FOR: Forest Ecology and Management

*Correspondence:

Johnny A. Uelmen Jr.

Department of Entomology

University of Wisconsin-Madison

Madison, WI 53706, USA

Phone: 920-979-9888

Email: uelmen@wisc.edu

**EFFECTS OF WINTER TEMPERATURES, SPRING DEGREE-DAY
ACCUMULATION, AND INSECT POPULATION SOURCE ON PHENOLOGICAL
SYNCHRONY BETWEEN FOREST TENT CATERPILLAR AND HOST TREES**

Johnny A. Uelmen Jr.¹, Richard L. Lindroth¹, Patrick C. Tobin², Peter B. Reich^{3,4}, Ezra G.
Schwartzberg^{1,5}, Kenneth F. Raffa¹

¹Department of Entomology, University of Wisconsin-Madison, Madison, WI 53706, USA,
uelmen@wisc.edu, richard.lindroth@wisc.edu, kfraffa@wisc.edu

²School of Environmental and Forest Sciences, University of Washington, Seattle, WA
98195, USA, pctobin@uw.edu

³Department of Forest Resources, University of Minnesota, St. Paul, MN 55108, USA,
preich@umn.edu

⁴Hawkesbury Institute for the Environment, University of Western Sydney, Penrith, 2751,
New South Wales, Australia.

⁵Adirondack Research, Saranac Lake, NY 12983, USA, ezra@adkres.org

Keywords: climate change, synchrony, phenology, forest, insect, plant-insect interactions,

Running Head: Insect defoliator asynchrony with host plants

ABSTRACT

Global climate change has the potential to dramatically alter multiple ecosystem processes, including herbivory. The development rates of both plants and insects are highly sensitive to temperature. Although considerable work has examined the effects of temperature on spring phenologies of plants and insects individually, few studies have examined how anticipated warming will influence their phenological synchrony. We applied elevated temperatures of 1.7 and 3.4°C in a controlled chamberless outdoor experiment in northeastern Minnesota, USA to examine the relative responses in onset of egg eclosion by forest tent caterpillar (*Malacosoma disstria* Hübner) and budbreak of two of its major host trees (trembling aspen, *Populus tremuloides* Michaux, and paper birch, *Betula papyrifera* Marshall). We superimposed four insect population sources and two overwintering regimes onto these treatments, and computed degree-day models. Timing of egg hatch varied among population source, overwintering location, and spring temperature regime. As expected, the development rates of plants and insects advanced under warmer conditions relative to ambient controls. However, budbreak advanced more than egg hatch. The degree of phenological synchrony between *M. disstria* and each host plant was differentially altered in response to warming. The interval by which birch budbreak preceded egg hatch nearly doubled from ambient to +1.7°C. In the case of aspen, the sequence changed from egg hatch preceding, to following, budbreak at +3.4°C. Additionally, under temperature regimes simulating future conditions, some insect populations currently south of our study sites became more synchronous with the manipulated hosts than did currently coexisting insect populations. These findings reveal how climate warming can alter insect-host plant interactions, through changes in phenological synchrony, possibly driving host shifts among

51 tree species and genotypes. They also suggest how herbivore variability, both among
52 populations and within individual egg masses, may provide opportunities for adaptation,
53 especially in species that are highly mobile and polyphagous.

INTRODUCTION

One of the least understood consequences of climate change is how warming temperature will influence phenological synchrony between insect herbivores and their host plants (Ayres and Lombardero 2000; Schwartzberg et al. 2014). Phenological synchrony is particularly critical to leaf feeders, as the availability and suitability of newly developing foliage strongly influence their success (van Asch and Visser 2013), and the frequency and incidence of outbreaks (Volney and Fleming 2000; Post and Forchhammer 2002; Liebhold et al. 2004; Haukioja 2005). Altered plant-herbivore relationships are likewise of concern from the perspective of arthropod biodiversity (Parmesan and Yohe 2003).

Boreal forests comprise the largest remaining intact terrestrial biome, and store approximately 32% of the world's forest carbon stock (Pan et al. 2011). In the southern boreal forest, mean annual temperatures have risen $\approx 1.5^{\circ}\text{C}$ since 1940 (Bale et al. 2002; Battisti et al. 2005; Netherer and Schopf 2010) and are expected to increase an additional 3-7° C in winter and 3-11°C in summer by 2100 (Kling et al. 2003). Even slight increases in mean annual temperature may be critical along the current lower latitudinal limits of boreal ecosystems, potentially contributing to forest dieback and regime shifts (Olsson 2010; Michaelian et al. 2011; Fisichelli et al. 2014; Reich et al. 2015).

Development outside a relatively narrow phenological window can have severe fitness consequences for early spring folivores (Quiring 1994; Lawrence et al. 1997; van Asch and Visser 2007). Larvae that hatch too late encounter tougher leaves, higher secondary metabolite concentrations, and decreased nitrogen and water concentrations, often resulting in longer development times (Hunter and Lechowicz 1992; Lindroth and Hwang 1996;

Jamieson et al. 2015). Hatching too early can result in starvation. The forest tent caterpillar (*Malacosoma disstria* Hübner), European gypsy moth (*Lymantria dispar dispar* Linnaeus), eastern spruce budworm (*Choristoneura fumiferana* Clemens), and jack pine budworm (*Choristoneura pinus* Freeman) provide examples of early season, eruptive defoliators, whose ranges overlap the ecotonal boundaries of the southern boreal forests in the Great Lakes region. These insects overwinter as pharate (1st instar within eggs) or 2nd instars, and begin feeding in synchrony with budbreak of their primary hosts (Parry et al. 1998).

We currently lack information on how an additional factor, dispersal, will affect future regimes. Specifically, the much higher dispersal rates of insects relative to plants could create novel interactions between more southerly insect populations and extant tree populations in northern latitudes (IPCC 2014). Consequently, potential range expansions of lepidopteran folivores under warming temperatures may have important ramifications for their population dynamics (Hodson 1941; Blais et al. 1955).

Malacosoma disstria is a gregarious leaf-feeding insect that has a relatively broad host range and can cause severe defoliation of deciduous trees throughout much of Canada and the United States (Trudeau et al. 2010). It extends from Nova Scotia to California, and northern Alberta to south Texas (Drooz 1985). Females oviposit all of their eggs in a single band encircling host twigs, from late June to early July. Egg masses range from 120 - 240 eggs in northern Minnesota (latitude 48°N) (Witter et al. 1975). The number of eggs per band is influenced by female size (which is strongly affected by larval host quality), latitude, and population density (Ives 1971; Witter et al. 1975; Smith and Goyer 1986; Parry et al. 2001). Larvae hatch in early April or May, undergo five instars of 7-10 days each, and pupate in early to late June. After 7-10 days, adults emerge, mate, and oviposit. Adults of

both sexes are strong fliers, and can disperse up to 19 km a year (Evenden et al. 2015).

When assisted by turbulent cold air masses, some have been reported to fly hundreds of kilometers (Brown 1965; Fullard and Napoleone 2001).

Two highly preferred hosts of *M. disstria* are trembling aspen (*Populus tremuloides* Michaux) and paper birch (*Betula papyrifera* Marshall). These are two of the most widely distributed trees in North America, extending from New England to the Pacific Northwest. Both are present in all Canadian provinces except Nunavut, and have isolated populations in high elevations extending to the southern United States (Howard 1996).

We investigated the effects of population source and temperature on the extent, timing, and duration of *M. disstria* egg hatch, and on phenological synchrony with trembling aspen and paper birch budbreak. Winter and spring temperatures were manipulated by moving egg masses, and artificially heating open-air outdoor experimental plots, respectively. Treatments mimicked anticipated temperatures within the region during the next 75-100 years (Kling et al. 2003; Wuebbles and Hayhoe 2004). The specific objectives were to (1) quantify the relative effects of increased temperature on timing of egg hatch by *M. disstria* populations collected along a latitudinal gradient, and (2) determine the effects of elevated temperatures, insect population source, and overwintering regime on the degree of phenological synchrony between insect egg hatch and host plant budbreak.

METHODS

Experimental design

We measured egg hatch among four *M. disstria* populations that were subjected to three overwintering regimes and three spring temperature regimes applied in replicated plots

at two sites. The two manipulated-treatment sites were in northeastern Minnesota along the ecotone boundary of southern boreal and northern temperate forests: Cloquet Forestry Center (CFC) near Cloquet, and Hubachek Wilderness Research Center (HWRC) near Ely (Fig. 1). Temperature treatments were applied using an outdoor, open-air mesoscale experiment termed ‘B4WarmED’ ([http://forestecology.cfans.umn.edu/ Research/B4WARMED](http://forestecology.cfans.umn.edu/Research/B4WARMED)), which, beginning in 2009, has simulated spring through autumn temperatures predicted from climate change models (see Reich et al. 2015 and Rich et al. 2015 for details). This infrastructure includes replicated heated plots that incorporate juvenile stands containing two hosts, trembling aspen and paper birch, and eight other native tree species, all from local (northern Minnesota) sources. Underground heating coils (Danfoss GX, Devi A/B, Denmark) and aboveground ceramic lamps (Salamander Model FTE-1000, United States) simultaneously manipulate soil and plant surface temperatures.

Three temperature treatments were administered: ambient controls, +1.7°C above ambient, and +3.4°C above ambient. These temperatures were selected to bracket the anticipated warming in the region during the next 75-100 years. Each experimental ring (plot) received one temperature treatment. There were six open-canopy rings per block, and three blocks per site, totaling 18 rings per site. Each block contained two rings per treatment, providing a total of 12 replicates per treatment across the two sites.

Experimental rings were 3 m in diameter. Heated rings had six ceramic lamps to administer +1.7°C and eight lamps to administer +3.4°C, evenly distributed around the perimeter. Control plots had 3 similarly distributed mock lamps. In 2012, temperature treatments commenced on 21 March in Cloquet and 27 March in Ely, and continued for

approximately 8 months. Each ring contained a thermal sensor that recorded aboveground temperature every 15 minutes.

Insect populations

Malacosoma disstria egg masses were collected in the fall of 2011 from naturally occurring populations in four regions across a latitudinal gradient (Fig. 1). Collections were from: 1) Prairie du Chien, WI (mid to late-December), southeast of the Wisconsin River along 180 m of a steep slope (42°58'27.98"N, 90°59'10.34"W), 2) Baraboo, WI (mid-October through early November), within an 800 m radius in the Baraboo Hills (43°25'12.53"N, 89°38'8.69"W), 3) Mille Lacs Lake (23 October), south of Isle, MN, along 275 m of a recreational trail (46° 8'30.15"N, 93°27'33.71"W), and 4) Bemidji, MN (24 October), from two locations 32 km apart: Potato Lake (47° 0'14.05"N, 95° 2'39.18"W) and Elbow Lake (47° 7'31.56"N, 95°34'8.55"W).

The number of egg bands ranged from 400 at Mille Lacs Lake to 100 at Prairie du Chien. Each egg band was inspected thoroughly, and those that were damaged, had many eggs missing, or were deformed were discarded. Healthy egg bands were tabulated for total numbers of eggs, missing eggs, and hatched eggs, and the assignment of each is in Uelmen 2014: App. 2 and 3B. Among the remaining healthy egg bands used, 52 had some missing eggs (mean = 2.28). The egg bands were sterilized by applying an aqueous solution of 1% Tween-20 and 5% bleach.

Partitioning and enclosure of overwintering egg bands

To account for the potential influence of winter environment on how egg bands respond to degree-day accumulation in the spring, and to test whether populations might differ in this regard, we also administered three overwintering regimes. In early December, half (36 per

population, 144 total) of the egg bands were brought to Madison, WI, and half were taken immediately to the B4WarmED sites, distributed evenly between Cloquet and Ely (Fig. 1). Egg bands were stored outdoors in mesh bags 152 cm above the ground.

In mid-March, just prior to initiation of annual warming treatments, the 144 egg bands that had overwintered in Madison were taken to the B4WarmED sites (72 each to Cloquet, Ely). At this time, all egg bands were placed in individual 7.5×12.5 cm mesh sleeves. Sleeves were fastened with binder clips, and suspended from 183 cm tall poles on a 60 cm radius rebar tie wire arm in the center of the experimental plot. Each of the 36 experimental plots contained 8 *M. disstria* egg bands: 1 per overwintering treatment (B4WarmED site vs. Madison) per population.

Assessment of insect and plant phenology

Once egg bands were in their respective experimental plots, they were monitored daily. It was typical for a few larvae to hatch 1-2 days before the remainder of the clutch, potentially skewing the results, so the time at which 50 eggs had hatched was designated as the date of hatch for each egg band. Observations on each egg band continued until 5 days after the last observed hatch. The duration of egg hatch was designated as the interval between when the first 50 and final larvae emerged. Two aspen and two birch trees per plot were evaluated daily for budbreak phenology. We defined budbreak as the time when leaf tips became visible (Schwartzberg et al. 2014).

Statistical analyses

We evaluated the effects of manipulated temperature, overwintering regime, hatch site, and population source on the timing and duration of egg hatch by *M. disstria*, and the effects of manipulated temperature and site on budbreak by trembling aspen and paper birch. We

also assessed phenological synchrony by calculating the difference between *M. disstria* hatch and host plant budbreak dates within the same temperature conditions. We used discrete analyses to characterize and quantify all sources of variation, and continuous analyses to integrate and expand the generality of results across a common temperature scale using the full power of the within-ring temperature recordings (15 minute intervals). Further, continuous models based on mean ring temperature allow us to model response differences between insects and plants, while continuous accumulated degree-day models facilitate comparison with other systems.

In the discrete models, we used a split-plot nested experimental design. Temperature was analyzed as three categorical treatments (ambient, +1.7°C and +3.4°C) across both hatch sites. The main factors were site, population source, and overwintering regime, unless otherwise stated. The formal hypothesis and model structure of egg hatch success, onset, and duration are located in SUPPLEMENTAL TEXT (Equation 1).

In the continuous models, the temperature measured within each ring (N=36) was treated as a continuous variable across both sites. These provide a common temperature scale derived from plot-specific data, and also account for the latitudinal difference between Cloquet and Ely. We used both mean ring temperature and accumulated degree-days. The mean ring temperature models allow us to calculate the intervals, in days, between budbreak and egg hatch. The accumulated degree-days model allows for the same types of comparisons but does not require averaging over a season.

Regression models were used to determine the relationships of date of egg hatch to mean ring temperature, and proportion of hatch to accumulated degree-days. We analyzed host

plant budbreak with a balanced two-way analysis of variance (SUPPLEMENTAL TEXT, Equation 2).

Regression models assessed the relationships between day of budbreak and mean ring temperature. Site was retained as a factor for plants because local conditions (i.e., soil) could potentially influence budbreak, in contrast to egg masses in mesh bags suspended from poles. Specific procedures for incorporating mean ring temperature and accumulated degree-days into continuous models are provided in the SUPPLEMENTAL TEXT (Equation 3).

An analysis of covariance was used to assess the influence of increased temperature on phenological synchrony between *M. disstria* and host plant budbreak. Regression models were used to determine the relationships between the differences in phenological events (egg hatch to birch/aspen budbreak) and temperature (SUPPLEMENTAL TEXT, Equation 4).

Statistical analyses were performed using Proc GLM, Proc MIXED (general linearized models) and Proc REG (regression) in SAS 9.3 and JMP 11.0.0 (SAS Institute Inc., Cary, NC). Results are reported (type III error) with corresponding *P* values of ≤ 0.05 as ‘significant’ and $0.05 < P \leq 0.10$ as ‘marginally significant’.

RESULTS

Overwintering survival of forest tent caterpillar eggs

The proportion of eggs that hatched was uniformly high, with an overall mean of 81.5% (SE= 0.83%) and an overall median of 84.5% (N= 284) (Table S1A). There were no significant effects of population source, overwintering regime, site, or experimentally manipulated temperature on egg hatch success (Table S1B). There was a marginally significant tendency for lower egg hatch at Ely than Cloquet (79.7% vs. 83.3%; $P=0.055$).

Five egg bands showed very few or no insect hatch, and were discarded. Detailed information on the total numbers of hatched and unhatched eggs in each band, and the treatment to which each band was assigned, are tabulated by Uelmen 2014: App. 2 and 3B.

Timing of forest tent caterpillar egg hatch

The timing of *M. disstria* egg hatch was strongly influenced by hatch site, temperature treatment, overwintering location, and population source (Table 1). There were no significant interactions. Overall, egg hatch ranged from 11 April to 8 May among all treatments, with a grand mean of 28 April (SE = 0.4 days) (Fig. 2), and a median of 1 May (N = 141). The median dates of egg hatch show similar relationships, with second quartiles ranging from 17 April to 6 May (Fig. S1).

As expected, hatch occurred first among egg bands exposed to +3.4 °C, then +1.7 °C, then ambient conditions. Across all populations, overwintering regimes, and hatch sites, mean egg hatch at +3.4°C occurred an average of 2.5 days before those at +1.7°C, which were 4 days before those at ambient temperatures. When populations and overwintering locations were pooled, egg hatch occurred earlier at Cloquet than Ely by 2 days at ambient temperature and +1.7 °C, and by 5 days at +3.4°C. There was a general trend for egg bands collected from southern populations to hatch before those from northern populations, but this pattern was not absolute. Overall, insects that overwintered in northeastern Minnesota hatched 3 days later than those that overwintered at the lower latitude, Madison, when all other factors were pooled.

Continuous models for mean ring temperature and accumulated degree-days likewise indicated a strong response of *M. disstria* egg hatch date to temperature (Table 2).

Population source had a significant effect on egg hatch, for both locally overwintered egg

masses and those overwintered in Madison, in the model based on mean ring temperature. Population had a significant effect on egg hatch on egg masses that overwintered in Madison in the accumulated degree-day model. Interactions were not analyzed, as they largely comprised the random effects ANCOVA model error. The r^2 values were substantially higher in the accumulated degree-day than mean ring temperature models.

In mean ring temperature analyses, egg masses that overwintered in Madison (mean date = 26 April, SE = 0.4; median date = 01 May; N = 143) hatched earlier than locally overwintered egg masses (mean date = 28 April, SE = 0.5; median date = 26 April; N = 141) by 2.5 days. The slopes of insect development versus temperature were similar between Madison and locally overwintered eggs in both the mean ring temperature (Fig. 3A) and accumulated degree-day (Fig. 3B) continuous models.

The hatch order of egg masses from various populations differed among wintering sites in the continuous models based on mean ring temperature. However, the order in which the end of hatching occurred among populations was not affected by wintering site. In the continuous models based on accumulated degree-days, populations under both wintering regimes had the same initial and end of hatch orders (Uelmen 2014: Fig. S4). As in the other analyses, r^2 values in the models employing accumulated degree-days were higher than those employing mean ring temperatures.

Duration of forest tent caterpillar egg hatch

Overall, the duration of egg hatch within a band averaged 5.0 (SE = 0.2) days, with a median of 5.0 days (N = 141). The duration of egg hatch was strongly influenced by treatment site, overwintering location, and population source (Table 1). Temperature treatment did not affect hatch duration, and there were no significant interactions among

factors. The mean duration of egg hatch ranged from 3.7 days (Mille Lacs Lake population, locally overwintered, Ely, +1.7 °C) to 8.7 days (Baraboo, Madison overwintered, Cloquet, +1.7 °C) (Fig. 4). Egg bands that overwintered in Ely had the shortest duration of egg hatch (mean days = 4.6, SE = 0.2; median days = 4.0; N = 70), followed by Cloquet (mean days = 5.3, SE = 0.2; median days = 6.0; N = 71) and Madison (mean days = 5.9, SE = 0.2; median days = 6.0; N = 142).

The onset and duration of egg hatch were inversely related (Fig. 5). Populations whose eggs hatched sooner also exhibited longer hatch durations. For example, egg masses that started to hatch on 12 April had an average hatch duration of 16 days, compared with egg masses that started to hatch on 04 May, which averaged 2 days. Populations from Baraboo and Mille Lacs Lake had the earliest egg hatches, but they also had the longest mean hatch durations (6.5 and 5.5 days, respectfully). The two latest hatching populations, Bemidji and Prairie du Chien, had the shortest mean durations of hatch (5 and 4.8 days, respectfully). Insect populations demonstrated higher variability in hatch durations in the accumulated degree-day model than in the day of hatch model. For both mean ring temperature and accumulated degree-day continuous models, Baraboo eggs were the first to complete hatching, but exhibited the greatest variability in hatch duration (11 days for degree-days and 6.5 days for mean ring temperature). Mille Lacs Lake eggs experienced the next highest variability in hatch duration, followed by Bemidji, and concluding with Prairie du Chien.

Budbreak phenology of trembling aspen and paper birch

The onset of budbreak by both aspen (grand mean = 25 April, SE = 1.0 days; median = 25 April; N = 68) and birch (grand mean = 19 April, SE = 0.9 days; median = 16 April; N = 69) were strongly influenced by temperature treatment (discrete analysis; Table 3). Site was

a significant factor for aspen budbreak ($P < 0.001$) and marginally significant for birch budbreak ($P = 0.087$). As expected, warmer experimental temperatures advanced host plant budbreak, which occurred first at +3.4 °C, then at +1.7 °C, then at ambient (Fig. 6). Also as expected, aspen budbreak occurred earlier in Cloquet than Ely. However, birch showed a marginally significant opposite trend, breaking bud earlier at Ely. Overall, budbreak occurred over 35 days for aspen (7 April to 12 May) and 30 days for birch (9 April to 9 May), among all treatments.

As temperatures increased, the interval between mean budbreak by these two tree species decreased. Birch budbreak occurred an average of ten days earlier than aspen budbreak at ambient temperatures, seven days earlier at +1.7 °C, and five days earlier at +3.4 °C. Mean and median host plant budbreak showed the same trend (Uelmen 2014: Fig. 6 and Table S3).

Increases in mean ring temperature likewise advanced estimates of budbreak by both aspen and birch (continuous analysis; Table 3). Site had a significant effect on aspen budbreak, but not on birch budbreak. The date of aspen budbreak and birch budbreak each showed negative linear relationships with increasing mean ring temperatures ($r^2 = 0.38$ and 0.27 , respectively). Birch broke bud 10 days earlier than aspen at ambient conditions, but this difference decreased to 5 days under the warmest simulated temperature conditions.

Aspen responded more strongly to temperature increases than did birch (slopes = -3.6 and -2.7 , respectively), and their phenologies converged.

Accumulating degree-days also advanced budbreak in both aspen and birch (Table 3B), although site was not a significant factor for either species. Aspen and birch budbreak each showed stronger positive linear relationships ($r^2 = 0.69$ and 0.67 , respectively) than in the mean ring temperature continuous model.

Structuring of phenological synchrony by insect population source, tree species and temperature

Manipulated spring temperatures advanced the timing of insect egg hatch and host plant budbreak, but the interval between budbreak and egg hatch differed between the two host plants and across temperature regimes. At ambient temperatures, aspen budbreak occurred later than *M. disstria* egg hatch, but slightly earlier than egg hatch at +1.7°C, and preceded egg hatch by even more at +3.4°C (Fig. 7). In contrast, birch budbreak occurred earlier than *M. disstria* egg hatch at all temperature regimes, and the interval between budbreak and egg hatch increased with increasing temperatures (Fig. 7).

With all factors pooled at ambient temperatures, mean birch budbreak occurred 5.5 days before mean egg hatch, and 9 days before mean aspen budbreak. At +1.7°C, birch budbreak advanced to 10 days before egg hatch, but decreased to 7 days before aspen budbreak. At +3.4°C, the interval between birch budbreak and egg hatch remained the same. However, aspen was only 5 days behind birch budbreak at the warmest temperatures. With all factors pooled at ambient temperatures, mean aspen budbreak occurred 3.5 days after mean egg hatch, at +1.7°C, aspen budbreak was 3 days before egg hatch, and at +3.4°C, aspen budbreak was 4.5 days before egg hatch.

Both insect egg hatch and aspen budbreak occurred earlier at Cloquet than Ely, consistent with a latitudinal effect. Host plant budbreak advanced more rapidly than insect egg hatch when subjected to increasing temperatures, with birch budbreak occurring earlier than aspen.

Comparisons of Insect vs. Host Response Based on Mean Ring Temperatures and Accumulated Degree-Days

Continuous models of analysis (both mean ring temperature and accumulated degree-day models) indicated strong temperature effects on the phenological relationship between *M. disstria* egg hatch and host plant budbreak (Table 4). Accumulated degree-days revealed strong responses between egg hatch and both host plant budbreak and mean ring temperature, indicating a strong response between egg hatch and aspen budbreak, but not birch budbreak. Population source did not affect this interval for either continuous temperature model. Interactions were not analyzed under the ANCOVA model, as the error consisted largely of random effects.

Both continuous models indicated that host plant budbreak responded more strongly than *M. disstria* egg hatch to high temperatures, altering phenological synchrony (Fig. 8A). Host plant budbreak had steeper slopes than *M. disstria* (accumulated degree-days: birch $r^2 = 0.718$, aspen $r^2 = 0.683$, *M. disstria* $r^2 = 0.501$, mean ring temperature: birch $r^2 = 0.267$, aspen $r^2 = 0.382$, *M. disstria* $r^2 = 0.195$).

With the exception of aspen budbreak under ambient mean ring temperatures, host plant budbreak occurred earlier than *M. disstria* egg hatch at all temperatures. Birch broke bud 3 degree-days before mean egg hatch, or 5 days under ambient mean ring temperatures, and 12.5 degree-days, or 12 days under the warmest simulated temperatures. Aspen broke bud 3 degree-days, or 7.5 days, after mean egg hatch, as manipulated by mean ring temperatures, and 4.5 degree-days, or 5 days under the warmest simulated temperatures (Fig. 8B). *Malacosoma disstria* population-specific synchrony data are in Fig. S2.

Both continuous models adequately explained host plant budbreak, insect egg hatch, and the phenological relationship between the two. The accumulated degree-day model provided a better goodness-of-fit, as indicated by stronger correlation coefficient values (Table 2).

This is also true for host plant budbreak (Table 3). Overall, the phenological relationship between *M. disstria* egg hatch and host plant budbreak is better explained by the accumulated degree-day model, as indicated by the more consistently significant p-values (Table 4) when compared with mean ring temperature.

DISCUSSION

We quantified how winter temperatures, spring temperatures, and insect population source influence development rates by an early-season herbivore, effects of spring temperatures on budbreak of two host tree species, and how anticipated climate may influence their phenological synchrony. As expected, experimental warming treatments that simulate predicted temperatures over the next 75-100 years advanced both host plant budbreak and insect egg hatch. However, host plants generally showed greater advances. At ambient temperatures, average egg hatch occurred shortly before, concurrently with, or shortly after, host budbreak depending on plant species, in agreement with prior work (Gray and Ostaff 2012; Parry et al. 1998; Schwartzberg et al. 2014). As temperatures increased, the relative phenologies shifted in the direction of more rapid plant than insect advance. This increased the interval between egg hatch and budbreak in relationships where plants currently become active first, and decreased and even changed the sequence in relationships where insects currently become active first. Some other systems have shown the opposite trend (Hunter and Elkinton 2000; Parmesan 2007), further illustrating the complexity of trophic responses to climate change.

Several key processes, which operate at multiple spatiotemporal scales, will determine how changes in phenological synchrony will influence the stability of plant–insect

interactions. At the scale of individuals, advances in budbreak relative to egg hatch typically lower insect performance due to poor nutritional quality and prolonged exposure to predators (Parry et al. 1998; Jones and Despland 2006; Jamieson et al. 2015). This could be particularly harmful to neonates feeding on birch, as they would encounter substantially more mature foliage. At a regional scale, *M. disstria* might compensate through dispersal: more southern populations might advance northward within the lifespan of individual trees, restoring prior temporal relationships between egg hatch and budbreak. This prospect is supported by the strong flight abilities of *M. disstria* (Brown 1965), the orders-of-magnitude difference in their generation time relative to their host trees, the variation in degree-day responses among populations across latitudes within dispersal range during the time frame being simulated, and the cold-hardiness of eggs from southern populations that would be oviposited by females that dispersed northward (Peltonen 2002). On a larger temporal scale, local populations of *M. disstria* might adapt to altered phenologies of their major host plants. This would require selection against individuals that hatched too late, which seems reasonable given the high degree of phenological synchrony in current populations (van Asch et al. 2013). Also, our data show high variation within populations and substantial variation within individual egg masses, both of which would facilitate local genetic adaptation. Additionally, the duration of hatch within an egg mass spans some of the plant phenological shifts we observed and also increases with warming temperatures, further providing opportunities for the insect to respond with adaptive genetic shifts.

At a finer spatial scale, oviposition on or larval movement to later-developing plants could influence performance of current *M. disstria* populations in a warmed climate (Gray and Ostaff 2012). Numerous later-developing species in this region, such as red oak

(*Quercus rubra* L.), cherry (*Prunus* spp.), and ash (*Fraxinus* spp.), are suitable hosts. Some alternative tree species would shift from a less synchronous to a more synchronous relationship with this polyphagous herbivore. Also, aspen shows strong variation in budbreak among clones, so some genotypes might become more synchronous than currently. This raises the possibility that genotypes that currently avoid herbivory through late budbreak may be less well chemically defended, due to trade-offs arising from metabolic costs (Hermes and Mattson 1992; Osier and Lindroth 2006), and hence become more susceptible with changing climate. Possibly slowing local adaptation is *M. disstria*'s behavior of usually confining feeding to a single tree (Despland and Noseworthy 2006), and the relatively short distance of early instar ballooning.

This study demonstrates asynchronous responses between insects and host plants in response to warming temperatures. These changes might favor the host plants. However, *M. disstria* appears to have multiple opportunities for adaptation, including switching to alternative host species, switching to more late-developing genotypes, local genetic shifts facilitated by substantial variation among eggs within individual masses, and migration by populations having different degree-day responses. Overall, this research provides realistic mesoscale examples for understanding and predicting responses to climate warming, and for understanding and predicting shifts in trophic interactions arising from climate change.

ACKNOWLEDGEMENTS

We thank B4WarmED site managers Artur Stefanski and Karen Rice, who provided technical expertise. Dr. Jun Zhu and Peter Crump (University of Wisconsin) provided valuable statistical modeling assistance. The Wisconsin DNR, Minnesota DNR and Jana

441 Albers, Christine Buhl, as well as local citizens provided assistance locating and collecting
 442 insects. This research was funded by the National Institute of Food and Agriculture, US
 443 Department of Agriculture (AFRI project 2011-67013-30147), the Office of Science (BER),
 444 US Department of Energy (grant no. DE-FG02-07ER64456), the University of Wisconsin
 445 College of Agricultural and Life Sciences, a UW Zoology Department teaching assistantship,
 446 a UW PEOPLE project assistantship, the Minnesota Department of Natural Resources, the
 447 University of Minnesota College of Food, Agricultural, and Natural Resources Sciences and
 448 the UM Wilderness Research Foundation. Reviews by two anonymous reviewers
 449 substantially improved this paper.

References

- 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**, 263-286.
- Bale, J. S., Masters, G. J., Hodkinson, I. D., Awmack, C., Bezemer, T. M., Brown, V. K., Butterfield, J., Buse, A., Coulson, J. C., Farrar, J., Good, J. E. G., Harrington, R., Hartley, S., Jones, T. H., Lindroth, R. L., Press, M. C., Symrnioudis, I., Watt, A. D., & Whittaker, J. B. (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology*, **8**, 1-16.
- Battisti, A., Stastny, M., Netherer, S., Robinet, C., Schopf, A., Roques, A., & Larsson, S. (2005) Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. *Ecological Applications*, **15**, 2084-2096.
- Brown, C. E. (1965) Mass transport of Forest Tent Caterpillar moths, *Malacosoma disstria* Hübner, by a cold front. *The Canadian Entomologist*, **97**, 1073-1075.
- Department of Forest Resources: College of Food, Agricultural Natural Resource Sciences, University of Minnesota (2010) <http://forestecology.cfans.umn.edu/B4WARMED.html>.
- Despland, E. & Noseworthy, M. (2006) How well do specialist feeders regulate nutrient intake? Evidence from a gregarious tree-feeding caterpillar. *Journal of Experimental Biology*, **209**, 1301-1309.
- Drooz, A. T. (1985) Insects of eastern forests. Misc. Publi No. 1426. Washington, DC; U.S. Department of Agriculture, Forest Service. 608 p.

- 471 Evenden, M. L., Whitehouse, C. M., & Jones, B. C. (2015) Resource allocation to flight in an
 472 outbreaking forest defoliator, the forest tent caterpillar, *Malacosoma disstria*.
 473 *Environmental Entomology*, doi: <http://dx.doi.org/10.1093/ee/nvv055>.
- 474 Fisichelli, N. A., Frelich, L. E., & Reich, P. B. (2014) Temperate tree expansion into adjacent
 475 boreal forest patches facilitated by warmer temperatures. *Ecography*, **37**, 152-161.
- 476 Fullard, J. H. & Napoleone, N. (2001) Diel flight periodicity and the evolution of auditory
 477 defences in the Macrolepidoptera. *Animal Behaviour*, **62**, 349-628.
- 478 Gray, D. R. & Ostaff, D. P. (2012) Egg hatch of forest tent caterpillar (Lepidoptera:
 479 Lasiocampidae) on two preferred host species. *Canadian Entomologist*, **144**, 790-797.
- 480 Haukioja, E. (2005) Plant defenses and population fluctuations of forest defoliators: mechanism-
 481 based scenarios. *Annales Zoologici Fennici*, **42**, 313-325.
- 482 Herms, D. A. & Mattson, W. J. (1992) The Dilemma of Plants: To Grow or Defend. *The*
 483 *Quarterly Review of Biology*, **67**, 283-335.
- 484 Hodson, A. C. (1941) An ecological study of the forest tent caterpillar, *Malacosoma disstria*
 485 Hbn. University of Minnesota Agricultural Experiment Station Technical Bulletin 148.
- 486 Howard, J. L. (1996) *Populus tremuloides*. In: Fire Effects Information System. U.S.
 487 Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire
 488 Sciences Laboratory. <http://www.fs.fed.us/database/feis/>.
- 489 Hunter, A. F. & Elkinton, J. S. (2000) Effects of Synchrony with Host Plant on Populations of a
 490 Spring-Feeding Lepidopteran. *Ecology*, **81**, 1248-1261.
- 491 Insect Pests on Upswing. *The Science News-Letter*, **81**, 342-343. 02 June 1962.

- 492 IPCC, 2014: Climate Change: Impacts, adaptation, and vulnerability. IPCC WGII AR5
 493 Summary for Policymakers. Figure SPM.5. [http://ipcc-](http://ipcc-wg2.gov/AR5/images/uploads/IPCC_WG2AR5_SPM_Approved.pdf)
 494 [wg2.gov/AR5/images/uploads/IPCC_WG2AR5_SPM_Approved.pdf](http://ipcc-wg2.gov/AR5/images/uploads/IPCC_WG2AR5_SPM_Approved.pdf).
- 495 Ives, W. G. H. (1971) The forest tent caterpillar in Alberta. Environmental Canada, Canadian
 496 Forest Service, Northern Forestry Centre Internal Report, NOR-4, Edmonton, Alberta.
- 497 Jamieson, M. A., Schwartzberg, E. G., Raffa, K. F., Reich, P. B., & Lindroth, R. L. (2015)
 498 Experimental climate warming alters aspen and birch phytochemistry and performance
 499 traits for an outbreak insect herbivore. *Global Change Biology*, doi: 10.1111/gcb.12842.
- 500 Jones, B. C. & Despland, E. (2006) Effects of synchronization with host plant phenology occur
 501 early in the larval development of a spring folivores. *Canadian Journal of Zoology*, **84**,
 502 628-633.
- 503 Kling, G. W., Hayhoe, K., Johnson, L., Magnuson, J., Polasky, S., Robinson, S., Shuter, B.,
 504 Wander, M., Wuebbles, D., & Zak, D. (2003) Confronting Climate Change in the Great
 505 Lakes Region. Union of Concerned Scientists, Ecological Society of America;
 506 Cambridge, MA, Washington, D.C. 92 pp.
- 507 Lawrence, R. K., Mattson, W. J., & Haack, R. A. (1997) White spruce and the spruce budworm:
 508 Defining the phenological window of susceptibility. *Canadian Entomologist*, **129**, 291-
 509 318.
- 510 Lindroth, R. L. & Hwang, S-Y. (1996) Clonal variation in foliar chemistry of quaking aspen
 511 (*Populus tremuloides* Michx.). *Biochemical Systematics and Ecology*, **24**, 357-364.
- 512 Liebhold, A., Koenig, W. D., & Bjornstad, O. N. (2004) Spatial synchrony in population
 513 dynamics. *Annual Review of Ecology and Systematics*, **35**, 467-490.

- 514 Michaelian, M., Hogg, E. H., Hall, R. J., & Arsenault, E. (2011) Massive mortality of aspen
 515 following severe drought along the southern edge of the Canadian boreal forest. *Global*
 516 *Change Biology*, **17**, 2084-2094.
- 517 Netherer, S. & Schopf, A. (2010) Potential effects of climate change on insect herbivores in
 518 European forests-general aspects and the pine processionary moth as specific example.
 519 *Forest Ecology and Management*, **259**, 831-838.
- 520 Olsson, R. (2010) Boreal Forest and Climate Change. *Air Pollution & Climate Secretariat*.
 521 <http://www.airclim.org/sites/default/files/documents/borealforest-regional.pdf>.
- 522 Osier, T. L. & Lindroth, R. L. (2006) Genotype and environment determine allocation to and
 523 costs of resistance in quaking aspen. *Oecologia*, **148**, 293-303.
- 524 Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L.,
 525 Shvidenko, A., Lewis, S. L., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W.,
 526 McGuire, A. D., Piao, S., Rautiainen, A., Sitch, S., & Hayes, D. (2011) A large and
 527 persistent carbon sink in the world's forests. *Science*, **333**, 988-993.
- 528 Parmesan, C., & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts
 529 across natural systems. *Nature*, **421**, 37-42.
- 530 Parmesan, C. (2007) Influence of species, latitudes and methodologies on estimates of
 531 phenological response to global warming. *Global Change Biology*, **13**, 1860-1872.
- 532 Parry, D., Spence, J. R., & Volney, W. A. (1998) Budbreak phenology and natural enemies
 533 mediate survival of first-instar forest tent caterpillar (Lepidoptera: Lasiocampidae).
 534 *Environmental Entomology*, **27**, 1368-1374.

- 535 Parry, D., Goyer, R. A., & Lenhard, G. J. (2001) Macrogeographic clines in fecundity,
 536 reproductive allocation, and offspring size of the forest tent caterpillar *Malacosoma*
 537 *disstria*. *Ecological Entomology*, **26**, 281-291.
- 538 Peltonen, M., Liebhold, A. M., Bjornstad, O. N., & Williams, D. W. (2002) Spatial synchrony in
 539 forest insect outbreaks: roles of regional stochasticity and dispersal. *Ecology*, **83**, 3120-
 540 3129.
- 541 Post, E., & Forchhammer, M. C. (2002) Synchronization of animal population dynamics by
 542 large-scale climate. *Nature*, **420**, 168-171.
- 543 Quiring, D. T. (1994) Influence of inter-tree variation in time of budburst of white spruce on
 544 herbivory and the behaviour and survivorship of *Zeiraphera Canadensis*. *Ecological*
 545 *Entomology*, **19**, 17-25.
- 546 Reich, P.B., Sendall, K. M., Rice, K., Rich, R. L., Stefanski, A., Hobbie, S. E., & Montgomery,
 547 R. A. (2015) Geographic range predicts photosynthetic and growth response to warming
 548 in co-occurring tree species. *Nature Climate Change*, **5**, 148-152
- 549 Rich, R. L., Stefanski, A., Montgomery, R. A., Hobbie, S.E., Kimball, B. A., & Reich, P. B.
 550 (2015) Design and performance of combined infrared canopy and belowground warming
 551 in the B4WarmED (Boreal Forest Warming at an Ecotone in Danger) experiment. *Global*
 552 *Change Biology*, **21**, 2334-2348.
- 553 Schwartzberg, E. G., Jamieson, M. A., Raffa, K. F., Reich, P. B., Montgomery, R. A., &
 554 Lindroth, R. L. (2014) Simulated climate warming alters phenological synchrony
 555 between an outbreak insect herbivore and host trees. *Oecologia*, **175**, 1041-1049.

- 556 Smith, J. D. & Goyer, R. A. (1986) Population fluctuations and causes of mortality for the forest
 557 tent caterpillar, *Malacosoma disstria* (Lepidoptera: Lasiocampidae), on three different
 558 sites in Southern Louisiana. *Environmental Entomology*, **15**, 1184-1188.
- 559 Uelmen, J (2014) Effects of Temperature Regimes and Population Source on the Success,
 560 Timing, and Host Plant Synchrony of Egg Hatch by *Malacosoma disstria*, master thesis,
 561 University of Wisconsin, Madison.
- 562 van Asch, M. & Visser, M. E. (2007) Phenology of forest caterpillars and their host trees: the
 563 importance of synchrony. *Annual Review Entomology*, **52**, 37-55.
- 564 Van Asch, M., Salis, L., Holleman, L. J. M., van Lith, B., and Visser, M. E. (2013) Evolutionary
 565 response of the egg hatching date of a herbivorous insect under climate change. *Nature*
 566 *Climate Change*, **3**, 244-248.
- 567 Volney, W. J. A. & Fleming, R. A. (2000) Climate change and impacts of boreal forest insects.
 568 *Agriculture, Ecosystems, and Environment*, **82**, 283-294.
- 569 Witter, J. A., Mattson, W. J., & Kulman, H. M. (1975) Numerical analysis of a forest tent
 570 caterpillar (Lepidoptera: Lasiocampidae) outbreak in northern Minnesota. *Canadian*
 571 *Entomologist*, **107**, 837-854.
- 572 Wuebbles, D. J. & Hayhoe, K. (2004) Climate change projections for the US Midwest.
 573 *Mitigation and Adaptation Strategies for Global Change*, **9**, 335-363.

574 **Table 1:** Results of ANOVA, relating the onset and duration (see Figure 4) of hatch of *M. disstria* egg bands under manipulated temperature regimes. A bolded value denotes significant factor at $P \leq 0.05$ (N = 288 egg bands).

Source	<i>Day of Hatch</i>			<i>Hatch Duration</i>		
	DF	F	P	DF	F	P
Model	27	11.18	<0.001	27	3.62	<0.001
Error	256			256		
Site	1	33.18	<0.001	1	29.43	<0.001
Temp.	2	61.13	<0.001	2	2.15	0.119
Overwinter	2	19.32	<0.001	2	11.57	<0.001
Population	3	19.02	<0.001	3	3.92	0.0092
Temp. *Population	6	0.34	0.822	6	0.79	0.575
Temp. *Overwinter	4	0.98	0.849	4	2.01	0.093
Overwinter*Population	6	1.37	0.228	6	1.03	0.409
Site*Population		Not Tested		3	1.33	0.264

575 **Table 2:** Results of ANCOVA relating the onset of egg hatch to mean ring temperature (A) and the proportion cumulative hatch to accumulated degree-days (B) for *M. disstria*. Coefficient values “a” (slope), “b” (intercept), and r^2 (correlation) comprise the linear values. A bolded value denotes significant factor at $P \leq 0.05$. Interactions are largely incorporated within error terms and not included.

	Source	Overwintering	a	b	r^2	DF	F	P
A	<i>Day of Hatch</i>							
	Model	<i>Locally</i>	-1.69	33.53	0.20	4	14.78	<0.001
	Error					136		
	Mean Ring Temp.					1	38.65	<0.001
	Population					3	7.04	0.002
	Model	<i>Madison</i>	-1.48	28.77	0.11	4	15	<0.001
B	Error					138		
	Mean Ring Temp.					1	21.65	<0.001
	Population					3	12.61	<0.001
	<i>Proportion Cumulative Hatch</i>							
	Model	<i>Locally</i>	0.00	-0.66	0.43	4	26.05	<0.001
	Error					136		
A	Accumulated Degree-days					1	82.4	<0.001
	Population					3	0.6	0.617
	Model	<i>Madison</i>	0.01	-0.60	0.53	4	43.73	<0.001
	Error					138		
	Accumulated Degree-days					1	104.74	<0.001
	Population					3	2.75	0.045

576

Table 3: Results of discrete (A) (see Figure 6) and continuous (B) models of aspen and birch budbreak in response to manipulated early spring temperatures. A bolded value denotes significant factor at $P \leq 0.05$ (N=68 for aspen, 69 for birch).

A ANOVA: Discrete model

Source	DF	F	P
<i>Aspen Budbreak</i>			
Model	5	26.58	<0.0001*
Error	62		
Temperature Treatment	2	56.22	<0.0001*
Site	1	19.97	<0.0001*
Temperature Treatment*Site	2	0.28	0.7597
<i>Birch Budbreak</i>			
Model	5	10.16	<0.0001*
Error	63		
Temperature Treatment	2	23.27	<0.0001*
Site	1	3.02	0.087
Temperature Treatment*Site	2	0.35	0.707
<i>Difference in plant budbreak</i>			
Model	5	37.09	<0.001
Error	131		
Temperature Treatment	2	65.14	<0.001
Species	1	55.9	<0.001
Temperature Treatment*Species	2	1.39	0.252

B ANOVA: Continuous model

Source	a	b	r ²	DF	F	P		
<i>Aspen Budbreak</i>								
Model	-3.614	52.511	0.382	2	35.44	<0.001		
Error				65				
Mean Ring Temp.				1	59	<0.001		
Site				1	14.72	0.0003		
<i>Birch Budbreak</i>								
Model	-2.664	34.924	0.267	2	14.56	<0.001		
Error				66				
Mean Ring Temp.				1	27.09	<0.001		
Site				1	1.38	0.244		
<i>Aspen Budbreak</i>								
Model	0.141	-12.816	0.688	7	1.49	<0.001		
Error				65				
Accumulated Degree-days				1	96.54	<0.001		
Site				1	0.79	0.378		
<i>Birch Budbreak</i>								
Model	0.15	-15.75	0.667	2	65.85	<0.001		
Error				66				
Accumulated Degree-days				1	127.5	<0.001		
Site				1	0.02	0.892		
<i>Difference in plant budbreak</i>								
<i>Mean Ring Temperature</i>	DF	F	P	<i>Accumulated Degree-Days</i>		DF	F	P
Model	3	35.15	<0.001	Model	71	2.79	<0.001	
Error	133			Error	65			
Mean Ring Temp.	1	64.51	<0.001	Species	1	53.2	<0.001	
Species	1	4.5	0.036	Plot	35	2.85	<0.001	
Mean Ring Temp.*Species	1	1.48	0.226	Plot*Species	35	1.58	0.056	

578

Table 4: Results of continuous models on the interval between *M. disstria* egg hatch and host plant budbreak. A bolded value denotes significant factor at $P \leq 0.05$.

Source	a	b	r ²	DF	F	P
<i>Egg hatch to aspen budbreak</i>						
Model	-2.13	19.355	0.199	4	8.75	<0.001
Error				138		
Mean Ring Temp.				1	32.25	<0.001
Population				3	0.89	0.449
<i>Egg hatch to birch budbreak</i>						
Model	-0.705	-1.274	0.02	4	0.87	0.484
Error				138		
Mean Ring Temp.				1	1.52	0.219
Population				3	0.65	0.587
<i>Egg hatch to aspen budbreak</i>						
Model	-0.374	8.439	0.05	4	2.64	0.036
Error				138		
Accumulated Degree-days				1	8.23	0.005
Population				3	0.3	0.826
<i>Egg hatch to birch budbreak</i>						
Model	-0.045	2.742	0.067	4	5.2	0.001
Error				138		
Accumulated Degree-days				1	18.61	<0.001
Population				3	0.63	0.598

Figure Legends

Figure 1: Locations of experimental sites at which *M. disstria* egg bands and host trees were subjected to manipulated spring temperatures (solid stars), insect population sources (circles), and overwintering sites of egg bands (open and solid stars). Experimental design is illustrated in accompanying flow diagram.

Figure 2: Mean dates of egg hatch among four *M. disstria* populations subjected to three manipulated temperature regimes and three overwintering regimes, during Spring 2012. Differences among sites, overwintering treatments, temperature treatments, and populations of *M. disstria* are significant (ANOVA, $df = 83$, $P < 0.0001$) (± 1 standard error). Statistics are provided in Table 1.

Figure 3: Relationship of proportion of cumulative *M. disstria* egg hatch to A) mean ring temperature and B) accumulated degree-days (threshold = 4.4°C) at the B4WarmED sites, Spring 2012. Data are shown separately for egg masses that overwintered at the treatment sites (northeast MN) or at a more southern location (Madison, WI). Widths of trendlines indicate 95% C.I. Statistics are in Table 2. Population source was significant for Madison-overwintered egg bands.

Figure 4: Mean duration of hatch of *M. disstria* egg bands subjected to three controlled spring temperature regimes and three overwintering regimes, 2012. Differences among sites, overwintering treatments, and populations of *M. disstria* are statistically significant (ANOVA, $df = 27$, $P = 0.001$). Temperature treatment was not significant (± 1 standard error). Statistics are provided in Table 1.

Figure 5: Inverse relationship between onset and within-band duration of egg hatch in *M. disstria*. Data are shown based on (A) hatch date and (B) accumulated degree-days. Data collected at the B4WarmED sites, Spring 2012 (ANOVA (A) $F_{1,282} = 132.17$, $P < 0.001$, $N = 284$) ($a = -1.526$, $b = 24.79$, $r^2 = 0.32$); ANOVA (B) $F_{1,282} = 98.20$, $P < 0.001$, $N = 284$) ($a = -9.91$, $b = 281.36$, $r^2 = 0.26$). Widths of trendlines indicate 95% C.I.

Figure 6: Mean date of budbreak among birch and aspen trees subjected to three temperature regimes at the B4WarmED sites, Spring 2012. Birch budbreak advanced earlier with warming temperatures (site was moderately significant) (ANOVA, $df = 5$, $P < 0.001$). Aspen budbreak advanced earlier with both warming temperatures, and varied between sites (ANOVA, $df = 5$, $P < 0.001$) (± 1 standard error). Statistics are provided in Table 3A.

Figure 7: Box and whisker plots displaying how synchrony of *M. disstria* egg hatch with aspen and birch budbreak varies with *M. disstria* population source and temperature treatment. Data show difference (days) between median budbreak and egg hatch at the B4WarmED sites, Spring 2012, under three temperature treatments. Negative x-values denote earlier budbreak than egg hatch (± 1 quantile).

Figure 8: Mean distribution of pooled populations of *M. disstria* and host plant phenology (A) and difference in timing between egg hatch and host plant budbreak (B) in relation to mean ring temperature at the B4WarmED sites, Spring 2012. Mean ring temperatures computed from the grand mean of daily averages from 36 plot-specific temperatures recorded from date of heating activation to date of last egg hatch. Negative values indicate plant budbreak occurred before insect egg hatch. Egg hatch and budbreak

623 always advanced with increasing temperature, but host plants advanced more rapidly.
624 Mean birch budbreak occurred before *M. disstria* egg hatch throughout the study. Widths
625 of trendlines indicate 95% C.I. Insects overwintered locally (N=144). Statistics are
626 provided in Table 2 for *M. disstria* and Table 3 for host plants.

Figure 1.

628 Figure 2.

629

Figure 3.

630 Figure 4.

631 Figure 5.

632 Figure 6.

633 Figure 7.

Figure 8.