

Simulated climate warming alters phenological synchrony between an outbreak insect herbivore and host trees

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Abstract As the world's climate warms, the phenologies of interacting organisms in seasonally cold environments may advance at differing rates, leading to alterations in phenological synchrony that can have important ecological consequences. For temperate and boreal species, the timing of early spring development plays a key role in plant–herbivore interactions and can influence insect performance, outbreak dynamics, and plant damage. We used a field-based, meso-scale free-air forest warming experiment (B4WarmED) to examine the effects of elevated temperature on the phenology and performance of forest tent caterpillar (*Malacosoma disstria*) in relation to the phenology of two host trees, aspen (*Populus tremuloides*) and birch (*Betula papyrifera*). Results of our 2-year study demonstrated that spring phenology advanced for both insects and trees,

with experimentally manipulated increases in temperature of 1.7 and 3.4 °C. However, tree phenology advanced more than insect phenology, resulting in altered phenological synchrony. Specifically, we observed a decrease in the time interval between herbivore egg hatch and budbreak of aspen in both years and birch in one year. Moreover, warming decreased larval development time from egg hatch to pupation, but did not affect pupal mass. Larvae developed more quickly on aspen than birch, but pupal mass was not affected by host species. Our study reveals that warming-induced phenological shifts can alter the timing of ecological interactions across trophic levels. These findings illustrate one mechanism by which climate warming could mediate insect herbivore outbreaks, and also highlights the importance of climate change effects on trophic interactions.

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Introduction

Anthropogenic climate warming has advanced the phenology of many plant and animal species in seasonally cold environments (Parmesan and Yohe 2003; Root et al. 2003; Parry et al. 2007). Because species demonstrate different sensitivities to variation in temperature, warming can result in phenological mismatches between organisms that interact across trophic levels (Parmesan 2006, 2007; Berggren et al. 2009; van der Putten et al. 2010). Shifts in phenological synchrony may have important ecological consequences (Berggren et al. 2009; van der Putten et al. 2010; Walther 2010; Liu et al. 2011). For instance, a key factor facilitating insect pest outbreaks in temperate and boreal forest

ecosystems is phenological synchrony with host trees (van Asch and Visser 2007; Foster et al. 2013). Due to increased tree mortality and forest dieback globally, understanding how climate change will influence forest insect pests and their host trees has become a particular concern in recent years (Volney and Fleming 2000; Logan et al. 2003; Jamieson et al. 2012; Raffa et al. 2013; Fettig et al. 2013; Weed et al. 2013).

While phenologies of both plants and insects are expected to advance with climate warming, less is known about whether organisms that interact across trophic levels will advance at similar rates and/or magnitudes (Bale et al. 2002; Van Asch and Visser 2007; Berggren et al. 2009). A growing number of examples demonstrates that insects and their host plants can show different sensitivities to increasing temperature trends, resulting in altered phenological synchrony (Visser and Holleman 2001; Memmott et al. 2007; Liu et al. 2011). While phenological tracking of host plants has been linked to enhanced performance of many defoliating insects (van Asch and Visser 2007), few studies have investigated potential warming-induced phenological shifts between outbreak herbivores and host trees.

The extent to which native folivores remain at low densities or undergo large-scale population increases can be influenced by the synchrony of larval feeding with vulnerable plant stages, especially for outbreak species (Bale et al. 2002; van Asch and Visser 2007; Foster et al. 2013). Phenological asynchrony may reduce insect folivore performance because larvae that emerge too early have little or no available food, and those that emerge too late are confronted with tougher foliage that is lower in nitrogen and potentially higher in defense chemicals (Parry et al. 1998; Bale et al. 2002; Nealis and Nault 2005; Jones and Despland 2006; van Asch and Visser 2007). Because phenological asynchrony with host trees can have strong fitness costs for folivores, insects have likely evolved mechanisms to reliably track the phenology of their hosts (van Asch and Visser 2007).

Temperature and photoperiod are the two key environmental cues affecting spring phenology of folivores and their host trees (van Asch and Visser 2007). Despite the relative importance of temperature in regulating insect and plant phenology, the underlying response mechanisms may be substantially different among species, and are further compounded by additional cues such as photoperiod and chilling requirements (Campbell and Sugano 1975; Hunter and Lechowicz 1992; van Asch and Visser 2007) and provenance (Campbell and Sugano 1975; Kriebel and Wang 1962). Furthermore, future temperature extremes may exceed historical conditions, which could affect the ability of insects to accurately track environmental signals and host phenology.

In this study, we examined the effects of simulated climate warming on the phenology of forest tent caterpillar (*Malacosoma disstria*) and two host tree species, trembling aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*). We investigated how projected increases in temperature may affect: (1) the phenology and synchrony of egg hatch and budbreak, and (2) larval performance, as measured by development time and pupal mass. We predicted that warming would lead to altered synchrony in the spring phenologies of insects and host trees due to differences in organismal sensitivity to temperature change and variation in response mechanisms to environmental cues.

Methods

Study system

Malacosoma disstria Hbn. is an early-season, generalist lepidopteran folivore that exhibits periodic outbreaks and is one of the most important native defoliating insects affecting North American forests (Mattson et al. 1991; Fitzgerald 1995). Pharate larvae overwinter inside eggs, which are clustered around branches in spumulin-covered egg bands. Larvae emerge in early spring, approximately at the time of budbreak of host trees, in particular *Populus* spp. (Fitzgerald 1995). Larvae feed gregariously during early instars, and can cause extensive damage to host-trees during outbreak years, including large-scale tree mortality events (Fitzgerald 1995; Donaldson and Lindroth 2008; Worrall et al. 2013).

Populus tremuloides is the most widely distributed tree species in North America and is the primary host for *M. disstria* in the northern range of the insect. Recent large-scale declines in *P. tremuloides* have been linked to the combination of climatic and biotic stressors, including defoliation by tent caterpillars (Worrall et al. 2013). Because *M. disstria* feeds on a variety of host trees, we also examined *Betula papyrifera*, which is also a common host tree of *M. disstria*, is likewise transcontinentally distributed, and occurs in the northern ranges of both *P. tremuloides* and *M. disstria*. Hereafter, these trees are referred to as aspen and birch.

Study site

We utilized a field-based, free-air climate change experiment, known as the B4WarmED (Boreal Forest Warming at an Ecotone in Danger) project, to investigate warming-induced changes in insect and tree phenology. B4WarmED study sites are located in northern Minnesota, USA, at the Cloquet Forestry Center in Cloquet, MN (46°40'45"N, 92°31'10"W) and Hubachek Wilderness Research Center

near Ely, MN (47°57'2"N, 91°44'55"W). Hereafter, these locations are referred to as Cloquet and Ely, respectively. The two research sites are positioned in the temperate-boreal transition zone, a region of overlapping range of northern temperate and southern boreal forest species. Climate warming in this region is expected to enhance survival of temperate species at the cold edge of their range while it reduces survival of boreal species (Kling et al. 2003).

Experimental design

The experimental design was a 3 (temperature treatment) × 2 (site) factorial, consisting of 6 replicate plots per temperature treatment (ambient, +1.7, +3.4 °C) at each of two sites for a total of 36 circular 3-m diameter plots. Each site contained three blocks with two temperature treatment replicates per block. Our study plots were located in open canopy habitats, which were clear-cut in 2007, prior to development of the B4WarmED infrastructure. In 2008, replicate individuals of ten native tree species were planted from bare-root nursery stock into each plot. At the beginning of our study period in 2011, we selected two trees per plot for each study species (aspen and birch).

Each warmed plot was individually temperature controlled to simultaneously manipulate soil and plant surface temperatures by +1.7 and +3.4 °C. Soil temperature was increased using underground soil heating cables (Danfoss GX, Devi A/B, Denmark), while plant surface temperature was increased using above-ground ceramic heating elements (Salamander Model FTE-1000). Temperatures for warming treatments were selected to bracket the range of anticipated warming in the region during the next 75–100 years (Kling et al. 2003; Wuebbles and Hayhoe 2004; Parry et al. 2007). Plots were warmed continuously (24 h/day) approximately eight months per year via feedback controls that operated independently at the plot-level scale to maintain experimental temperature differentials relative to ambient, unheated plots within a block. Temperature treatment start times at each site for each year were determined by a set of criteria that included persistence of snow cover and five consecutive days of daily average temperatures exceeding 1 °C (early-mid April in 2011 and late March in 2012). See Supplemental Material (ESM 1) for exact temperature treatment start and stop dates.

Forest tent caterpillar egg bands were collected from naturally occurring populations in Wisconsin and Minnesota. In 2011, we collected egg bands from Sauk County, Wisconsin (43.43°N, 89.94°W) from mid-March to early-April, and stored eggs at 2 °C until deployment into field plots in mid-April. In 2012, we used a population closer to our experimental sites and overwintered egg bands at the sites. Specifically, we collected egg bands from Mille Lacs County, Minnesota (45.93° N, 93.63° W) in late October,

2011, and stored two equal sets outside at the Ely and Cloquet sites.

Phenology and performance measurements

To examine warming effects on insect phenology, phenological synchrony with host plants, and insect performance, we reared enclosed forest tent caterpillars from the egg to pupal stage in study plots. One to five days prior to initiation of warming treatments in mid-April, we attached egg bands to either the apical or lateral shoot of two aspen and two birch trees per plot. We used mesh sleeves (~1 × 1.5 m) to enclose insects onto branches.

To examine budbreak phenology, we surveyed trees weekly, with more frequent monitoring (every 1–3 days) for trees nearing budbreak. Budbreak date was recorded when at least one bud within the mesh sleeve broke, (i.e., the tips of individual leaves within a bud became visible). Early springtime insect phenology was censused at the same times as plant phenology. We assigned egg bands to one of five classes at each census date, based on numbers of hatched larvae: 0, 1–5, 6–20, 21–50, and >50. We closely monitored egg bands approaching the 21–50 range, and recorded the day that larval masses reached that stage as the date of egg hatch.

In 2011, we culled second stadium larvae to reduce the number of individuals enclosed on a single branch, to ensure an adequate supply of food. To better accommodate the gregarious behavior of early-instar larvae and reduce their mortality, we altered our approach in 2012 by not removing larvae until they had reached the late third instar. When a cohort reached the third stadium, larval aggregations were culled to 15–20 individuals. In both years, insects were further culled during the late fourth stadium of the cohort to avoid crowding and ensure larvae would have adequate food. Additionally, we moved enclosed larvae from branch to branch within a tree, approximately every 1–2 weeks to maintain the foliage supply for fourth and fifth instars. A minimum cohort of six larvae was maintained on each tree until pupation, when possible. Pupae were collected from mesh enclosures 1–3 days after the onset of cocoon construction, moved indoors so they could develop through pupation, and then weighed ~3 days later. Pupation date was recorded as the day pupae were collected from plots, averaged by tree.

Statistical analysis

To evaluate phenological synchrony, we calculated the difference in time (days) between forest tent caterpillar egg hatch and host tree budbreak on a per tree basis. To assess larval development time, we estimated the time to pupation, based on the number of days from egg hatch to pupation on

Table 1 Effects of warming treatment, tree species, and their interaction on response variables, including budbreak date, egg hatch and pupation dates, phenological synchrony between egg hatch and budbreak, development time from egg hatch to pupation, and pupal mass

	2011			2012		
	Temperature	Species	Temperature × species	Temperature	Species	Temperature × species
Budbreak	49.4 (2,28)***	297.6 (1,33)***	0.10 (2,33)	81.2 (2,28)***	46.9 (1,33)***	1.20 (2,33)
Egg hatch	42.7 (2,28)***	0.29 (1,33)	0.58 (2,33)	44.7 (2,28)***	0.005 (1,33)	0.29 (2,33)
Pupation	27.6 (2,41)***	20.3 (1,41)***	0.18 (1,41)	51.1 (2,21)***	27.3 (1,18)***	1.50 (2,33)
Synchrony	16.1 (2,28)***	166.8 (1,33)***	0.34 (1,33)	5.60 (2,28)**	34.1 (1,33)***	1.50 (2,33)
Development time	17.3 (2,41)***	28.6 (1,41)	0.47 (2,41)	43.1 (2,58)***	22.8 (1,57)***	1.11 (2,60)
Pupal mass	0.91 (2,41)	0.64 (1,41)	1.05 (2,41)	2.34 (2,60)	0.83 (1,60)	1.93 (2,60)

Values are *F* statistics with degrees of freedom shown in parentheses

Significant effects: *** ($P < 0.001$), ** ($0.001 \leq P < 0.01$), * ($0.01 \leq P < 0.05$)

Table 2 Summary statistics for treatment effects within tree species

	Budbreak date	Egg hatch date	Pupation date	Synchrony	Development time	Pupal mass
Aspen						
2011	40.3 (2,33)***	31.2 (2,33)***	12.4 (2,19)***	4.7 (2,33)*	6.2(2,19)*	1.1 (2,19)
2012	38.1 (2,33)***	10.8 (2,33)***	35.5 (2,30)***	5.9 (2,33)**	3.1(2,30)*	0.9 (2,30)
Birch						
2011	23.5 (2,33)***	14.9 (2,33)***	16.1 (2,23)***	8.0 (2,33)**	13.2 (2,23)***	0.4 (2,23)
2012	19.3 (2,33)***	20.5 (2,33)***	18.0 (2,31)***	0.4 (2,33)	0.5 (2,31)	3.3 (2,31)*

Values are *F* statistics with degrees of freedom shown in parentheses

Significant effects in bold: *** ($P < 0.001$), ** ($0.001 \leq P < 0.01$), * ($0.01 \leq P < 0.05$)

a per tree basis. All response variables analyzed were averaged within plots across trees of each species, making plot the experimental replicate ($N = 12$ plots per temperature treatment group). For plant and insect phenological data, statistical models included temperature treatment, species, and their interaction as fixed effects, while site, block [site], and plot [block, site] were random effects (brackets denote nesting). To examine the effects of warming on pupal weight and development time, we were not able to use block as a factor, because low survivorship of larvae to the pupal stage (in particular in 2011) resulted in unbalanced representation across blocks (i.e., missing data cells in the factorial design). Thus, we used a statistical model that included temperature treatment, species, and their interaction as fixed effects, and site as a random effect. We initially included pupal sex as a factor in statistical models. There was no significant treatment by sex interaction effect and the main treatment effects were similar for models with or without pupal sex. Ultimately, we decided to use models without sex as a factor, because we lacked those data for some pupae.

We analyzed data using linear mixed models with the restricted maximum likelihood (REML) method in JMP[®] Pro v. 10.0 (SAS Institute Inc.). For significant results, we

followed-up with univariate analyses to examine treatment effects within tree species. Tukey-HSD post hoc tests were used to evaluate significant differences among treatments at $\alpha = 0.05$.

Results

Plant and insect phenology

The timing of aspen and birch budbreak, as well as forest tent caterpillar egg hatch and pupation, advanced in response to warming in both 2011 and 2012 (Tables 1, 2; Figs. 1, 2, 3). Overall, early spring phenology of trees was more sensitive to elevated temperature than was egg hatch of insects. In the first year of the study (2011), a 3.4 °C increase in temperature advanced budbreak ~5–7 days for aspen and birch, while egg hatch advanced 3–4 days. More substantial changes in phenology were observed in the second year of the study, with budbreak advancing 15 days for aspen and 10 days for birch, and larvae emerging from eggs 8–9 days earlier in +3.4 °C treatment plots compared with ambient plots. Likewise, larvae pupated 12–14 days earlier in both years in warmed plots (Fig. 3). Budbreak

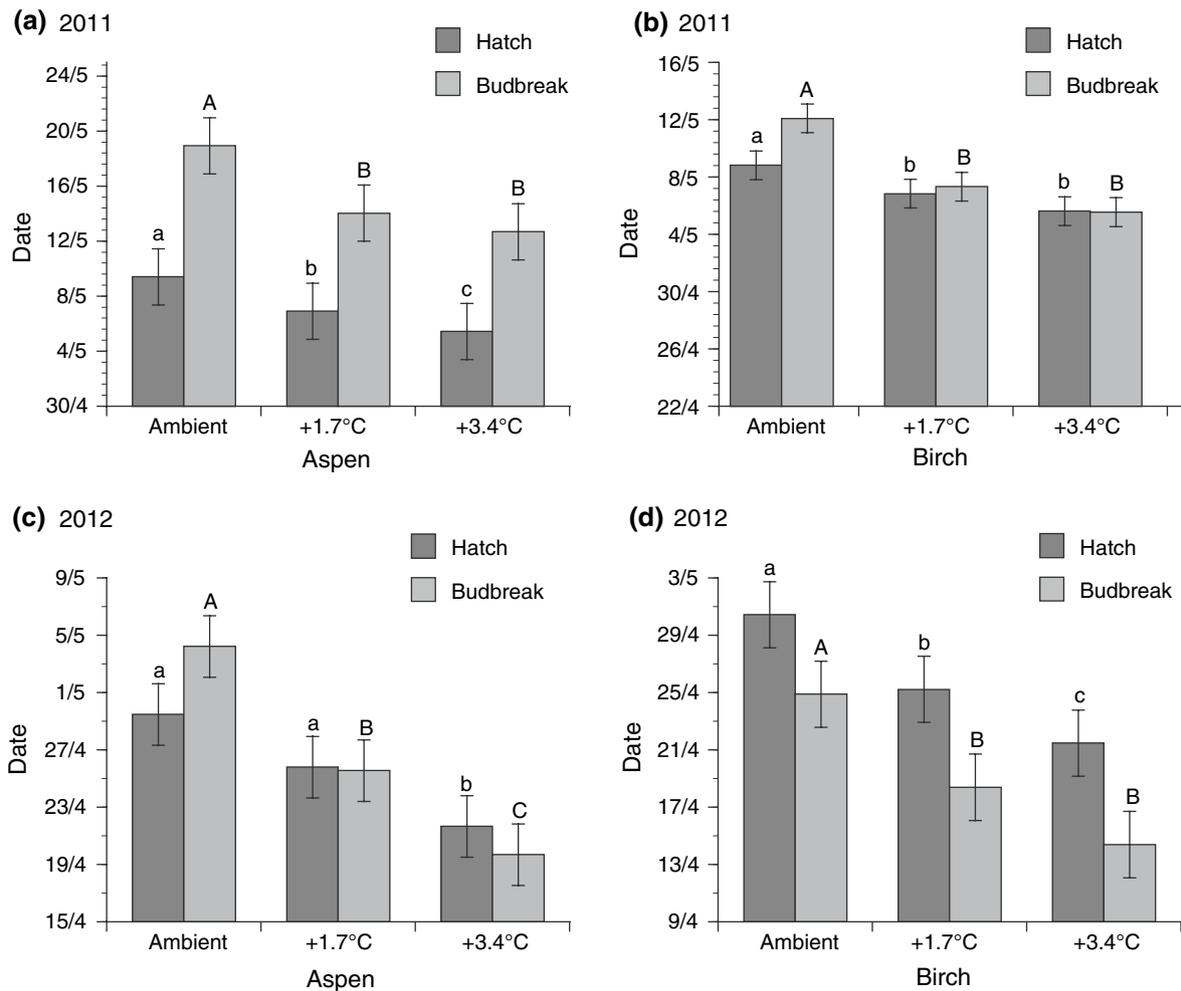


Fig. 1 Timing of egg hatch relative to budbreak for aspen (a, c) and birch (b, d). The date (day/month) range is consistent among graphs, but dates shift along the y-axis to accommodate temporal differences. Values are least square mean \pm SE ($N = 12$ plots per treatment). *Let-*

ters indicate significant differences from post hoc analyses of within-species differences at $P < 0.05$. *Lowercase letters* are used for egg hatch and *uppercase letters* for budbreak

and pupation dates differed significantly between tree species, whereas egg hatch date was not affected by tree species (Table 1). Across temperature treatments, budbreak occurred 7 days earlier in birch than in aspen in both years (Fig. 1), whereas forest tent caterpillar pupation dates were ~7 days later on birch compared with aspen (Fig. 3). Temperature treatment did not interact with species to significantly affect any response variable (Table 1). Moreover, the vast majority of results presented in this paper demonstrate continuous linear responses to increasing temperatures, across the three levels.

Phenological synchrony between insects and host trees

Warming treatments affected the interval between egg hatch and tree budbreak. Specifically, tree phenology advanced to a greater extent in response to heating treatments than

did insect phenology (Tables 1, 2; Figs. 1, 2). In 2011, egg hatch occurred prior to aspen and birch budbreak, and the mean interval between insect and host tree phenological stages decreased by ~2–3 days with a 3.4 °C increase in temperature. In both study years, host tree species significantly differed in the degree of synchrony with forest tent caterpillar (Tables 1, 2), although the species effect varied across years. For insects on aspen, the interval between egg hatch and budbreak decreased under elevated temperatures in 2011, and phenologies became more synchronous under both elevated temperatures in 2012 (Fig. 2). In both years, budbreak was more responsive to warming than was egg hatch (Fig. 1). In contrast, egg hatch and birch budbreak became fully synchronous under elevated temperatures in 2011, but increasingly asynchronous under elevated temperatures in 2012 (Fig. 2), although the shift in synchrony was not statistically significant in the latter case. As was

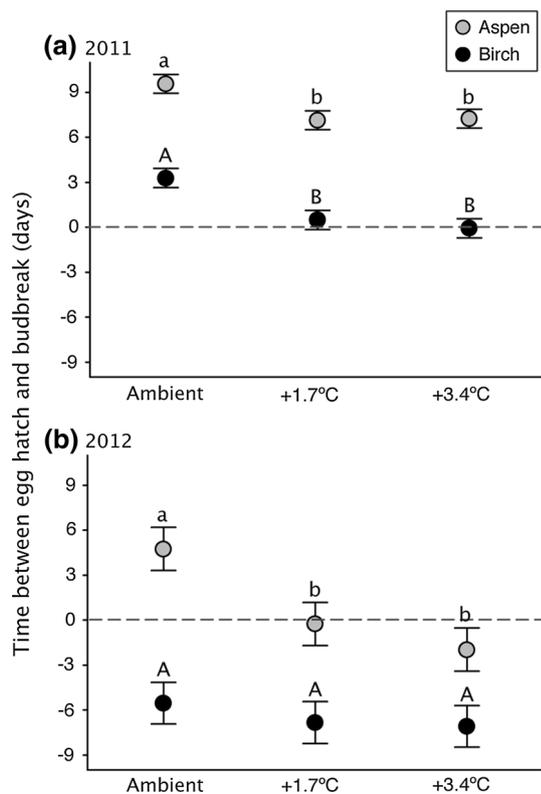


Fig. 2 Time between egg hatch and budbreak. *Negative values* denote budbreak prior to egg hatch. Values are least square mean \pm SE ($N = 12$ plots per treatment). *Letters* indicate significant differences from post hoc analyses of within-species differences at $P < 0.05$. *Lowercase letters* are used for aspen and *uppercase letters* for birch

observed for aspen, budbreak in birch was more responsive to warming than was egg hatch (Fig. 1).

Larval development time and performance

Larval development time (egg hatch to pupation) significantly decreased with warming during both years (Tables 1, 2; Fig. 4a, b). In 2011, increasing temperatures by 3.4 °C reduced larval development time by 9 days across host species, with similar trends for larvae reared on both aspen and birch (Fig. 4a). The effect of temperature on development time was less pronounced in 2012; across host species, mean development time was 3 days shorter for larvae in +3.4 °C plots compared with larvae in the ambient treatment (Fig. 4b). During both years, larvae developed faster on aspen than on birch, completing pupation ~ 7 days earlier. Across species, pupal mass was not significantly affected by temperature treatment or host species in either year (Tables 1, 2; Fig. 4c, d). Subsequent univariate analyses, however, indicated significant treatment effects on pupal mass for larvae reared on birch in 2012 (Table 2; Fig. 4d).

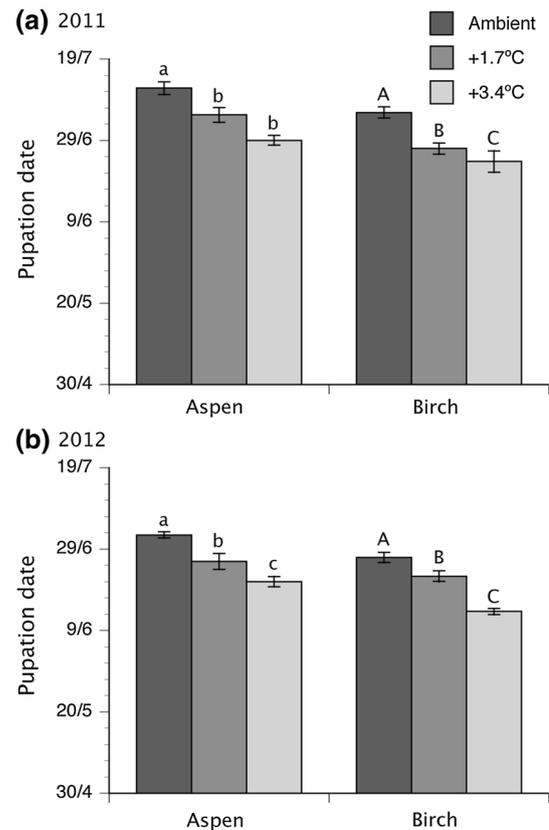


Fig. 3 Date of pupation of forest tent caterpillar larvae developing on aspen and birch in each study year. Values are the mean date \pm SE ($N = 12$ plots per treatment). *Letters* indicate significant differences from post hoc analyses of within-species differences at $P < 0.05$. *Lowercase letters* are used for aspen and *uppercase letters* for birch

Discussion

Experimental warming within the outdoor open-air mesocosms successfully simulated a higher temperature profile predicted for 75–100 years in the future. Under these manipulated conditions, both egg hatch and budbreak advanced in response to elevated temperatures, but the magnitude of these advances in phenology differed under our temperature treatment. These results suggest that increased temperature will not only advance phenology, but these advances may differ among species that interact in space and time. Specifically in our study, host trees exhibited a greater sensitivity to temperature than the insect folivores, a pattern opposite to expectation (Parmesan 2007), resulting in altered phenological synchrony between the two interacting species. Such climate-induced shifts in timing between associated organisms across trophic levels could have important ecological consequences (Parmesan 2006). Our results indicate that changes in phenological synchrony and elevated temperatures do not necessarily lead to direct effects on insect performance (e.g., pupal

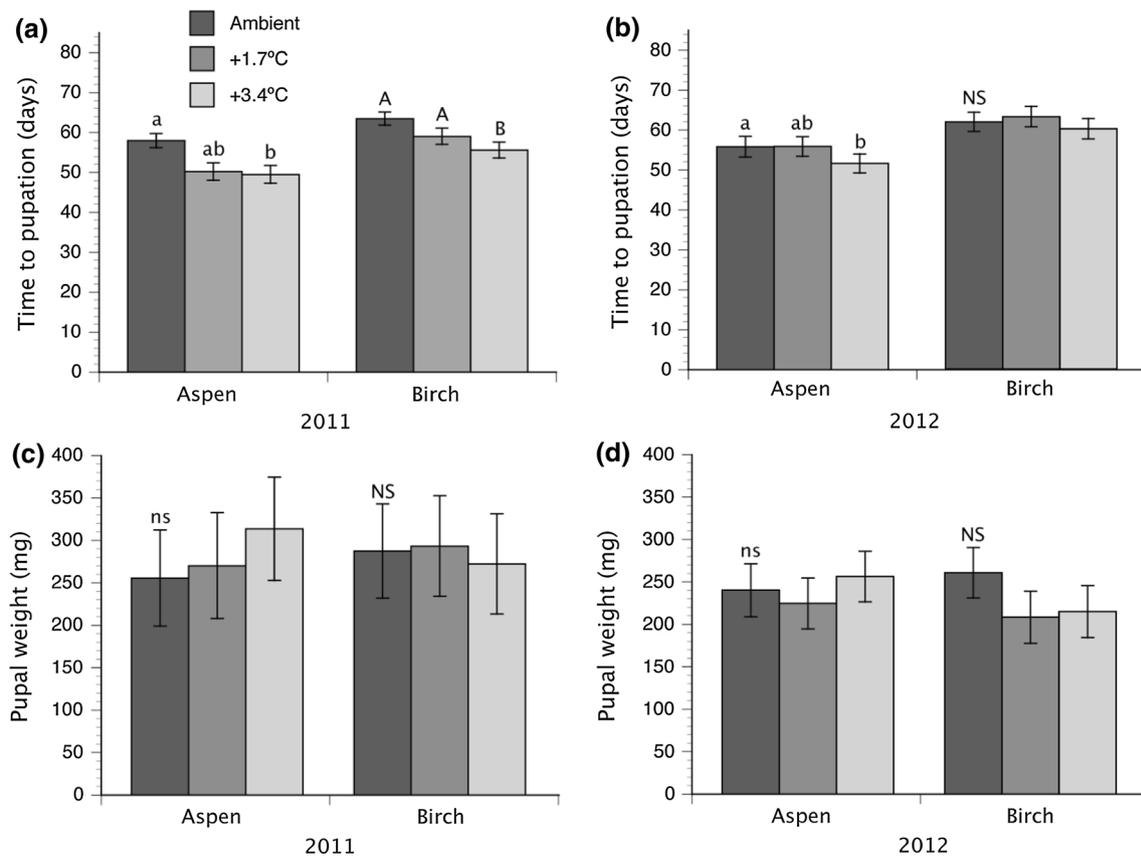


Fig. 4 Development time (a, c) and pupal weights (b, d). Values are least square mean \pm SE ($N = 12$ plots per treatment). Letters indicate significant differences from post hoc analyses of within-species dif-

ferences at $P < 0.05$. Lowercase letters are used for aspen and uppercase letters for birch

mass), but can affect insect development time and have the potential to affect the relationship between these closely interacting species.

Despite variation in yearly temperatures, shifts in phenological synchrony were consistent across host species, demonstrating a greater advance in plant phenology compared to insect phenology in response to warming for both aspen and birch. Variation in response of caterpillars and their host trees to elevated temperature resulted in increased phenological synchrony between egg hatch and budbreak in 2011. Likewise, in 2012, increased temperature resulted in increased synchrony between egg hatch and budbreak on aspen. In contrast, for insects on birch in 2012, elevated temperatures resulted in a trend for decreased synchrony, although mean differences in synchrony were not statistically significant. Altered phenological synchrony observed in both years can be explained by budbreak being more responsive to warming than was egg hatch. In other words, our data suggest that the phenological advance of budbreak was greater than the phenological advance of egg hatch under increased temperature, which manifested in altered phenological synchrony. This result is counter to our

predictions that insect phenology would advance more than plant phenology. Based on a meta-analysis showing spring advancement in phenologies (Parmesan 2007), we expected that insects would show a greater advance in phenology as compared to plants in response to temperature treatments.

We observed consistent differences in timing of bud-break across species. Birch always broke bud prior to aspen at each treatment temperature regime. However, the date of egg hatch was independent of the tree species on which they hatched (i.e., egg hatch was not plant-mediated and its occurrence was dependent on temperature). Historic records indicate consistency of forest tent caterpillar egg hatch at or shortly before budbreak in aspen (Rose 1958, Parry et al. 1998 and references therein) with very high survival when hatching up to 10 days prior to budbreak, especially at lower ambient temperatures (Hanec 1966). In our experiments, under ambient conditions, forest tent caterpillar eggs hatched prior to budbreak in aspen and just before or after budbreak in birch, aligning with historic records.

The phenological relationship between *M. disstria* and these two host trees under simulated climate warming was consistently affected by temperature treatment across years,

despite annual variation in timing of egg hatch in relation to budbreak under ambient conditions. As such, the timing of budbreak in relation to egg hatch consistently advanced or receded in response to temperature treatments, even when budbreak and egg hatch were temporally reversed with one another. Regardless, the between-year variation in synchrony under ambient conditions may not be due to climatic differences between years and could be due to several other factors. For example, insects used in 2011 were obtained from Sauk County, Wisconsin, while those in 2012 originated from Mille Lacs Lake, MN. Moreover, in 2011, insects were collected and moved to the two research sites in northern Minnesota in early spring, whereas in 2012 they were collected in late fall and overwintered within the research sites. It is possible that either the population source of eggs or their overwintering conditions may have affected egg hatch phenological response to spring temperatures. This difference from year to year highlights the potential effect of overwintering condition and/or population source on egg hatch. We recognize that time periods between egg hatch and budbreak may depend on geography and population phenotypes. However, our study sites experienced two distinctly different weather patterns in 2011 and 2012, with temperatures in the former being relatively normal, while in the latter were unusually warm. Between-year variation in spring weather likely resulted in differences in dates of bud break and egg hatch, however the effect of temperature on altered phenological synchrony across these two years provides confidence that the overall trends we observed are relatively robust.

Forest tent caterpillars are likely well-adapted to variation in temperature from year to year and an important part of this adaptation may be to emerge slightly prior to budbreak, rather than in perfect synchrony, as a way to “hedge their bets” (Gray and Ostaff 2012) for years in which temperatures are warmer than average. We currently lack the information needed to infer how warming-induced phenological shifts between forest tent caterpillar and its hosts will influence the fitness of either insects or trees, but it is likely that fitness could be affected by a combination of time between egg hatch and the onset of feeding, the quality of host tissue at the start of feeding, as well as the combination of these factors. There is some evidence that insect folivores can survive quite well when hatched prior to budbreak, although survival likely depends on temperature post hatching (Hunter 1993). Other evidence suggests that feeding too early can be disadvantageous to folivores, such as gypsy moth (*Lymantria dispar*) larvae (Stoyenoff et al. 1994), due to lack of available food. Late-hatching folivores are also disadvantaged due to the tougher and potentially more chemically defended foliage they encounter (Palo 1984; Parry et al. 1998; Visser and Holleman 2001; Nealis and Nault 2005; Jones and Despland 2006;

van Asch and Visser 2007; Gray 2008; Thomson 2009). Moreover, Parry et al. (1998) documented increased predation and slowed development of forest tent caterpillars that enclosed later. While we did not document differences in pupal weight among temperature treatments, it is possible that temperature treatments may have affected early instar survival. We culled populations to maintain appropriate defoliation rates on plants, and as a result, any effects of temperature treatment on early instar survival may have gone unnoticed.

Little is known about how plants and their associated insect herbivores might evolve and adapt to a changing climate. While the tight synchrony of insects with their host plants is evidence that adaptation has maintained phenological synchrony over time (Dixon 2003), it is not clear that this selection pressure can continue to maintain synchrony in the future as climate changes much faster than it has during the evolutionary history of insects and their hosts.

Our results demonstrate the effect of simulated warming on phenological synchrony between a forest folivore and two of its host trees. As temperature increased, budbreak advanced to a greater extent than did egg hatch, resulting in an increase in phenological synchrony in three of four cases (year \times tree species) when egg hatch in ambient conditions preceded budbreak. This research provides a robust example of how species that interact closely can track climate warming differently, manifesting in altered phenological synchrony with potential consequences for insect outbreak dynamics.

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