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# Effects of winter temperatures, spring degree-day accumulation, and insect population source on phenological synchrony between forest tent caterpillar and host trees



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

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#### 1. 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

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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, 2007), 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

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stock (Pan et al., 2011). In the southern boreal forest, mean annual temperatures have risen ≈1.5 °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).

M. 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 to 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.

#### 2. Methods

#### 2.1. 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), 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,  $+1.7\,^{\circ}\text{C}$  above ambient, and  $+3.4\,^{\circ}\text{C}$  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 opencanopy 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.

#### 2.2. Insect populations

*M. 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

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