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Density-Dependent Survival in the Larval Stage of an Invasive Insect: Dispersal vs. Predation

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DENSITY-DEPENDENT SURVIVAL IN THE LARVAL STAGE OF AN INVASIVE INSECT:
DISPERSAL VS. PREDATION

A Thesis Presented

by

ADAM PEPI

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

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ABSTRACT

DENSITY-DEPENDENT SURVIVAL IN THE LARVAL STAGE OF AN INVASIVE INSECT: DISPERSAL VS. PREDATION

SEPTEMBER 2015

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1. The success of invasive species is often thought to be due to release from natural enemies. This hypothesis relies on the assumption that species are regulated by top-down forces in their native range and implies that species are likely to be regulated by bottom-up forces in the invasive range. Neither of these assumptions has been consistently supported with insects, a group which include many highly destructive invasive pest species.
2. Winter moth (*Operophtera brumata*) is an invasive defoliator in North America that appears to be regulated by mortality in the larval stage in its invasive range. To assess whether regulation in the invasive range is caused by top-down or bottom-up forces, we sought to identify the main causes of larval mortality.
3. To measure the importance of different sources of winter moth larval mortality, we used observational and manipulative field studies to measure dispersal, predation, parasitism, disease. We measured the response of larval dispersal in the field to multiple aspects of foliar quality, including total phenolics, pH 10 oxidized phenolics, trichome density, total nitrogen,

total carbon, and carbon-nitrogen ration. We also used manipulative laboratory studies to measure the presence of cannibalism and dispersal.

4. Tree-level declines in density were driven by density-dependent larval dispersal of early instars with very little mortality caused by other factors. Later instar larvae dispersed at increased rates from previously damaged vs. undamaged foliage, and field larval dispersal rates were related to proportion of oxidative phenolics in 2015, suggesting that larval dispersal may have been mediated by an induced decline in foliar quality.

5. We conclude that winter moth population densities are regulated in New England by density-dependent larval dispersal possibly mediated by phenolic oxidative capacity. The suggested role of host plant quality in mediating dispersal means that winter moth population densities in New England appear to be regulated by bottom up forces, aligning with the assumptions of the natural enemy release hypothesis. This is the first study known to the authors presenting data showing a negative effect on insect herbivore performance from pH 10 oxidized phenolics.

Keywords: population dynamics; density-dependence; trophic interactions; tannins; intraspecific competition; ballooning

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CHAPTER 1

DENSITY-DEPENDENT SURVIVAL IN THE LARVAL STAGE OF AN INVASIVE INSECT: DISPERSAL VS. PREDATION

1.1 Introduction

Human activity has resulted in the purposeful or accidental introduction of non-native species worldwide, some of which reach far higher densities in their introduced range than in their native range (Mack *et al.* 2000). This phenomenon is commonly considered to be due to the removal of mortality from natural enemies that regulate densities of the species in its native range, and is known as the enemy release hypothesis (Keane & Crawley 2002). This hypothesis is based on the assumption that most species are regulated by top-down factors such as predators, disease, or parasitoids in their native range, and implies that such species are more likely to be regulated by bottom-up factors in their introduced range. The lack of top-down control for invasive species has been a central justification for the introduction of non-native natural enemies for biological control (Van Driesche *et al.* 2010), and an abundance of clear cases of thorough control of invasive pest species after the introduction of natural enemies from their region of origin – particularly by specialist parasitoids – exist [*e.g.*, the control of red scale (*Aonidiella aurantii* Maskell [Diaspididae]) on citrus by *Aphytis* spp. (Murdoch 1994) and winter moth (*Operophtera brumata* L. [Geometridae]) by *Cyzenis albicans* Fall. (Tachinidae) and *Agrypon flaveolatum* Gravenhorst (Ichneumonidae) (Roland 1994; Roland & Embree 1995)]. These successes have helped lead to a general hypothesis that populations of insect herbivores are regulated by specialist parasitoids (*e.g.*, Berryman 1996, 2002). However, the evidence that parasitoids drive population dynamics of native

insect species, especially cyclic dynamics, and that the enemy release hypothesis is a primary driver of invasiveness is inconsistent (*e.g.*, Rosenheim 1998; Myers & Cory 2013 for the role of specialist parasitoids, and Colautti et al. 2004 for the importance of the enemy release hypothesis). This suggests that such assumptions about how populations are regulated are often oversimplified, or apply to some species and not others.

Forest Lepidoptera are a group that has been intensively studied with regards to identifying factors that are important drivers of insect population dynamics (Myers 1988; Myers & Cory 2013), and studies on winter moth and autumnal moth (*Epirrita autumnata* Borkh.[Geometridae]) in particular illustrate the complexity of the issue well. For example, ten-year cyclic outbreaks of these geometrids in Fennoscandia have alternatively been proposed to be driven by delayed density-dependent mortality from specialist parasitoids (Tanhuanpää *et al.* 2002; Klemola *et al.* 2010), or by delayed induced resistance of host plants (Haukioja & Neuvonen 1987). Delayed induced resistance has not been supported as an explanation for geometrid cycles in more recent work (Haukioja 2005; Myers & Cory 2013), while the role of predators and parasitoids has accumulated evidence but remains controversial (Schott *et al.* 2012; Myers & Cory 2013). In a manipulative study, Klemola *et al.* (2010) found that exclusion of parasitoids resulted in continuing growth of a population of outbreaking autumnal moths in Finland, whereas Schott et al. (2010) found no relationship between parasitism rate and population growth rate in winter moth and autumnal moth populations in a spatiotemporally extensive observational study in coastal Norway. Similarly, some work has suggested that variation in generalist predator communities can influence the propensity of winter and autumnal moth to outbreak (Tanhuanpää *et al.* 1999;

Raymond *et al.* 2002), but other work has found no such relationship (Hansen, Ims & Hagen 2009; Schott *et al.* 2013). Despite decades of work on these species, beginning with classic work by Varley & Gradwell (1968) and Feeny (1970), a clear explanation of the factors driving winter or autumnal moth population dynamics remains elusive.

One aspect of winter moth population dynamics that has rarely been directly investigated but holds potential significance is larval dispersal. Dispersal has been considered a process of central importance in population dynamics, but as in the case of winter moth, historically has been less studied than other regulatory factors (Taylor 1990; Cappuccino 1995). Density-dependent dispersal occurs in insects (Denno *et al.* 1991; Berger 1992; Denno & Peterson 1995; Herzig 1995; Fonseca & Hart 1996; Rhainds, Gries & Chew 1997; Rhainds *et al.* 2002), as well as a broad variety of other taxa (Lambin, Aars & Piertney 2001). In insects, density-dependent dispersal has been especially well documented in sap-feeding insects, especially in the orders Hemiptera and Thysanoptera (Denno & Peterson 1995), but less so in Lepidoptera or other chewing insects (Morris & Mott 1963; Lance & Barbosa 1979; Berger 1992; Rhainds, Gries & Chew 1997; Rhainds *et al.* 2002).

Lepidopteran species commonly disperse as early instar larvae by ballooning on silken threads with wind currents that transport them to new host plants (Bell *et al.* 2005). This seems to be especially common in species with wingless females, at least among Geometridae and Lymantriinae within Erebidae (Roff 1990; Hunter 1995; Bell *et al.* 2005). Passive dispersal strategies like ballooning can lead to heavy mortality, since the ability of larvae to land on a suitable host is largely due to chance (Cox & Potter 1986; Terry, Bradley & Duyn 1989). For such behavior to occur, it is expected that the possible benefits of

dispersal must outweigh the costs. Evolutionary models predict that dispersal can increase individual fitness when competition for resources is sufficiently high in the potential disperser's high density local population, even if dispersal carries a high risk of mortality (Travis, Murrell & Dytham 1999).

Winter moth is a polyphagous geometrid moth species with one generation per year, with flightless adult females and winged adult males that emerge, mate, and lay their eggs on the bark of host plants in the late fall and early winter. The larvae hatch in early spring and disperse by ballooning onto opening buds of deciduous trees and feed on young leaf tissue (Embree 1965; Varley & Gradwell 1968). Mortality at this initial dispersal stage, if hatch is not closely synchronized with budburst, has widely been considered to be an important factor that affects population fluctuations in winter moth (Embree 1965; Varley & Gradwell 1968; Holliday 1977; Wint 1983; Hunter 1992; van Dongen *et al.* 1997; Visser & Holleman 2001; Tikkanen & Julkunen-Tiitto 2003) and other spring-feeding lepidopteran populations (Feeny 1970; Hunter & Elkinton 2000; Jepsen *et al.* 2009), although there is some evidence to the contrary (Hunter, Watt & Docherty 1991; Dewar & Watt 1992; Kerslake & Hartley 1997). Some authors (Embree 1965; Varley & Gradwell 1968) have suggested that dispersal of winter moth larvae occurs only immediately after hatch, but Edland (1971) showed that winter moth larvae can continue to balloon through the second instar. The possibility of population-level effects from larval dispersal after the beginning of feeding has so far remained unexplored.

In the present study, we investigated the importance of larval dispersal to winter moth population dynamics in New England, where winter moth has been present as an outbreaking

invasive species since at least the early 1990s, at times causing severe defoliation (Elkinton *et al.* 2010). Long term monitoring in New England years (J. S. Elkinton & G. H. Boettner, unpublished data) has found larval densities much higher than previous studies in other locations (Embree 1965; Varley & Gradwell 1968), along with strongly density-dependent mortality during the larval stage. Mortality during the larval stage appears to be the main factor affecting variation in population size between years. To investigate the causes of density-dependent declines in population density during the larval stage of winter moth, we measured density declines due to dispersal, predation, parasitism and disease in the field, and dispersal and cannibalism in the laboratory. We also examined the response of larval dispersal to density of conspecifics, and foliar quality of host plants.

1.2 Materials and methods

1.2.1 Laboratory manipulation of winter moth larval density

To assess the presence of different causes of mortality of early instar winter moth larvae across a range of densities, we conducted laboratory rearing experiments. Winter moth adults reared from June 2013 and 2014 collections of larvae on Vancouver Island in British Columbia, Canada, were bred in the laboratory, and resulting eggs were used for rearing experiments (all other experiments were conducted with larvae from Massachusetts, USA). To create a range of densities, eggs were counted into groups of 5, 10, 20, 40, and 80 and were stored at 1 °C. These reflect the natural range of densities found in individual buds in Massachusetts. During spring 2014 and 2015, eggs were warmed for five days at 20 °C until they turned blue, signifying imminent hatch. Counted groups of eggs were then attached to twigs with a single developing bud using a small piece of marking tape placed in plastic

containers (drink cups, 8 cm diameter top x 15 cm depth, Fabri-Kal, Kalamazoo, MI, USA) and ventilated with fine mesh. Twenty replicate containers of each density treatment were set up, except for the 5 egg treatment which had 40 replicates. Containers were kept at 20 °C under 14 hrs per day of artificial light. Twigs of red oak (*Quercus rubra* L.), red maple (*Acer rubrum* L.), and apple (*Malus domestica* L.) were collected from Amherst, Massachusetts, when buds had expanded sufficiently to expose green tissue and were thus available for winter moth larvae to enter and feed . Twigs were placed in cups and were embedded in moist plaster of Paris (for the apple trials) or set in water with a layer of paraffin wax solidified on the surface, to hydrate twigs and prevent death of larvae by drowning.

For each container, number of eggs hatched, live and dead larvae, head capsules, and location of larvae in buds or on container sides was recorded. This information was recorded for half of the containers after a period of five days following the point at which >80% of larvae had hatched, and for the second half at seven days (red oak and red maple trials) or 10 days (apple trial) after >80% hatch. Number of head capsules was used to assess cannibalism; presence of detached head capsules above the number of second instar larvae (each of which would leave a head capsule from molting) was considered to be evidence of cannibalism. The location of dead larvae was used to assess the dispersal rates of larvae. Proportion of surviving larvae relative to initial density and host species was analyzed with logistic regression using a quasibinomial distribution to correct for overdispersion.

1.2.2 Field density monitoring

To assess dispersal rates in the field, 20 buds or developing leaf clusters were collected weekly from each of 5 apple, 11 red maple, and 13 red oak trees (total N=29)

spread across four sites in eastern Massachusetts [West Bridgewater (42.021916, -70.982450); Hanson (42.049473, -70.8730180; 42.060583, -70.843865); Freetown (41.794359, -71.053035)] from April 21 until June 6 in 2014. The same sample trees at the same sites along with two additional red oak and red maple sample trees at Freetown (total N=33) were sampled from April 25 until May 31 in 2015. Each leaf cluster was dissected, and the number of live or dead winter moth larvae, the instar of each larva was recorded. To assess defoliation, thirty leaves collected from sample trees on 6 June 2014 and 31 May 2015 were scored by visual estimation into 10 defoliation classes, from 0% to 100% defoliated. An additional two to four bud or leaf clusters in 2014 were collected at every sample tree and date, and brought back to the laboratory and frozen at -20° C for subsequent chemical analysis. In 2015, pooled leaf material from 20 buds or leaf clusters from each sample tree that had been collected for density counts was frozen at -80° C for chemical analysis.

To assess the relationship between density and dispersal, a period of the larval stage within which to measure declines in density was identified. Density of larvae in buds climbs at the beginning of the season as larvae hatch, and as buds develop sufficiently for larvae to enter. Towards the end of the larval stage the number of larvae per leaf cluster decline as larvae drop off of foliage to pupate in the soil beneath the host tree. Therefore data from the beginning and end of the larval stage was not considered (*i.e.*, after May 16 2014 and May 15 2015) in our analyses. To determine the beginning of the period within which to measure dispersal, first, average larval densities per bud cluster for each week were calculated. Second, the date of peak average larval density for the majority of sample trees of each host species was determined (In 2014, this was May 3 for red maple and red oak and was April 27 for apple. In 2015 this was May 1 for all tree species). Third, the proportion of larvae

remaining was measured as a proportion of total larval count from 20 leaf clusters from each tree on a date before pupation (May 16 2014 and May 15 2015), out of the total initial (peak) larval count from that tree. Some sample trees had more larvae in samples before pupation than at the initial larval count. These results were likely due to sample error, and from the delayed phenology of a few sample trees that delayed the entry of larvae into buds until after the dates used to assess initial densities. These counts (N=6 in 2014, N=10 in 2015) were changed to the same value as the initial counts for those sample trees. Dispersal rates of winter moth larvae in response to initial density and tree species of each sample tree was analyzed using a logistic generalized mixed model (Bolker *et al.* 2009). Site was included as a random effect, and an observation-level random effect (sample tree) was also included in the model to account for overdispersion (Elston *et al.* 2001; Browne *et al.* 2005; Harrison 2014).

1.2.3 Early larval dispersal manipulation and predator exclusion

To experimentally assess the relative importance of predation and dispersal in observed declines of early instar winter moth larvae in the field, we set up a predator exclusion and dispersal manipulation experiment in May 2015. This was conducted on trees along a gas pipeline right-of-way at Freetown-Fall River State Forest in Freetown, Massachusetts, with natural populations of first and second instar winter moth larvae in May 2015. Twenty pairs of buds were manipulated in either of two treatments on each of 10 red oak trees on May 2, approximately at peak larval densities. The ‘no dispersal or predation’ treatment (N=100) consisted of cloth bags designed to prevent larval dispersal and predation. The ‘dispersal only’ treatment consisted of 30 μm mesh bags designed to allow most first and

second instar larvae to disperse but to prevent most predation. A 30 μm size limit would exclude most predaceous insects including ants, wasps and predacious beetles. After six days manipulated buds and 10 pairs of unmanipulated (control) buds from each sample tree were collected for dissection (total N=300). Differences in final larval densities by treatment were analyzed using a Poisson generalized mixed model, with treatment by sample tree as a random effect, and an observation-level random effect (clusters of two buds) to account for overdispersion.

1.2.4 Late larval predator exclusion

To assess the predation rates on late instar winter moth larvae in the field, predator exclusion manipulations were conducted at Freetown-Fall River State Forest May 2013 and 2014, with natural populations of fourth and fifth instar winter moth larvae. Red oak trees were selected, and the number of larvae and leaf clusters on a single section of branch per tree were counted *in situ*, and one of three treatments were applied: no predation, no avian predation, and a control treatment. The ‘no predation’ treatment consisted of a fine mesh bag (silk screening mesh, 10 μm mesh) which was intended to exclude all predation and prevent larval dispersal. The ‘no avian predation’ treatment consisted of a wire tomato hoop encased in coarse mesh (bird netting, 1.5 cm mesh) intended to allow larval dispersal and invertebrate predation but to prevent avian predation. The control treatment consisted only of a wire tomato hoop, which allowed larval dispersal and all predation. Replicates (2013, N=59; 2014, N=45) were grouped into blocks of three with one tree randomly assigned to each treatment. After six or seven days, leaf clusters from treated branches were removed, taken to the laboratory and frozen, and the number of larvae per branch counted. The proportion

surviving was compared across treatments in a logistic generalized mixed model with block as a random effect to account for spatial non-independence. Similar to the field monitoring of larval density, some sample branches had more larvae per branch at final count than at the initial count; such differences were assumed to be due to sample error or undercounting of initial densities, and these counts (2013, N=33; 2014, N=11) were adjusted to the same value as the initial counts for that sample branch.

1.2.5 Larval dispersal from defoliated leaves

To assess the effects of previous damage to foliage on larval dispersal rates, during May 2013-2015, foliage was collected haphazardly from red maple and red oak trees with undamaged leaves, and with foliage previously damaged by naturally occurring winter moth herbivory, and was placed in moist floral foam in mesh ventilated 19 liter buckets, separated by tree species (see Table 1.1 for details of experimental design including sample sizes). Late instar larvae were collected from the field and placed on foliage in each bucket. Every 24 hours, the numbers of larvae on the side, bottom, or lid of the bucket were counted, and the larvae returned to the foliage. The proportion of dispersing larvae was then compared across treatments using logistic generalized mixed models, with bucket as a random effect to account for non-independence due to repeated measurements of individual buckets in 2013 and 2014, and year as a random effect in the overall model of all years.

1.2.6 Foliar quality

To determine the relationship between foliar quality and larval dispersal rates in the field density monitoring experiment, samples collected from sample trees one week after peak larval density were analyzed for multiple aspects of foliar quality. Phenolic content,

oxidative phenolics, nitrogen content, and carbon content from May 11 2014 samples and the same data plus trichome density from May 8 2015 samples were measured, as follows: leaves for chemical analysis were freeze-dried and ground with a mortar and pestle. Total foliar phenolics and the proportion of oxidative phenolics were analyzed using a modified Folin-Ciocealtea assay following the method of Salminen & Karonen (2011) using absorbance measurements from a microplate reader (Spectramax M2, Molecular Devices, California, USA). Total phenolics were calculated using gallic acid standards and species-specific phenolic standards from Sephadex LH-20 gravity column chromatography (Sephadex LH-20, GE Healthcare Bio-Sciences, Pennsylvania, USA), also after Salminen and Karonen (2011). Proportion of oxidative phenolics measurements were read from extracts diluted to 1.0 ± 0.3 mg/ml gallic acid equivalents (due to difficulties with precise dilution). Total oxidative phenolics were calculated as the product of the proportion of active phenolics and total phenolic content. Total nitrogen and carbon analysis of 5 mg of leaf material was conducted with a combustion analyzer (ECS 4010, Costech Analytical Technologies, California, USA) using acetanilide standards. Phenolic, nitrogen, and carbon measures were obtained from a single pooled sample for each sample tree that consisted of two to six leaf clusters per tree in 2014 and 20 leaf clusters in 2015. Trichome density was measured using the average number of trichomes intersecting a 1 mm line on 20 leaves from each sample tree. Measures of foliar quality in each year by sample tree and tree species were analyzed for their effect on larval survival in logistic generalized mixed models with site-level and observation-level random effects.

1.2.7 Statistical analysis

All statistical analysis was conducted in R (R Core Team 2013, version 3.02). Mixed models were run using the lme4 package (Bates *et al.* 2014), and significance tests of mixed models were made using parametric likelihood ratio bootstrap tests with the function PBmodcomp from the package pbrtest (Halekoh & Højsgaard 2014), except for the early larval dispersal manipulation predation exclusion experiment, for which Wald chi-square tests were used to calculate p-values because of model convergence failure with PBmodcomp. Marginal (fixed effects, R^2_m) and conditional (fixed and random effect, R^2_c) coefficients of determination were calculated for mixed models using the function rsquare.GLMM from the package MuMIn (Nakagawa & Schielzeth 2013). Plotting was implemented in R using the ggplot2 package (Wickham 2009).

1.3 Results

1.3.1 Laboratory density manipulation

In the laboratory experiments, larval survival in cup trials significantly decreased with increasing log conspecific density (log odds $\beta = -0.022$, $\chi^2 = 208.1$, $P < 0.001$, Fig. 1.1), and differed by tree species ($\chi^2 = 36.2$, $P < 0.001$). Mortality was almost entirely due to starvation after dispersal: 97.2% of recovered dead larvae had crawled out of buds and died on the inside of the cup. In all laboratory trials, there was negligible evidence of cannibalism. Less than 10% of the cups had any evidence of cannibalism, and even in those cups mortality due to cannibalism was not the main cause of mortality.

1.3.2 Field density monitoring

In the field, proportion of larvae remaining on sample trees decreased significantly with increasing initial density in both years (2014: log odds $\beta=-1.113$, $\chi^2=9.3$ $P=0.008$, $R^2_m=0.122$, $R^2_c=0.102$, 2015: log odds $\beta=-1.461$, $\chi^2=23.2$, $P=0.001$, $R^2_m=0.123$, $R^2_c=0.123$, Fig. 1.2), and differed significantly between tree species (2014: $\chi^2=18.4$, $P=0.003$, 2015: $\chi^2=14.2$, $P=0.001$, Fig. 1.2).

From samples collected in field density monitoring, the percent of dead larvae in leaf samples peaked on April 22 (22%) in 2014 and May 1 (3%) in 2015 and decreased as the season progressed (Fig. 1.3). Most dead larvae were neonates that failed to establish in buds. No ectoparasitoids or visible endoparasitoids were observed in any larvae, and no adult parasitoids emerged.

At the end the feeding season, defoliation, as measured by the logit-transformed proportion eaten of sample tree leaves was more closely related to peak densities than to pre-drop densities in 2014, though significantly related to both (May 3 2014 density: $AIC_c=102.90$, $F_{1,23}=11.03$, $P=0.003$, May 16 2014 density: $AIC_c=67.78$, $F_{1,23}=107.5$, $P<0.001$, Fig. 1.4). In 2015, neither peak nor pre-drop density was significantly related to defoliation, and neither was a better predictor than the other (May 1 2015 density: $AIC_c=60.68$, $F_{1,23}=0.0003$, $P=0.965$, May 15 2015 density: $AIC_c=60.53$, $F_{1,23}=0.59$, $P=0.450$, Fig. 1.4). An interaction between tree species and density was included in the defoliation models.

1.3.3 Early larval dispersal manipulation and predator exclusion

Larval densities significantly different between the no dispersal or predation, dispersal only, and control treatments ($\chi^2=53.7$, $P<0.001$, Fig 1.5). The no dispersal or predation treatment (cloth bags) had the highest mean densities (8.9 ± 0.45 larvae per two buds), the dispersal only treatment (mesh bags) had intermediate densities (5.1 ± 0.79 larvae per two buds), and the control treatment (unbagged) had the lowest densities (2.5 ± 0.26 larvae per two buds).

1.3.4 Late larval predator exclusion

Over both years of the larval predator exclusion experiment, there was no significant difference in larval survival between the no predation, no avian predation and control treatments (2013: $\chi^2=2.762$, $P=0.243$; 2014: $\chi^2=0.781$, $P=0.623$; Fig. 1.6), and overall larval survival was quite high (2013: $80.4\% \pm 3.9\%$; 2014: $71.8\% \pm 3.7\%$).

1.3.5 Larval dispersal from defoliated leaves

In the combined analysis of all trial of the larval dispersal from defoliated leaves experiments, the rate of larval dispersal was significantly elevated on defoliated leaves, with 35% more larvae dispersing per day from defoliated foliage ($\chi^2=20.10$, $P=0.001$), with no difference between tree species ($\chi^2=0.46$, $P=0.528$). All four trials showed the same trend (Fig. 1.7), though there were differences in significance level between individual trials (Table 1.1).

1.3.6. Foliar quality

Proportion of oxidative phenolics and derived measures (ox. phenolics x gallic acid equivalent phenolics, ox. phenolics x self standard equivalent phenolics) were significantly related to proportion of remaining larvae in 2015, but not in 2014, although the fitted effects in both years were negative (Table 1.2, Figure 1.8). None of the other measures of foliar quality were significantly related to larval survival (Table 1.2).

1.4 Discussion

We hypothesize that *ex-situ* mortality after density-dependent dispersal represents the major cause of mortality during the winter moth larval stage, because of the strong density-dependent dispersal of early instar larvae in the field, the dispersal behavior of larvae in the laboratory, and the increase in densities when dispersal is prevented in the field. We also hypothesize that larval dispersal is mediated by host plant quality, specifically phenolic oxidative capacity, based on the response of larval dispersal to damaged foliage, and the relationship between the phenolic oxidative capacity of host tree foliage and larval dispersal rates in the field. Though the evidence is not unequivocal, our results are the first to suggest a negative relationship between larval performance and pH 10 phenolic oxidative capacity as measured using methods from Salminen and Karonen (2010).

As with most other work on the population-level effects of insect dispersal, we are unable to account for the fate of larvae after they disperse. Dispersal may not necessarily constitute mortality, as we have suggested. However, since the combined average population density of all sample trees declined after the week in which most dispersal occurred (Fig. 1.2; May 3-11 2014 & May 1-8 2015), it does not appear that dispersal simply represents the

redistribution of spatially heterogeneous population density to a more even distribution, but that dispersal causes some localized regulation of larval densities on high density trees through mortality of larvae occurring likely as a result of starvation or predation after dispersal.

In previous work on the larval stage of winter moth in Nova Scotia, Embree (1965) suggested that larval survival increased with density at lower densities and decreased with density at higher densities. He speculated that the former was due to saturation of avian or other predators and the latter was due to either starvation or other aspects of larval competition. Our findings are consistent with these higher density effects, though our results suggest that mortality occurs mainly due to larval dispersal and not *in-situ* starvation, since larvae disperse well before resource limits are reached. Although starvation may occur after larvae disperse, it does not appear to drive the decision to disperse. In contrast to Embree (1965), we found no evidence of increasing survival with density at lower densities, and also found little evidence of direct starvation, except on two apple trees that were completely defoliated in 2014. Our findings confirm that winter moth in North America does undergo density-dependent larval survival, but most likely due to dispersal.

The lack of differences in survival of late instar larvae predator exclusion treatments and controls show that predators have little impact in winter moth populations, and that top-down regulation by predation is probably not an important cause of larval mortality for outbreak populations of winter moth in North America. This finding is consistent with those of Embree (1965). Roland, Hannon & Smith (1986) observed density-dependent predation by a flock of pine siskins (*Spinus pinus* Wilson) on a population of winter moth. However, they argued that bird predation was unlikely to be an important regulator of winter moth density,

due to the inconsistent presence of bird predators, and the lack of any numerical response by birds to the presence of a winter moth food resource due to territorialism. The lack of a numerical response as well as habitat requirements of nesting birds other than food availability are probably what resulted in low rates of predation in our studies.

The significant larval mortality in outbreak populations of winter moth presented here contrasts with those of low-density populations. Multiple studies including classic work by Varley and Gradwell (1968) in England and by Roland (1994) in British Columbia, Canada, provide substantive evidence that low-density populations of winter moth are regulated by density-dependent predation by pupal predators. Our results are consistent with those of Holliday (1977), who showed that there was negligible mortality of winter moth during the larval stage of winter moths in a low density population on apples in England. We also observed virtually no change in density over the larval stage on sample trees with low densities of larvae (Fig 1.2). In contrast, when densities were high, we observed a large drop in larval density of the early instars, presumably due to dispersal.

The intermediate densities in the fine mesh bag treatment in the early larval dispersal manipulation and predation exclusion experiment, could indicate that predation occurs on early larval instars alongside dispersal. However, the fine mesh in that treatment was designed to exclude nearly all invertebrate predators such as ants or predatory wasps, but to allow at least some dispersal, particularly of first and second instar winter moth larvae. It seems likely that the fine mesh reduced dispersal because larvae attempting to leave the buds would have been intercepted by the mesh bags. This probably explains why the densities in that treatment were higher than on the unbagged branches. In other words the mesh bags likely reduced the amount of dispersal, though not as much as cloth bags. In addition, since

we have shown that there is negligible predation on late instar larvae through a lack of an increase in survival from predator exclusion treatments in the late larval predator exclusion experiment, it seems unlikely that there would be significant predation on early instar larvae given that later instars would probably be more desirable to most predators, especially large predators such as birds.

The absence of parasitism or other mortality in later instars in the field monitoring samples reflects the fact that winter moth lacks parasitoids and pathogens with significant population-level impacts in New England releases (J. S. Elkinton & G. H. Boettner, unpublished data). The complete absence of larval parasitoids in these samples is consistent with the results of long term population and biological control release monitoring collections from 2004 to present in New England, except where the tachinid parasitoid *C. albicans* has been established from releases (J. S. Elkinton & G. H. Boettner, unpublished data). European populations of winter moth by contrast are attacked by as many as 18 species of parasitoids (Vindstad *et al.* 2013). Winter moth in North America, as a new invader, is similar in this respect to the geometrid *Agriopsis aurantiaria* Hübner, which has recently invaded northern Fennoscandia, where it has only one larval parasitoid (Vindstad *et al.* 2013). It is possible that it takes several decades at least for native (generalist) parasitoids to adapt to a novel invader, which might explain the complete absence of larval parasitoids of winter moth in New England.

Similarly, mortality from disease is negligible (H. J. Broadley, J. S. Elkinton and J. P. Burand, unpublished data). Few larvae die of any cause during mass rearing for biological control release monitoring (2013: 1.1%, 2014: 3.2%, from numbers of cadavers found in rearing containers, H. J. Broadley, J. S. Elkinton and J. P. Burand, unpublished data). Of

those, only some are infected with disease. The 28% infection rate of larvae by *O. brumata* nucleopolyhedrovirus reported by Burand et al. (2011) represents the proportion of larvae infected out of the number of larvae that had died in rearing; although percent larval mortality in rearings were not recorded for the years of that study, they were likely also very small. Disease mortality in winter moth is almost always far less than that observed with many other forest Lepidoptera, such as gypsy moth, *Lymantria dispar* L. (Elkinton & Liebhold 1990), or the western tent caterpillar, *Malacosoma californicum* Packard (Myers & Cory 2013).

Even in the absence of any apparent regulation from disease, parasitism, or predation, complete defoliation by winter moths of red oak and red maple trees is rare in New England (J. S. Elkinton & G. H. Boettner, unpublished data), and was also rare for Garry oaks (*Quercus garryana* Douglas ex Hook) in British Columbia before the release of biological control agents there (Roland & Myers 1987). This pattern holds even if the larvae establish at high densities at the beginning of the feeding season, and may be a result of early instar larval dispersal in response to high densities of conspecifics even when there is still abundant foliage available. Defoliation is commonly used as an index of larval densities in many studies of forest defoliators (e.g., Liebhold *et al.* 1995), but in the present case density-dependent dispersal behavior weakened the relationship between peak larval densities and defoliation levels in 2014, and there were no relationships between either peak or pre-drop larval densities and defoliation in 2015. This illustrates the significant effect of larval dispersal behavior on the level of damage caused by winter moths.

The choice by larvae to disperse can confer a fitness advantage if the risk of mortality from remaining is sufficiently high relative to the likelihood of finding a suitable host (Travis *et al.* 1999). Dispersal behavior would seem likely to result in larval densities tracking host plant carrying capacity, as has been observed in some other herbivores (Cappuccino 1995; Solbreck 1995). However, in this case the tracking of host plant carrying capacity is clearly imperfect, because very often there is only moderate defoliation at the end of the feeding season on trees that experience high dispersal rates. This suggests that dispersal may in part be caused by reduced host plant quality induced by damage from high herbivore densities, a process that has precedence with other cases of density dependent dispersal in insects (Denno & Peterson 1995). The larval dispersal from defoliated leaves experiment, together with oxidative phenolics data, provide evidence that winter moth larval dispersal may be indeed be mediated by induced host plant defense, although proportion of oxidative phenolics was only related to larval survival rates in 2015 and not 2014.

The role of phenolics (specifically tannins) in plant-herbivore interactions has been the subject of a long and contradictory string of research. For example, Feeny (1970) suggested that the spring feeding habit of winter moth evolved to avoid the increasing content of condensed tannins in developing oak leaves, and Schultz & Baldwin (1982) showed that feeding by gypsy moths on oaks caused induction of tannins and suggested that larval growth might be affected. Such early work assumed that the primary function of tannins was herbivore resistance through protein precipitation, a mechanism which was not consistently found to effect herbivores (Ayres *et al.* 1996). More recent work by Appel (1993) and Salminen & Karonen (2011) has suggested that tannins may have anti-herbivore effects through oxidative activity in high pH guts (*i.e.*, most insect herbivores) and protein

precipitation in low pH guts (*i.e.*, mammalian herbivores). The present study, to the authors' knowledge, is the first to show evidence suggestive of anti-herbivore effects from the oxidative capacity of phenolics in foliage.

Previous work has suggested that the winter moth parasitoid *C. albicans* responds to winter moth-damaged foliage, and it is possible that winter moth larval dispersal has developed as an enemy avoidance response. *C. albicans* lays microtype eggs on the edges of partially defoliated leaves and winter moth larvae become parasitized when they ingest them while feeding. Roland (1986) and Hassell (1968) postulated the existence of a volatile chemical released by winter moth damaged leaves that attracts the flies. Roland (1986) showed that *C. albicans* aggregate to defoliated oak but not apple leaves, and identified the volatile compound borneol in Garry oak foliage to be an attractant for *C. albicans* (Roland, Denford & Jimenez 1995). *C. albicans* was the principal agent responsible for the decline of high density populations of winter moth in Nova Scotia as part of successful biological control program against that species in the 1950s and on Vancouver Island in the 1970s (Roland & Embree 1995). It is possible that the dispersal behavior we have documented in early larval stages at high density evolved to avoid defoliated leaves and thus lessen attack by this parasitoid. If winter moth larvae disperse in response to a chemical signal present in damaged oak but not apple foliage, it could explain the high levels of defoliation found on apple trees and not on oak trees in British Columbia by Roland and Myers (1987) and the lack of heavy defoliation on red oak and red maple in New England. In the present study, complete defoliation was observed only on apple (Fig. 1.4) and never on red oak or red maple.

1.5 Conclusion

Density dependent mortality during the larval stage is the main factor driving variation in winter moth population densities (J. S. Elkinton & G. H. Boettner, unpublished data). If the major cause of winter moth larval mortality is *ex-situ* mortality after the dispersal of early instars in response to conspecific density and oxidative phenolics which our results show, then dispersal mediated by a decline in host plant quality is the main factor regulating winter moth population densities in the absence of its co-evolved natural enemies. Dispersal has not previously been considered a major regulating factor of winter moth population densities, and our present study adds to the growing body of evidence showing that density-dependent dispersal is an important density regulating factor in insect populations (Denno *et al.* 1991; Berger 1992; Denno & Peterson 1995; Herzig 1995; Rhainds *et al.* 1997, 2002). Previous work on winter moth has identified asynchrony of larval hatch with budburst as a major determinant of winter moth population density change (Varley and Gradwell 1968; Embree 1965; Jepsen *et al.* 2009) and dispersal of first instars may be an additional component of this phenomenon. None of these previous studies focused on dispersal *per se* or identified it as being density dependent.

If winter moth larval dispersal is triggered by pH 10 oxidative phenolics as our results suggest then we can conclude that winter moth populations are regulated by a bottom-up process, confirming assumptions of the natural enemy release hypothesis. However, further work, such as laboratory leaf-painting dispersal studies with phenolic extracts of greater or lesser oxidative capacity, would be necessary to conclusively demonstrate that the pH 10 oxidative capacity of foliage is the mechanism that causes winter moth larvae to disperse. In any case, our results provide preliminary confirmatory evidence of the suggestion by

Salminen and Karonen (2011) that the oxidative activity of phenolics in a pH 10 environment is likely to have biologically significant effects on herbivores.

Table 1.1. Experimental design and likelihood ratio parametric bootstrap significance tests for larval dispersal from defoliated leaves experiments. Listed from left to right are trial number, year of trial, length in days of trial, species included in trial, number of buckets in defoliated and undefoliated treatments, total ‘replicates’ included in model of measurements of dispersal rate for each bucket and day, number of larvae placed in each bucket, model results for treatment effects, and model results for tree species effects. P-values in bold are significant to the 0.05 level.

Trial	Year	Length	Species	Defoliated	Undefoliated	N (buckets x days)	Larvae/bucket	Treatment	Tree species
1	2013	2 days	Oak & Maple	12	12	48	25	$\chi^2=5.414$, P=0.035	$\chi^2=0.192$, P=0.666
2	2014	5 days	Oak & Maple	12	12	120	25	$\chi^2=26.332$, P=0.001	$\chi^2=0$, P=1.000
3	2014	6 days	Oak & Maple	12	12	144	25	$\chi^2=9.814$, P=0.004	$\chi^2=0.163$, P=0.711
4	2015	1 day	Oak	24	18	42	20	$\chi^2=0.115$, P=0.757	N/A
							Overall model:	$\chi^2=20.1$, P=0.001	$\chi^2=0.462$, P=0.528

Table 1.2. Year, sample size, slopes, marginal r-squared, condition r-squared, likelihood ratio test chi-squared values, and parametric bootstrap significance tests from models of effects of leaf quality on declines in larval density. P-values in bold are significant to the 0.05 level.

Variable	Year	N	β (log odds)	R ² m	R ² c	χ^2	P
Percent phenolics, gallic acid equivalents	2014	26	-0.021	0.0473	0.0895	8.214	0.658
Percent phenolics, self-standard equivalents	2014	26	-0.009	0.0473	0.0896	8.222	0.699
Proportion oxidative phenolics	2014	22	-1.029	0.0474	0.0689	25.078	0.489
Proportion oxidative phenolics x percent phenolics, gallic acid equivalents	2014	22	-0.024	0.0393	0.0786	24.003	0.566
Proportion oxidative phenolics x percent phenolics, self-standard equivalents	2014	22	-0.013	0.0394	0.0785	24.053	0.558
Percent phenolics, gallic acid equivalents	2015	33	0.020	0.0066	0.0486	0.391	0.574
Percent phenolics, self-standard equivalents	2015	33	0.008	0.0067	0.0479	0.273	0.628
Proportion oxidative phenolics	2015	26	-1.158	0.0310	0.1121	66.674	0.018
Proportion oxidative phenolics x percent phenolics, gallic acid equivalents	2015	26	-0.037	0.0204	0.0834	64.258	0.024
Proportion oxidative phenolics x percent phenolics, self-standard equivalents	2015	26	-0.018	0.0185	0.0814	64.096	0.031
Percent nitrogen	2014	27	-0.407	0.0732	0.1190	1.475	0.225
Percent carbon	2014	27	0.010	0.0664	0.1078	0.015	0.903
Ratio percent carbon: percent nitrogen	2014	27	0.150	0.0763	0.1266	2.247	0.134
Percent nitrogen	2015	24	0.307	0.0333	0.0333	1.070	0.300
Percent carbon	2015	24	0.132	0.0334	0.0334	1.308	0.253
Ratio percent carbon: percent nitrogen	2015	24	-0.065	0.0306	0.0306	0.482	0.488
Trichomes per linear mm	2015	33	-0.025	0.0156	0.0708	2.840	0.092

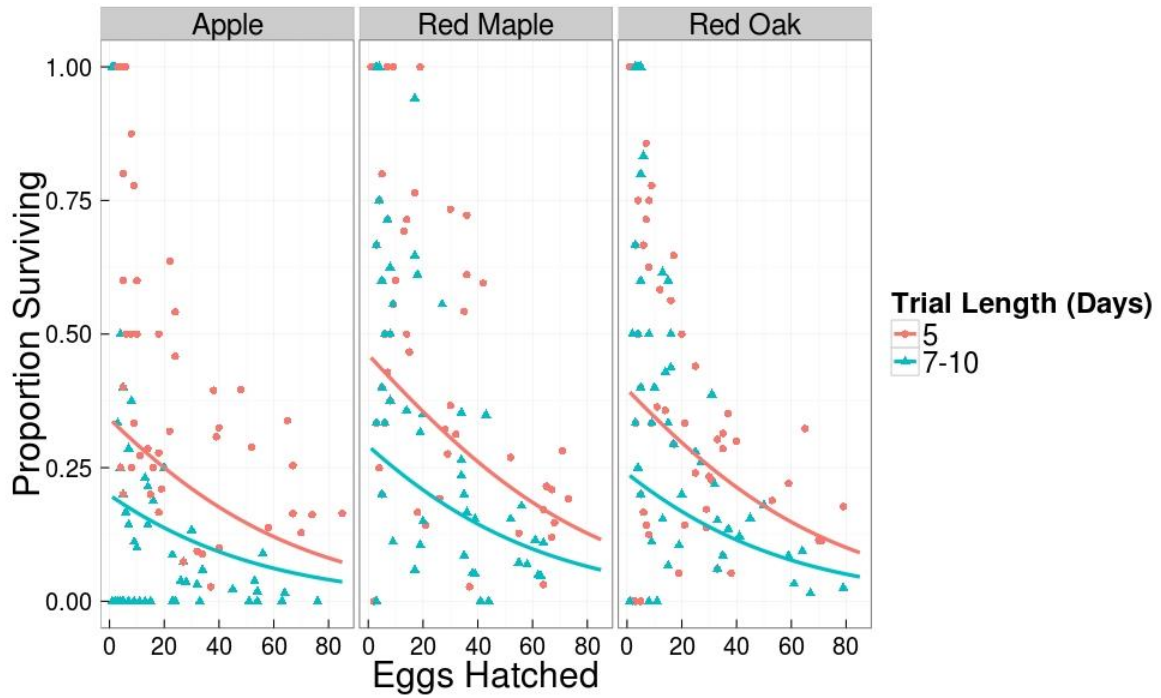


Figure 1.1. Logistic regression of larval survival in each cup by initial number of hatched larvae per cup from the laboratory density manipulation experiment, on three host species, after trial lengths of 5 days, 7 days (red oak and red maple), and 10 days (apple).

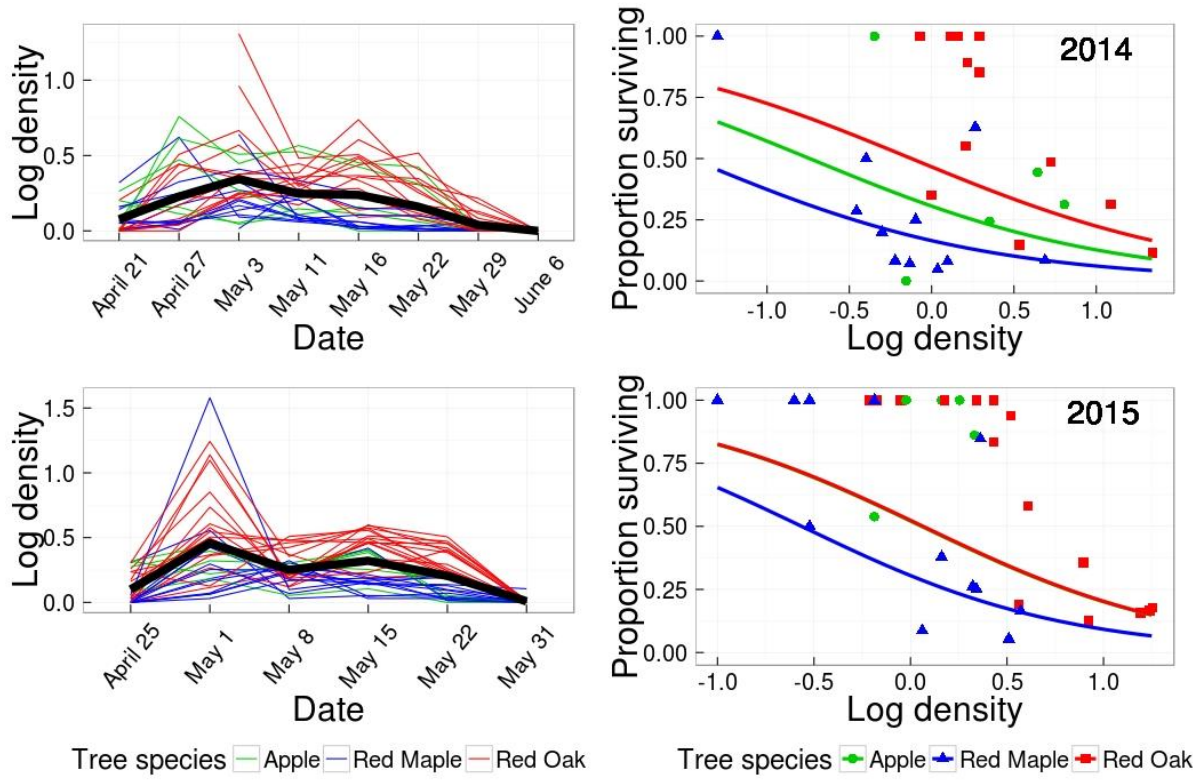


Figure 1.2 Time series of log winter moth larval densities (left) by sample tree (narrow lines) and overall mean (broad line), and predicted proportion of larvae remaining (survival) by density from proportional logistic mixed models of density dependent winter moth larval dispersal (right), in 2014 (top) and 2015 (bottom). Host species are shown by color and line type. In 2015, the apple and red oak regression lines are nearly identical and are overlapping.

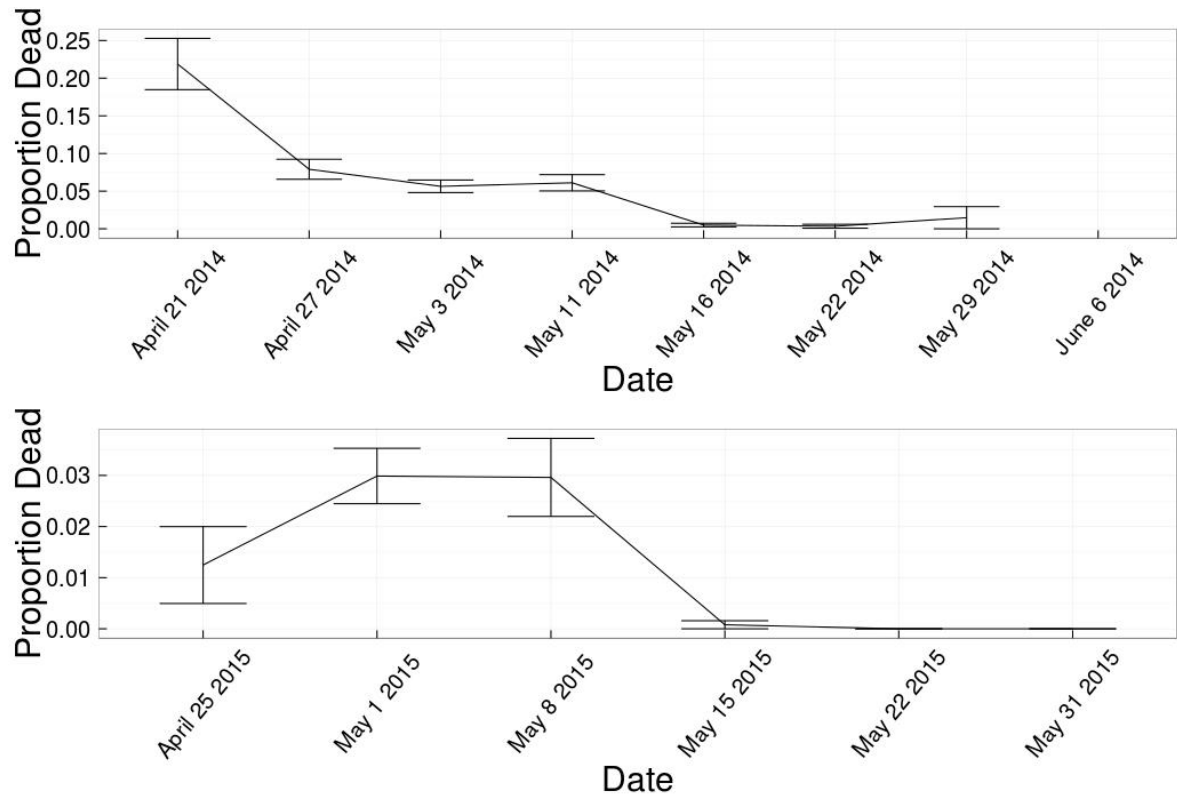


Figure 1.3 Time series of proportion of larvae dead out of total larvae on that sample date from all samples in field monitoring collections in 2014 (top) and 2015 (bottom) with ± 1 standard error. Note difference in y axis scale between years.

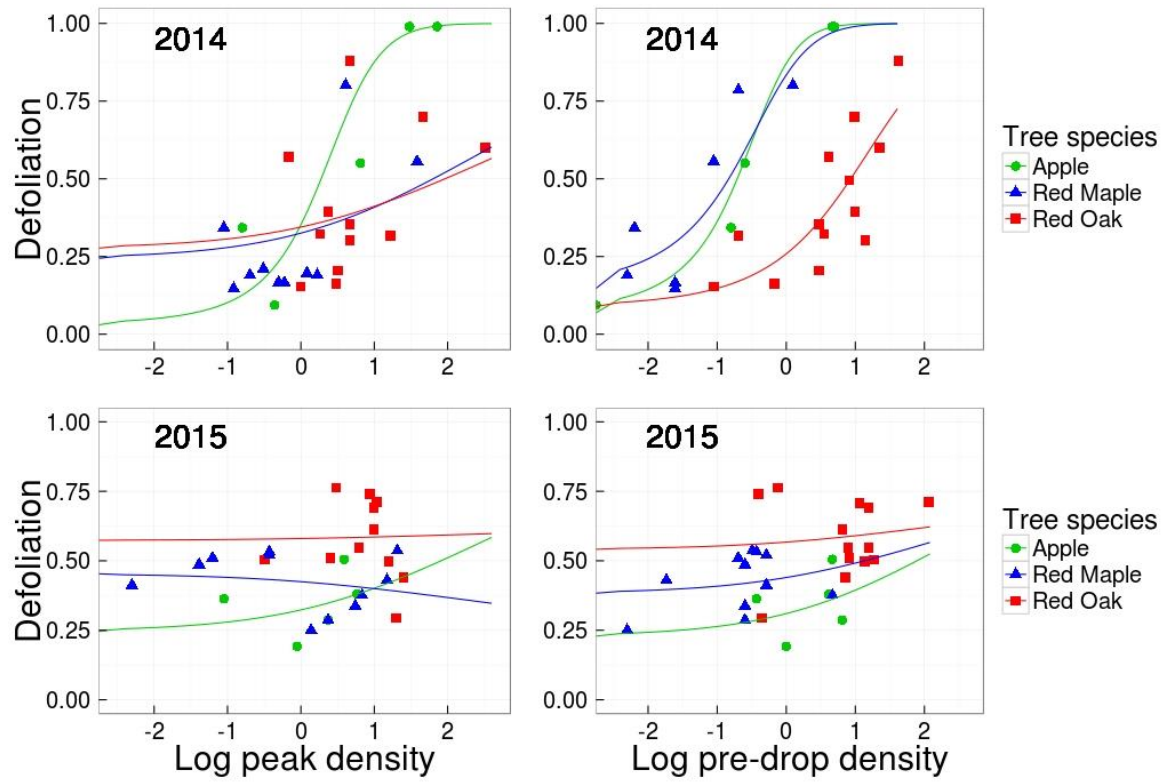


Figure 1.4. Backtransformed linear models of logit proportion defoliated (30 leaves per sample tree), by peak and pre-drop densities (left and right) in 2014 and 2015 (top and bottom).

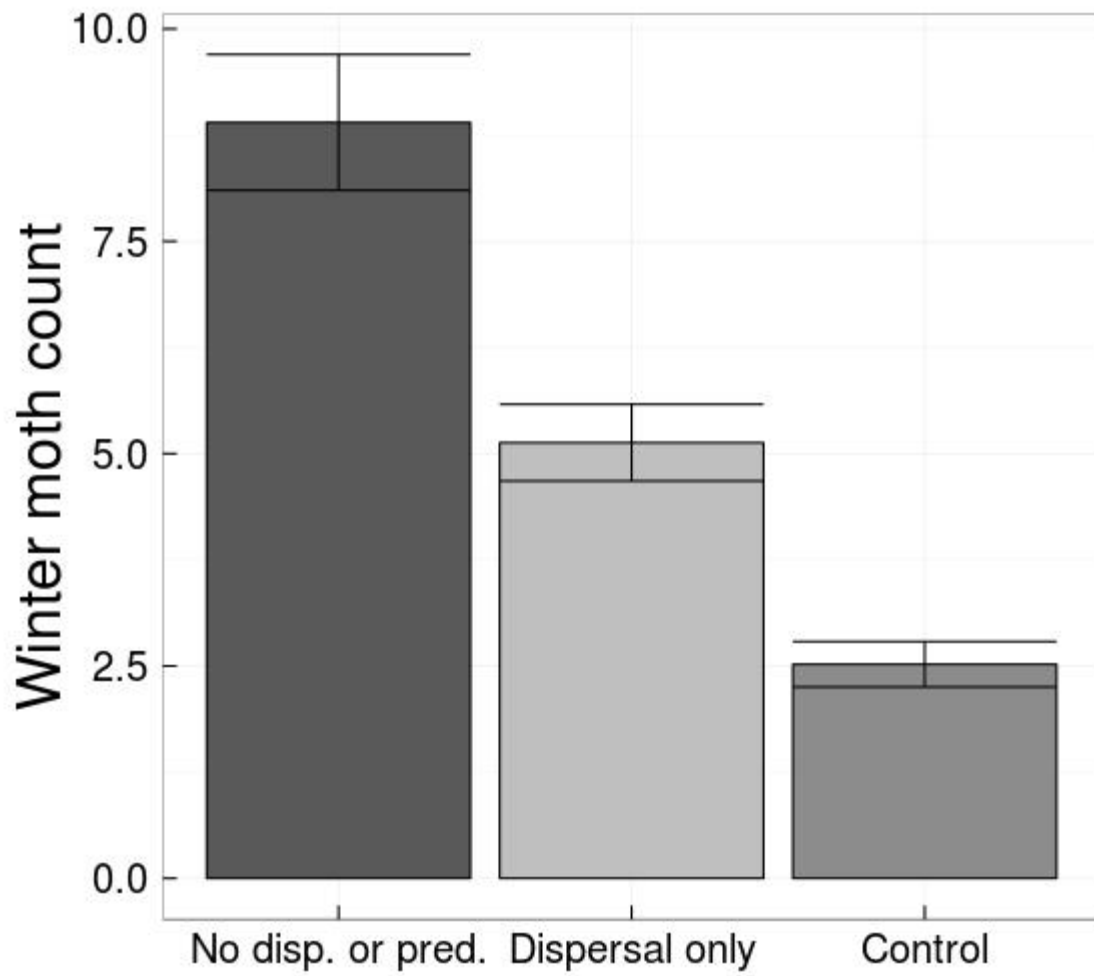


Figure 1.5. Mean and ± 1 standard error by year and treatment of early larval dispersal manipulation and predator exclusion experiment

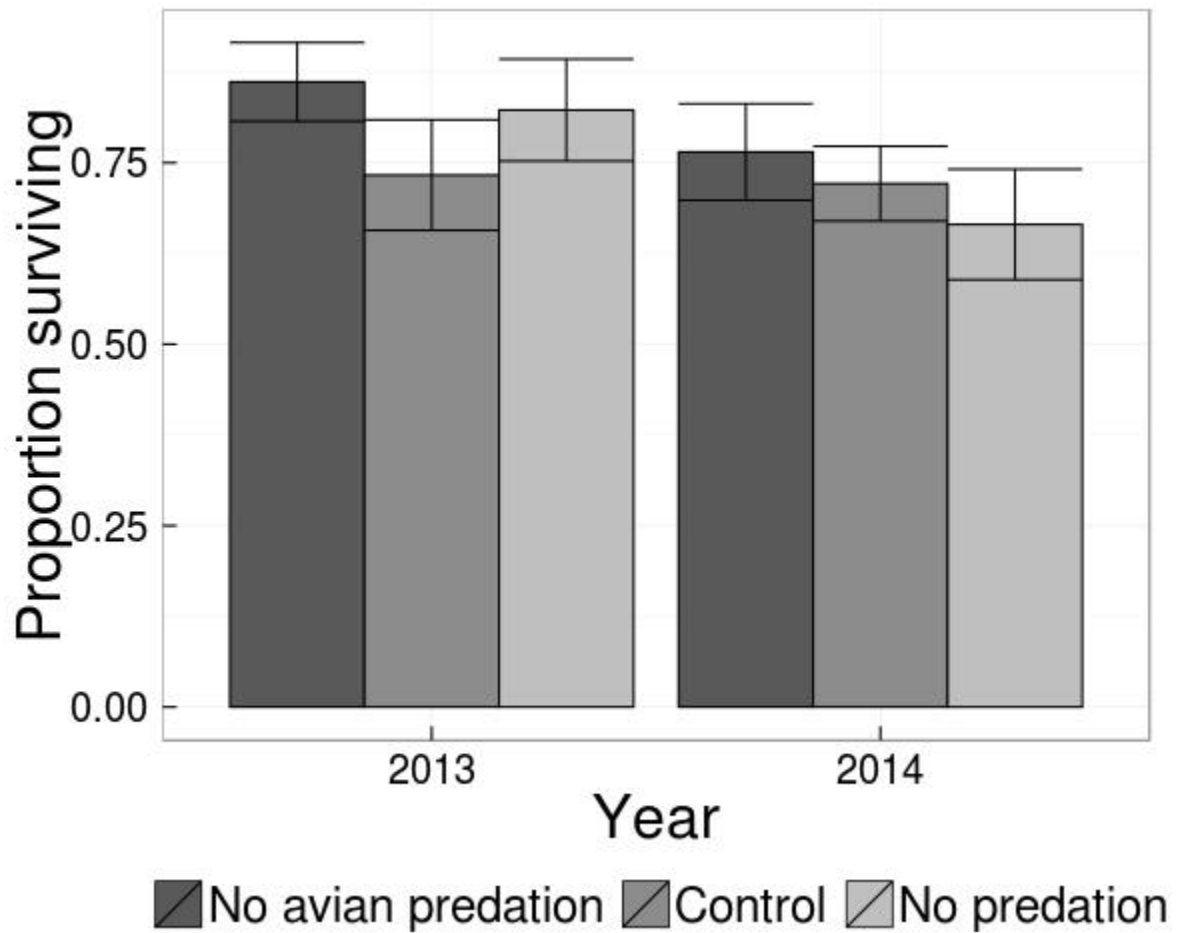


Figure 1.6. Mean and ± 1 standard error by year and treatment of late larval predator exclusion experiment. The fine mesh treatment excludes all predation and prevented larval dispersal, the coarse mesh treatment allows larval dispersal and invertebrate predation but prevents avian predation, and the wire support control treatment allows larval dispersal and all predation.

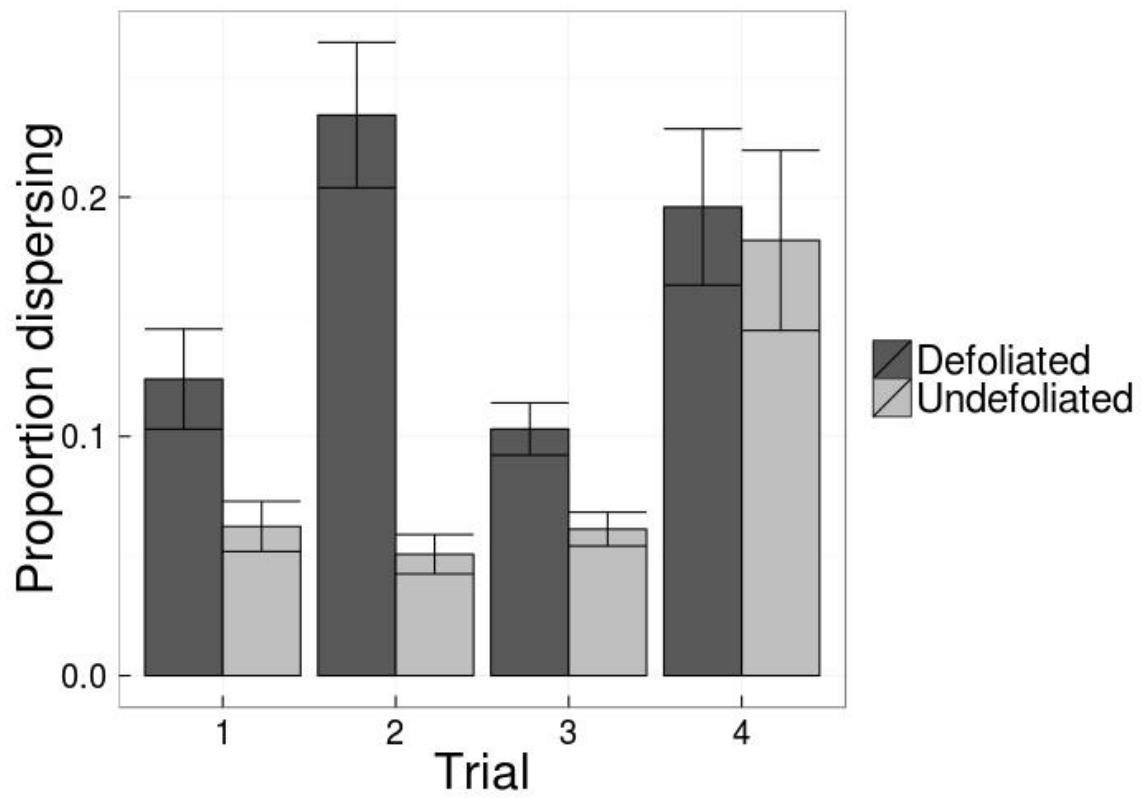


Figure 1.7. Mean and ± 1 standard error of proportion of larvae dispersed from defoliated and undefoliated leaves in four trials, from 2013 (trial 1), 2014 (trials 2 and 3), and 2015 (trial 4, see also Table 1.1).

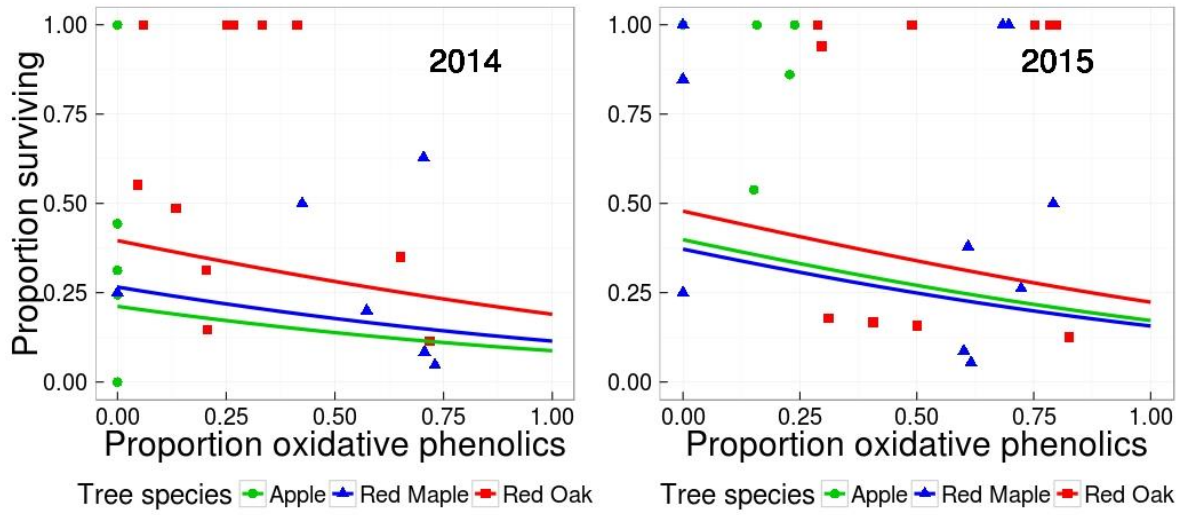


Figure 1.8. Proportion of larvae remaining on sample trees by proportion of oxidative phenolics of analyzed leaf material from sample trees, in 2014 and 2015.

REFERENCES

- Appel, H. M. (1993) Phenolics in ecological interactions: the importance of oxidation. *Journal of Chemical Ecology* **19**, 1521-1552.
- Ayres, M.P., Clausen, T.P., MacLean S. F., Redman, A.M. & Reichardt, P.B. (1997) Diversity structure and antiherbivore activity in condensed tannins. *Ecology* **78**, 1696–1712.
- Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014) lme4: Linear mixed-effects models using Eigen and S4. ArXiv e-print; in press, *Journal of Statistical Software*. doi: <http://arxiv.org/abs/1406.5823>.
- Bell, J.R., Bohan, D.A., Shaw, E.M. & Weyman, G.S. (2005) Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. *Bulletin of Entomological Research*, **95**, 69–114.
- Berger, A. (1992) Larval movements of *Chilo partellus* (Lepidoptera: Pyralidae) within and between plants: timing, density responses and survival. *Bulletin of Entomological Research*, **82**, 441–448.
- Berryman, A.A. (1996) What causes population cycles of forest Lepidoptera? *Trends in Ecology and Evolution*, **11**, 28–32.
- Berryman, A.A. (ed.). (2002) *Population Cycles: The Case for Trophic Interactions*. Oxford University Press, New York.
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J. S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* **24**: 127-135.
- Browne, W. J., Subramanian, S. V., Jones, K. & Goldstein, H. (2005) Variance partitioning in multilevel logistic models that exhibit overdispersion. *Journal of the Royal Statistical Society A*, **168**, 599–613.
- Burand, J.P., Kim, W., Welch, A., & Elkinton, J.S. (2011) Identification of nucleopolyhedrovirus in winter moth populations from Massachusetts. *Journal of Invertebrate Pathology*, **108**, 217-219.
- Cappuccino, N. (1995) Chapter 1 - Novel approaches to the study of population dynamics. *Population Dynamics* (eds. P.W. Price & N. Cappuccino), pp. 3–16. Academic Press, San Diego.
- Colautti, R.I., Ricciardi, A., Grigorovich, I.A. & MacIsaac, H.J. (2004) Is invasion success explained by the enemy release hypothesis? *Ecology Letters*, **7**, 721–733.

- Cox, D.L. & Potter, D.A. (1986) Aerial dispersal behavior of larval bagworms, *Thyridopteryx ephemeraeformis* (Lepidoptera: Psychidae). *The Canadian Entomologist*, **118**, 525–536.
- Denno, R.F. & Peterson, M.A. (1995) Chapter 6 - Density-dependent dispersal and its consequences for population dynamics. *Population Dynamics: New Approaches and Synthesis* (eds. P.W. Price & N. Cappuccino), pp. 113–130. Academic Press, San Diego.
- Denno, R.F., Roderick, G.K., Olmstead, K.L. & Dobel, H.G. (1991) Density-related migration in planthoppers (Homoptera : Delphacidae): the role of habitat persistence. *The American Naturalist*, **138**, 1513–1541.
- Dewar, R.C. & Watt, A.D. (1992) Predicted changes in the synchrony of larval emergence and budburst under climatic warming. *Oecologia*, **89**, 557–559.
- Edland, T. (1971) Wind dispersal of winter moth larvae *Operophtera brumata* L. (Lep., Geometridae) and its relevance to control measures. *Norsk Entomologisk Tidsskrift*, **18**, 103–105.
- Elkinton, J.S. & Liebhold, A.M. (1990) Population dynamics of gypsy moth in North America. *Annual Review of Entomology*, **35**, 571–96.
- Elkinton, J.S., Boettner, G.H., Sremac, M., Gwiazdowski, R., Hunkins, R.R., Callahan, J., Scheufele, S.B., Donahue, C.P., Porter, A.H., Khramian, A., Whited, B.M. & Campbell, N.K. (2010) Survey for winter moth (Lepidoptera: Geometridae) in northeastern North America with pheromone-baited traps and hybridization with the native Bruce spanworm (Lepidoptera: Geometridae). *Annals of the Entomological Society of America*, **103**, 135–145.
- Elston, D. A., Moss, R., Boulinier, T., Arrowsmith, C., & Lambin, X. (2001) Analysis of aggregation, a worked example: numbers of ticks on red grouse chicks. *Parasitology*, **122**, 563-569.
- Embree, D.G. (1965) The population dynamics of the winter moth in Nova Scotia, 1954-1962. *Memoirs of the Entomological Society of Canada*, **46**, 1–57.
- Feeny, P. (1970) Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology*, **51**, 565–581.
- Fonseca, D.M. & Hart, D.D. (1996) Density-dependent dispersal of black fly neonates is mediated by flow. *Oikos*, **75**, 49–58.

- Halekoh, U. & Højsgaard, S. (2014) A Kenward-Roger approximation and parametric bootstrap methods for tests in linear mixed models - the R package pbrtest. *Journal of Statistical Software*, **59**, 1–30.
- Hansen, N.M., Ims, R.A. & Hagen, S.B. (2009) No impact of pupal predation on the altitudinal distribution of autumnal moth and winter moth (Lepidoptera : Geometridae). *Environmental Entomology*, **38**, 627–632.
- Harrison, X. (2014). Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ* **2**:e616 doi: <https://dx.doi.org/10.7717/peerj.616>
- Hassell, M.P. (1968) The behavioural response of a tachinid fly (*Cyzenis albicans* (Fall.)) to its host, the winter moth (*Operophtera brumata* (L.)). *Journal of Animal Ecology*, **37**, 627–639.
- Haukioja, E. (2005) Plant defenses and population fluctuations of forest defoliators : mechanism-based scenarios. *Annales Zoologici Fennici*, **42**, 313–325.
- Haukioja, E. & Neuvonen, S. (1987) Insect population dynamics and induction of plant resistance: the testing of hypotheses. *Insect Outbreaks* (eds. P. Barbosa & J.C. Schultz), pp. 411–423. Academic Press, San Diego.
- Herzig, A.L. (1995) Effects of population density on long-distance dispersal in the goldenrod beetle *Trirhabda virgata*. *Ecology*, **76**, 2044–2054.
- Holliday, N.J. (1977) Population ecology of winter moth (*Operophtera brumata*) on apple in relation to larval dispersal and time of bud burst. *Journal of Applied Ecology*, **14**, 803–813.
- Hunter, A.F. (1995) The ecology and evolution of reduced wings in forest macrolepidoptera. *Evolutionary Ecology*, **9**, 275–287.
- Hunter, A.F. & Elkinton, J.S. (2000) Effects of synchrony with host plant on populations of a spring-feeding lepidopteran. *Ecology*, **81**, 1248–1261.
- Hunter, M.D. (1992) A variable insect–plant interaction: the relationship between tree budburst phenology and population levels of insect herbivores among trees. *Ecological Entomology*, **17**, 91–95.
- Hunter, M.D., Watt, A.D. & Docherty, M. (1991) Outbreaks of the winter moth on Sitka spruce in Scotland are not influenced by nutrient deficiencies of trees, tree budburst, or pupal predation. *Oecologia*, **86**, 62–69.

- Jepsen, J.U., Hagen, S.B., Karlsen, S. & Ims, R.A. (2009) Phase-dependent outbreak dynamics of geometrid moth linked to host plant phenology. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 4119–4128.
- Keane, R.M. & Crawley, M.J. (2002) Exotic plant invasions and the enemy hypothesis. *Trends in Ecology & Evolution*, **17**, 164–170.
- Kerslake, J.E. & Hartley, S.E. (1997) Phenology of winter moth feeding on common heather: Effects of source population and experimental manipulation of hatch dates. *Journal of Animal Ecology*, **66**, 375–385.
- Klemola, N., Andersson, T., Ruohomäki, K. & Klemola, T. (2010) Experimental test of parasitism hypothesis for population cycles of a forest lepidopteran. *Ecology*, **91**, 2506–2513.
- Lambin, X., Aars, J. & Pieltney, S.B. (2001) Dispersal, intraspecific competition, kin competition, and kin facilitation: a review of the empirical evidence. *Dispersal* (eds. J. Clobert, J.O. Wolff, J.D. Nichols, E. Danchin & A.A. Dhondt), pp. 110–122. Oxford University Press, New York.
- Lance, D. & Barbosa, P. (1979) Dispersal of larval Lepidoptera with special reference to forest defoliators. *The Biologist*, **61**, 90–110.
- Liebhold, A.M., Elkinton, J.S., Zhou, C., Hohn, M.E., Rossi, R.E., Boettner, G.H., Boettner, C.W., Burnham, C. & McManus, M.L. (1995) Regional correlation of gypsy moth (Lepidoptera: Lymantriidae) defoliation with counts of egg masses, pupae, and male moths. *Environmental Entomology*, **24**, 193–203.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000) Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications*, **10**, 689–710.
- Morris, R.F. & Mott, D.G. (1963) Dispersal and the spruce budworm. *Memoirs of the Entomological Society of Canada*, **31**, 180–189.
- Murdoch, W.W. (1994) Population regulation in theory and practice. *Ecology*, **75**, 271–287.
- Myers, J.H. (1988) Can a general hypothesis explain population cycles of forest Lepidoptera? *Advances in Ecological Research*, **18**, 179–242.
- Myers, J.H. & Cory, J.S. (2013) Population cycles in forest Lepidoptera revisited. *Annual Review of Ecology, Evolution, and Systematics*, **44**, 565–592.

- Nakagawa, S. & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, **4**, 133–142. doi: 10.1111/j.2041-210x.2012.00261.x
- R Core Team. (2013) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Raymond, B., Vanbergen, A., Watt, A., Hartley, S.E., Cory, J.S. & Hails, R.S. (2002) Escape from pupal predation as a potential cause of outbreaks of the winter moth, *Operophtera brumata*. *Oikos*, **98**, 219–228.
- Rhainds, M., Gries, G. & Chew, P.S. (1997) Adaptive significance of density-dependent ballooning by bagworm larvae, *Metisa plana* (Walker) (Lepidoptera: Psychidae). *The Canadian Entomologist*, **129**, 927–931.
- Rhainds, M., Gries, G., Ho, C.T. & Chew, P.S. (2002) Dispersal by bagworm larvae, *Metisa plana*: Effects of population density, larval sex, and host plant attributes. *Ecological Entomology*, **27**, 204–212.
- Roff, D.A. (1990) The evolution of flightlessness in insects. *Ecological Monographs*, **60**, 389–421.
- Roland, J. (1986) Parasitism of winter moth in British Columbia during build-up of its parasitoid *Cyzenis albicans*: Attack rate on oak v. apple. *Journal of Animal Ecology*, **55**, 215–234.
- Roland, J. (1994) After the decline : what maintains low winter moth density after successful biological control ? *Journal of Animal Ecology*, **63**, 392–398.
- Roland, J., Denford, K.E. & Jimenez, L. (1995) Borneol as an attractant for *Cyzenis albicans*, a tachinid parasitoid of the winter moth, *Operophtera brumata* L. (Lepidoptera: Geometridae). *The Canadian Entomologist*, **127**, 413–421.
- Roland, J. & Embree, D.G. (1995) Biological control of the winter moth. *Annual Review of Entomology*, **40**, 475–492.
- Roland, J., Hannon, S.J. & Smith, M.A. (1986) Foraging pattern of pine siskins and its influence on winter moth survival in an apple orchard. *Oecologia*, **69**.
- Roland, J. & Myers, J.H. (1987) Improved insect performance from host-plant defoliation: winter moth on oak and apple. *Ecological Entomology*, **12**, 409–414.
- Rosenheim, J. A. (1998) Higher-order predators and the regulation of insect herbivore populations. *Annual Review of Entomology*, **43**, 421–447.

- Salminen, J.P. & Karonen, M. (2011) Chemical ecology of tannins and other phenolics: we need a change in approach. *Functional Ecology*, **25**, 325–338.
- Schott, T., Hagen, S.B., Ims, R.A. & Yoccoz, N.G. (2010) Are population outbreaks in sub-arctic geometrids terminated by larval parasitoids? *Journal of Animal Ecology*, **79**, 701–708.
- Schott, T., Ims, R.A., Hagen, S.B. & Yoccoz, N.G. (2012) Sources of variation in larval parasitism of two sympatrically outbreaking birch forest defoliators. *Ecological Entomology*, **37**, 471–479.
- Schott, T., Kapari, L., Hagen, S.B., Vindstad, O.P.L., Jepsen, J.U. & Ims, R. A. (2013) Predator release from invertebrate generalists does not explain geometrid moth (Lepidoptera: Geometridae) outbreaks at high altitudes. *The Canadian Entomologist*, **145**, 184–192.
- Schultz, J.C. & Baldwin, I.T. (1982) Oak leaf quality declines in response to defoliation by gypsy moth larvae. *Science* **217**, 149–151
- Solbreck, C. (1995) Chapter 14 - Long-term population dynamics of a seed-feeding insect in a landscape perspective. *Population Dynamics* (eds. P.W. Price & N. Cappuccino), pp. 279–301. Academic Press, San Diego.
- Tanhuanpää, M., Ruohomäki, K., Kaitaniemi, P. & Klemola, T. (1999) Different impact of pupal predation on populations of *Epirrita autumnata* (Lepidoptera; Geometridae) within and outside the outbreak range. *Journal of Animal Ecology*, **68**, 562–570.
- Tanhuanpää, M., Ruohomäki, K., Turchin, P., Ayres, M.P., Bylund, H., Kaitaniemi, P., Tammaru, T. & Haukioja, E. (2002) Population cycles of the autumnal moth in Fennoscandia. *Population Cycles: The Case for Trophic Interactions* (ed A.A. Berryman), pp. 142–155. Oxford University Press, New York.
- Taylor, A.D. (1990) Metapopulations, dispersal, and predator-prey dynamics : An overview. *Ecology*, **71**, 429–433.
- Terry, I., Bradley, J.R. & Duyn, J.W. (1989) Establishment of early instar *Heliothis zea* on soybeans. *Entomologia Experimentalis et Applicata*, **51**, 233–240.
- Tikkanen, O.P. & Julkunen-Tiitto, R. (2003) Phenological variation as protection against defoliating insects: The case of *Quercus robur* and *Operophtera brumata*. *Oecologia*, **136**, 244–251.
- Travis, J.M.J., Murrell, D.J. & Dytham, C. (1999) The evolution of density-dependent dispersal. *Proceedings of the Royal Society B: Biological Sciences*, **266**, 1837–1842.

- Van Dongen, S., Backeljau, T., Matthysen, E. & Dhondt, Andre, A. (1997) Synchronization of hatching date with budburst of individual host trees (*Quercus robur*) in the winter moth (*Operophtera brumata*) and its fitness consequences. *Journal of Animal Ecology*, **66**, 113–121.
- Van Driesche, R.G., Carruthers, R.I., Center, T., Hoddle, M.S., Hough-Goldstein, J., Morin, L., Smith, L., Wagner, D.L., Blossey, B., Brancatini, V., Casagrande, R., Causton, C.E., Coetzee, J.A., Cuda, J., Ding, J., Fowler, S.V., Frank, J.H., Fuester, R., Goolsby, J., Grodowitz, M., Heard, T. A., Hill, M.P., Hoffmann, J.H., Huber, J., Julien, M., Kairo, M.T.K., Kenis, M., Mason, P., Medal, J., Messing, R., Miller, R., Moore, A., Neuenschwander, P., Newman, R., Norambuena, H., Palmer, W. A., Pemberton, R., Perez Panduro, A., Pratt, P.D., Rayamajhi, M., Salom, S., Sands, D., Schooler, S., Schwarzländer, M., Sheppard, A., Shaw, R., Tipping, P.W. & van Klinken, R.D. (2010) Classical biological control for the protection of natural ecosystems. *Biological Control*, **54**, S2–S33.
- Varley, G. & Gradwell, G. (1968) *Population Models for the Winter Moth*. Blackwell Scientific Publications, Oxford.
- Vindstad, O.P.L., Schott, T., Hagen, S.B., Jepsen, J.U., Kapari, L. & Ims, R. A. (2013) How rapidly do invasive birch forest geometrids recruit larval parasitoids? Insights from comparison with a sympatric native geometrid. *Biological Invasions*, **15**, 1573–1589.
- Visser, M.E. & Holleman, L.J.M. (2001) Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proceedings of the Royal Society B: Biological Sciences*, **268**, 289–294.
- Wickham, H. (2009) *ggplot2: elegant graphics for data analysis*. Springer, New York.
- Wint, W. (1983) The role of alternative host-plant species in the life-cycle of a polyphagous moth, *Operophtera brumata* (Lepidoptera: Geometridae). *Journal of Animal Ecology*, **52**, 439–450.