar spruce budworm larvae from hibernation under field conditions in Minnesota. Annals of the Entomological Society of America, 75, 175–177. https://doi.org/10.1093/aesa/54.2.175

Beck, S. D. (1983). Insect thermoperiodism. Annual Review of Entomology, 28, 91–108. https://doi.org/10.1146/annurev.en.28.011833.000515

Berg, E. E., Henry, J. D., Fastie, C. L., Volder, A. D. D., & Matsuoaka, S. M. (2006). Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: Relationship to summer temperatures and regional differences in disturbance regimes. Forest Ecology and Management, 227, 219–232. https://doi.org/10.1016/j.foreco.2006.02.038

Blais, J. R. (1957). Some relationships of the spruce budworm, Choristoneura fumiferana (Clem.) to black spruce, Picea mariana (Moench) Voss. Forestry Chronicle, 33, 364–372. https://doi.org/10.5558/tfc33364-4

Bogournou, F., De Grandpre, L., Pureswaran, D. S., & Kneesnow, D. (2017). Temporal variation in plant neighbourhood effects on defoliation of primary and secondary hosts by an outbreak herbivore. Ecosphere, 8. https://doi.org/10.1002/ecs2.1759

Burnham, K. P., & Anderson, D. R. (2002). Model selection and multimodel inference: A practical information-theoretic approach, 2nd ed. New York, NY: Springer.

Buse, A., & Good, J. (1996). Synchronization of larval emergence in winter moth (Operophthera brumata L.) and budburst in pedunculate oak (Quercus robur L.) under simulated climate change. Ecological Entomology, 21, 335–343. https://doi.org/10.1046/j.1365-2311.1996.t01-1-00001.x

Chuine, I. (2010). Why does phenology drive species distribution? Philosophical Transactions of the Royal Society B: Biological Sciences, 365, 3149–3160. https://doi.org/10.1098/rstb.2010.0142

Doria, L., & Kettlea, E. G. (1982). A review of entomological survey and assessment techniques used in regional spruce budworm, Choristoneura fumiferana (Clem.), surveys and in the assessment of operational spray programs. Report of the Committee for Standardization of Survey and Assessment Techniques, Eastern Spruce Budworm Council. Government of Quebec, Ministry of Energy and Resources, Ste-Foy, Quebec. 43 p.

Forrest, J., & Miller-Rushing, A. J. (2010). Toward a synthetic understanding of the role of phenology in ecology and evolution. Philosophical Transactions of the Royal Society B: Biological Sciences 365, 3101–3112. https://doi.org/10.1098/rstb.2010.0145

Fuentealba, A., Pureswaran, D. S., Bauce, E., & Despland, E. (2017). How does synchrony with host plant affect the performance of an outbreaking insect defoliator? Oecologia, 184, 847–857.

Fuentealba, A., Sagne, S., Pureswaran, D. S., Bauce, É., & Despland, E. (2018). Defining the window of opportunity for feeding initiation by second instar spruce budworm larvae. Canadian Journal of Forest Research, 48, 285–291. https://doi.org/10.1139/cjfr-2017-0133

Greenbank, D. O. (1963). Host species and the spruce budworm. The dynamics of epidemic spruce budworm populations. Memoirs of the Entomological Society of Canada, 31, 219–223.

Gunderson, C. A., Edwards, N. T., Walker, A. V., O’Hara, K. H., Campion, C. M., & Hanson, P. J. (2012). Forest phenology and a warmer climate – Growing season extension in relation to climatic provenance. Global Change Biology, 18, 2008–2025. https://doi.org/10.1111/j.1365-2486.2011.02632.x

Hagen, S. B., Jepsen, J. U., Ims, R. A., & Yoccoz, N. G. (2007). Shifting altitudinal distribution of outbreak zones of winter moth, Operophthera brumata in sub-arctic birch forest: A response to recent climate warming? Ecography, 30, 299–307. https://doi.org/10.1111/j.0906-7590.2007.04981.x

Hansen, E. M., & Bentz, B. J. (2003). Comparison of reproductive capacity among univoltine, semivolitine, and re-emerged parent spruce beetles (Coleoptera: Scolytidae). Canadian Entomologist, 135, 697–712. https://www.fs.usda.gov/treesearch/pubs/43480

Hansen, E. M., Bentz, B. J., Powell, J. A., Gray, D. R., & Vandygriff, J. C. (2011). Preupal diapause and instar IV developmental rates of the spruce beetle, Dendroctonus rufipennis (Coleoptera: Curculionidae, Scolytinae). Journal of Insect Physiology, 57, 1347–1357. https://doi.org/10.1016/j.jinsphys.2011.06.011

Harrington, R., Woinwood, I., & Sparks, T. (1999). Climate change and trophic interactions. Trends in Ecology & Evolution, 14, 146–150. https://doi.org/10.1016/S0169-5347(99)01604-3

Haynes, K. J., Allstadt, A. J., & Klimetzek, D. (2014). Forest defoliator outbreaks under climate change: Effects on the frequency and severity of outbreaks of five pine insect pests. Global Change Biology, 20, 2004–2018. https://doi.org/10.1111/gcb.12506

Hill, J. K., Griffiths, H. M., & Thomas, C. D. (2011). Climate change and evolutionary adaptations at species range margins. Annual
Review of Entomology, 56, 143–159. https://doi.org/10.1146/annurev-ento-120709-144746

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. Biometrical Journal, 50, 346–363. https://doi.org/10.1002/bimj.200810425

Huang, J., Deslauriers, A., & Rossi, S. (2014). Xylem formation can be modeled statistically as a function of primary growth and cambium activity. New Phytologist, 203, 831–841. https://doi.org/10.1111/nph.12859

Jepsen, J. U., Kapari, L., Hagen, S. B., Schott, T., Vindstad, O. P. L., Nilssen, A. C., & Ims, R. A. (2011). Rapid northwards expansion of a forest insect pest attributed to spring phenology matching with sub-Arctic birch. Global Change Biology, 17, 2071–2083. https://doi.org/10.1111/j.1365-2486.2010.02370.x

Lawrence, R. K., Mattson, W. J., & Haack, R. A. (1997). White spruce and the spruce budworm: Defining the phenological window of susceptibility. Canadian Entomologist, 129, 291–318. https://doi.org/10.4039/Ent129291-2

Logan, J. A., Régnière, J., & Powell, J. A. (2003). Assessing the impacts of global warming on forest pest dynamics. Frontiers in Ecology and the Environment, 1, 130–137. https://doi.org/10.1890/1540-9295(2003)001[0130:ASTGMW]2.0.CO;2

Lysyk, T. J. (1989). Stochastic model of eastern spruce budworm (Lepidoptera: Tortricidae) phenology on white spruce and balsam fir. Journal of Economic Entomology, 82, 1161–1168. https://doi.org/10.1093/jea/82.4.1161

Mazerolle, M. J. (2016). AICcmodavg: Model selection and multimodel inference based on QAIC(c). R package version 2.0-4. Retrieved from http://CRAN.R-project.org/package=AICcmodavg

Menzel, A., Sparks, T. H., Estrella, N., Koch, E., Aasa, A., Ahas, R., ... Zust, A. (2006). European phenological response to climate change matches the warming pattern. Global Change Biology, 12, 1969–1976. https://doi.org/10.1111/j.1365-2486.2006.01193.x

Ministère des Forêts, de la Faune et des Parcs (2016). Aires infestées par Choristoneura fumiferana (Clem.) (Lepidoptera: Tortricidae) et simulation de son histoire saisonnière. Québec, Canada. Report L AU-X-137E.

Mjaseth, R. R., Hagen, S. B., Yoccoz, N. G., & Imms, R. A. (2005). Phenology and abundance in relation to climatic variation in a sub-arctic insect herbivore-mountains birch system. Oecologia, 145, 53–65. https://doi.org/10.1007/s00442-005-0089-1

Nealis, V. G., & Régnière, J. (2004). Insect-host relationships influencing disturbance by the spruce budworm in a boreal mixedwood forest. Canadian Journal of Forest Research, 34, 1870–1882. https://doi.org/10.1139/x04-061

Numainville, G., & Desponts, M. (2004). Les stades de débourrement des bourgeons foliaires de l'épinette noire. Guide no 7. Ministère des Ressources naturelles, Direction de la recherche forestière, Gouvernement du Québec, Quebec, Canada.

Ouranos (2015). Summary of the synthesis on climate change knowledge in Quebec, 2015th ed (p. 13). Montreal, QC: Ouranos.

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. Nature, 421, 37–42. https://doi.org/10.1038/nature01286

Pinheiro, J. C., & Bates, D. M. (2000). Mixed-effect models in S and S-PLUS. New York, NY: Springer Verlag.

Pinheiro, J. C., Bates, D. M., DebRoy, S., Sarkar, D., & Team, R. C. (2016). Linear and nonlinear mixed effects models. R package version 3.1-127. Retrieved from http://CRAN.R-project.org/package=nlme

Pureswaran, D. S., De Grandpré, L., Paré, D., Taylor, A., Barrette, M., Morin, H., ... Kneeshaw, D. D. (2015). Climate-induced changes in host tree-insect phenology may drive ecological state-shift in boreal forest. Ecology, 96, 1480–1491. https://doi.org/10.1890/13-2366.1

R Core Team (2016). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org

Régnière, J. (1987). Temperature-dependent development of eggs and larvae of Choristoneura fumiferana (Clem.) (Lepidoptera: Tortricidae) and simulation of its seasonal history. Canadian Entomologist, 119, 717–728. https://doi.org/10.4039/Ent119717-7

Régnière, J. (1990). Diapause termination and changes in thermal responses during postdiapause development in larvae of the spruce budworm, Choristoneura fumiferana. Journal of Insect Physiology, 36, 727–735. https://doi.org/10.1016/0022-1910(90)90046-I

Régnière, J. (1996). Generalized approach to landscape-wide seasonal forecasting with temperature-driven simulation models. Environmental Entomology, 25, 869–881. https://doi.org/10.1093/ee/25.5.869

Régnière, J., & Bolstad, P. (1994). Statistical simulation of daily air temperature patterns in eastern North America to forecast seasonal events in insect pest management. Environmental Entomology, 23, 1368–1380. https://doi.org/10.1093/ee/23.6.1368

Régnière, J., Powell, J., Bentz, B., & Nealis, V. (2012). Effects of temperature on development, survival and reproduction of insects: Experimental design, data analysis and modeling. Journal of Insect Physiology, 58, 634–647. https://doi.org/10.1016/j.jinsphys.2012.01.010

Régnière, J., & St-Amant, R. (2007). Stochastic simulation of daily air temperature and precipitation from monthly normals in North America north of Mexico. International Journal of Biometeorology, 51(5), 415–430. https://doi.org/10.1007/s00484-006-0078-z

Régnière, J., St-Amant, R., & Bechard, A. (2014). BioSim 10 user’s manual. Natural Resources Canada, Canadian Forest Service, Information Report LAU-X-137E.

Reichenbach, N. G., & Stairs, G. R. (1984). Response of the western spruce budworm (Lepidoptera: Tortricidae) to temperature and humidity: Developmental rates and survivorship. Environmental Entomology, 13, 611–618. https://doi.org/10.1093/ee/13.2.611

Rossi, S. (2015). Local adaptations and climate change: Converging sensitivity of bud break in black spruce provenances. International Journal of Biometeorology, 59, 827–835. https://doi.org/10.1007/s00484-014-0900-y

Saucier, J.-P., Robitaille, A., Grondin, P., Bergeron, J.-F., & Gosselin, J. (2011). Les régions écologiques du Québec méridional (4e ed). Quebec, Canada.

Saucier, J.-P., Grondin, P., Robitaille, A., Gosselin, J., Morneau, C., Richard, P. J. H., ... Payette, S. (2009). Écologie forestière. Manuel de forêtérieur. 2nd ed (pp. 165–316). Québec, QC: Éditions MultiMondes, Ordre des ingénieurs forestiers du Québec.

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution, 1, 103–113. https://doi.org/10.1111/j.2041-210X.2010.00012.x

Schwartzberg, E. G., Jamieson, M. A., Raffa, K. F., Montgomery, R. A., & Lindroth, R. L. (2014). Simulated climate warming alters phenological synchrony between an outbreak insect herbivore and host trees. Oecologia, 175, 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

Stireman, J. O., Dyer, L. A., Janzen, D. H., Singer, M. S., Lill, J. T., Marquis, R. J., ... Diniz, I. R. (2005). Climatic unpredictability and parasitism of caterpillars: Implications of global warming. Proceedings of the
Swaine, J. M., & Craighead, F. C. (1924). Studies on the spruce budworm. Canadian Department of Agriculture Technical Bulletin, 37.

Tran, J. K., Ylioja, T., Billings, R. F., Régnière, J., & Ayres, M. P. (2007). Impact of minimum winter temperatures on the population dynamics of Dendroctonus frontalis. Ecological Applications, 17, 882–899. https://doi.org/10.1890/06-0512

Trier, T. M., & Mattson, W. J. (1997). Needle mining by the spruce budworm provides sustenance in the midst of privation. Oikos, 79, 241–246. https://doi.org/10.2307/3546009

Van Asch, M., Tienderen, P. H. V., Holleman, L. J. M., & Visser, M. E. (2007). Predicting adaptation of phenology in response to climate change, an insect herbivore example. Global Change Biology, 13, 1596–1604. https://doi.org/10.1111/j.1365-2486.2007.01400.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

Visser, M. E., & Holleman, L. J. M. (2001). Warm springs disrupt the synchrony of oak and winter moth phenology. Proceedings of the Royal Society B Biological Science, 268, 289–294. https://doi.org/10.1098/rspb.2000.1363

Voigt, W., Perner, J., Davis, A. J., Eggers, T., Schumacher, J., Bahrmann, R., Sander, F. W. (2003). Trophic levels are differentially sensitive to climate. Ecology, 84, 2444–2453. https://doi.org/10.1890/02-0266

Weed, A. S., Ayres, M. P., & Hicke, J. (2013). Consequences of climate change for biotic disturbances in North American forests. Ecological Monographs, 83, 441–470. https://doi.org/10.1890/13-0160.1

Werner, R. A., Holsten, E. H. (1985a). Effect of phloem temperature on development of spruce beetles in Alaska. In L. Safranyik (Ed), The role of the host in the population dynamics of forest insects (pp. 155–163). Proc IUFRO Conference. Canadian Forest Service.

Werner, R. A., Holsten, E. H. (1985b). Factors influencing generation times of spruce beetles in Alaska. Canadian Journal of Forest Research, 15, 438–443. https://doi.org/10.1139/x85–070

Werner, R. A., Holsten, E. H., Matsuoka, S. M., & Burnside, R. E. (2006). Spruce beetles and forest ecosystems in south-central Alaska: A review of 30 years of research. Forest Ecology and Management, 227(3), 195–206. https://doi.org/10.1016/j.foreco.2006.02.050

Williams, D. W., Liebhold, A. M. (2002). Climate change and the outbreak ranges of two North American bark beetles. Agricultural and Forest Entomology, 4(2), 87–99. https://doi.org/10.1046/j.1461–9563.2002.00124.x

Wolkovich, E. M., Cook, B. I., Allen, J. M., Crimmins, T. M., Betancourt, J. L., Travers, S. E., Cieland, E. E. (2012). Warming experiments underpredict plant phenological responses to climate change. Nature, 485(7399), 494–497. https://doi.org/10.1038/nature11014

How to cite this article: Pureswaran DS, Neau M, Marchand M, De Grandpré L, Kneeshaw D. Phenological synchrony between eastern spruce budworm and its host trees increases with warmer temperatures in the boreal forest. Ecol Evol. 2019;9:576–586. https://doi.org/10.1002/ece3.4779