

# Combined Effects of Natural Enemies and Competition for Resources on a Forest Defoliator: A Theoretical and Empirical Analysis

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**ABSTRACT:** Explanations for the dynamics of insect outbreaks often focus on natural enemies, on the grounds that parasitoid and pathogen attack rates are high during outbreaks. While natural enemy models can successfully reproduce outbreak cycles, experiments have repeatedly demonstrated the importance of resource quality and abundance. Experiments, however, are rarely invoked in modeling studies. Here we combine mechanistic models, observational data, and field experiments to quantify the roles of parasitoid attacks and resource competition on the jack pine budworm, *Choristoneura pinus*. By fitting models to a combination of observational and experimental data, we show that parasitoid attacks are the main source of larval budworm mortality at low and intermediate budworm densities but that resource competition is the main source of mortality at high densities. Our results further show that the effects of resource competition become more severe with increasing host tree age and that the effects of parasitoids are moderated by strong competition between parasitoids for hosts. Allowing for these effects in a model of insect outbreaks leads to realistic outbreak cycles, while a host-parasitoid model without resource competition produces an unrealistic stable equilibrium. The effects of resource competition are modulated by tree age, which in turn depends on fire regimes. Our model therefore suggests that increases in fire frequency due to climate change may interact in complex ways with budworm outbreaks. Our work shows that resource competition can be as important as natural enemies in modulating insect outbreaks, while demonstrating the usefulness of high-performance computing in experimental field ecology.

**Keywords:** host-parasitoid model, plant-insect interactions, insect outbreak, mathematical model, jack pine budworm, nonlinear fitting.

## Introduction

Ecologists have long debated whether the population dynamics of herbivorous insects are driven by natural enemies or by the quality and density of resources (Lawton and McNeill

1979). This question is part of a larger discussion about the relative importance of top-down versus bottom-up mechanisms (Hunter and Price 1992). In insect ecology, this debate has seen at least a superficial resolution in the sense that there is clear evidence for effects of natural enemies on some species (Turchin 2003) and clear evidence for effects of resources on others (Denno et al. 2002; Gratton and Denno 2003). A difficulty with this resolution, however, is that it emphasizes either-or explanations, whereas it seems likely that both natural enemies and resources often play important roles (Moreau et al. 2018).

Here we ask instead, Under what conditions are natural enemies more important than resources or resources more important than natural enemies? Our study system consists of the jack pine budworm, *Choristoneura pinus*; the budworm's jack pine host, *Pinus banksiana*; and the parasitoid insects that attack the budworm (McCullough 2000). Jack pine budworm has cyclical outbreaks at intervals of 6–12 years and is representative of a large group of outbreaking forest-defoliating insects that damage economically important timber (Liebhold and Kamata 2000).

In attempting to explain insect outbreaks, theoreticians have traditionally focused on the role of natural enemies. Parasitoids and pathogens are often significant causes of mortality during outbreaks (Myers 1993; Klemola et al. 2002), and host-parasitoid and host-pathogen models can qualitatively reproduce time series data on defoliator densities (Varley et al. 1974; Anderson and May 1980). Host-pathogen and host-parasitoid models have dominated the literature, but more formal comparisons of models to data have provided mixed support for these natural enemy models. In the case of the larch budmoth, *Zeiraphera diniana*, Turchin et al. (2003) showed that budmoth density data are indeed best explained by a host-parasitoid model. In the case of the pine looper, *Bupalus piniarius*, however, Kendall et al. (2005) provided evidence for both a host-parasitoid model and a maternal-effects model, with the best model varying across sites.

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Modeling studies have also traditionally focused on observational time series data, but using time series data alone can lead to incorrect inferences about underlying mechanisms (Cobey and Baskerville 2016). Indeed, experiments have often revealed clear effects of resource quality (Hunter and Schultz 1993) or abundance (Myers et al. 2011) on insect population dynamics. To disentangle the effects of parasitoids and resources on the jack pine budworm, we therefore collected a combination of observational and experimental data on larval mortality, and we used statistical model selection (Burnham and Anderson 2004) to determine which of several competing models provides the best explanation for our data.

Model selection confirmed that parasitoids and resource competition both have strong effects on larval budworm survival. Model selection further suggested that competition for resources is modulated by tree quality, such that competition is more severe on older jack pines and that parasitoid competition for hosts restricts parasitoid-induced mortality. Resource competition is therefore the most important source of mortality at high budworm densities, while parasitoids are more important at low and intermediate densities.

To understand the significance of these results for budworm outbreaks, we extended our models to allow for long-term budworm and parasitoid population dynamics. A model with only host-parasitoid interactions produces outbreaks with an unrealistically small amplitude, because in this system the parasitoids compete strongly for hosts. A model with parasitoids and resource competition but not tree quality produces outbreaks with an unrealistically large amplitude, because the effects of quality strongly modulate resource competition. Including quality in the models then produces cycles with amplitudes that are closest to the amplitudes of outbreaks seen in nature. These long-term models are preliminary because they do not include the effects of fire, which can alter forest dynamics, but they make an important general point. Classical theory has long argued that parasitoids and other natural enemies are likely to be destabilizing, while resource competition is likely to be stabilizing (Gotelli 2008). The destabilizing effects of density dependence in our models, as well as the stabilizing effects of parasitoids, thus demonstrate that a combination of natural enemies and resource competition can lead to dynamics that cannot be easily intuited from classical theory.

Our work provides a rare example of the effects of competition for resources on complex population dynamics. More concretely, our approach demonstrates the usefulness of carrying out robust empirical tests of ecological theory, especially in combination with advanced nonlinear fitting techniques. The economic and conservation value of jack pine forests (McCullough 2000) means that our work also has implications for jack pine management. Fire plays a

key role in maintaining jack pine forests, a role that will likely be altered as climate change increases fire risk (Abatzoglou and Williams 2016). Given that defoliation has also been shown to alter fire risk in mixed spruce/jack pine forests (James et al. 2017), our results suggest that the effects of climate change on North American forests will be modulated by the effects of natural enemies and tree quality on insect outbreaks.

## Model Construction

### *Budworm Natural History*

We used our knowledge of budworm biology to construct a set of mechanistic models of larval budworm survival. We then used our models to design experiments and to analyze the resulting data. By analyzing our data using mechanistic models, we developed a better understanding of the roles of parasitoid attacks and plant quality in larval survival than if we had used, for example, generalized linear models.

Jack pine budworm is a defoliating Lepidopteran insect native to Canada and the northern United States. It feeds almost exclusively on jack pine, a major component of North American forests (Mallett and Volney 1990; Hall et al. 1993; McCullough 2000). At intervals of 6–12 years, budworm outbreaks cause extensive defoliation and tree death, with insects persisting at low densities in the intervening years (Dixon and Benjamin 1963; McCullough and Kulman 1991; Volney 1992; Nealis et al. 1997). Tree death and canopy defoliation can in turn lead to increased frequency and severity of wildfires (Stocks 1987a; Flower et al. 2014; James et al. 2017). Parasitoid-induced mortality in the jack pine budworm is high during outbreaks (Nealis and Lysyk 1988), but larval mortality is also strongly affected by the density of jack pine pollen cones, which are an important food source for early-stage larvae (Nealis and Lomic 1994). Management of jack pine forests has significant economic and conservation implications (Probst 1986) because jack pine is important in the logging industry and because young jack pine stands provide breeding grounds for the endangered Kirtland's warbler (*Setophaga kirtlandii*). Wildfires play an important role in jack pine forests. By releasing jack pine seeds from their serotinous cones, they allow for postfire regeneration (Volney et al. 1995).

Like many outbreaking insects, the budworm has a single generation per year (Hunter 2001), with the nonfeeding adults reproducing in late summer (McCullough 2000). Larvae hatch at the end of the summer and overwinter without feeding, reemerging in the spring to feed on pollen cones and eventually pine needles (Nealis et al. 2003). Previous work has shown that parasitoids impose severe mortality on budworm larvae (Nealis 1987), and therefore all of our models include mortality due to parasitoid attacks. In our study

populations, parasitoid-induced mortality was largely due to two Hymenopteran parasitoids, the Braconid *Apanteles fumiferana* and the Ichneumonid *Glypta fumiferana*, which together accounted for >99% of all of the parasitoids we observed. In addition, a few insects were parasitized by species of hard-to-distinguish Diptera in the family Tachinidae, and in the interest of simplicity we grouped these latter species together.

When a female parasitoid attacks a newly hatched budworm larva in late summer, it uses its ovipositor to deposit a single egg directly into the body of the larva. The parasitoid larva that results can then overwinter within its host larva, and such larvae give rise to the next generation of parasitoids. Budworm larvae emerge from hibernacula and begin feeding in early May, and parasitoids begin to emerge from parasitized larvae after a week or two of host feeding activity. Parasitism results in host death, so infected larvae have no chance of surviving to adulthood. A previous study concluded that the most common jack pine budworm parasitoids have only a single generation per year (Nealis and Lysyk 1988), but that study relied solely on measures of infection rates at single time points. Because we quantified infection rates during each week of the larval feeding period, we are able to show that additional parasitoid attacks occur during the larval feeding period in the spring. Budworm parasitoids thus can have at least two generations each year, even though jack pine budworm has only one generation each year.

Budworm densities are very high during outbreaks, and larvae compete intensely for resources. Some versions of our models therefore include direct density-dependent mortality. The main larval food source is pollen cones, the male strobili produced by jack pine trees (Nealis et al. 1997; McCullough 2000). Larval survival is believed to be lower on young trees and older trees, which produce fewer pollen cones than trees of intermediate age (McCullough 2000). As a measure of host tree quality, we therefore used the diameter at breast height (DBH), a standard measure of tree age. Cores from a subset of jack pines confirmed that counts of tree rings are strongly positively correlated with DBH ( $r^2 = 0.75$ ,  $F_{1,14} = 41.23$ ,  $P < .01$ ; see the appendix, available online).

As we will show, the parasitoids in our study had multiple generations during a single larval feeding period. To describe parasitoid attacks, we therefore used a susceptible-exposed-infected-removed (SEIR) model from mathematical epidemiology (Keeling and Rohani 2008). The SEIR model allows for multiple disease generations, which in our case are equivalent to parasitoid generations. The model also includes a distributed delay between parasitoid attack and host death, an important feature of parasitoid development times. We allowed the three parasitoid species in the models to differ in their attack rates and development times, but the models are nested, such that if the effects of two or all three species are sufficiently similar, they can be grouped together. In our

models, the parasitoid class  $P$  corresponds to the infected class  $I$  of SEIR models. This structure makes it possible for emerging adult parasitoids in the model to parasitize hosts in the same larval host generation. In our case, the removed (or  $R$ ) class of SEIR models consists of individuals that have died. As in SEIR models, these individuals do not affect the dynamics of the system, and we therefore do not include an equation for the  $R$  class.

Our simpler models can all be derived from our most complex model, so here we present only the most complex model (we present the remaining models in the appendix):

$$\frac{dS}{dt} = \overbrace{-\frac{\alpha\phi SP}{1 + \rho P}}^{\text{parasitoid attacks}} - \overbrace{\gamma_1 S^{\gamma_2} \left( S + \sum_{j=1}^m E_j \right)}^{\text{direct density dependence}} \times \overbrace{\left( (Q - \eta_1)^2 + \eta_2 \right)}^{\text{nonlinear DBH effects}} \tag{1}$$

$$\frac{dE_1}{dt} = \frac{\alpha\phi SP}{1 + \rho P} - \gamma_1 E_1^{\gamma_2} \left( S + \sum_{j=1}^m E_j \right) \times \left( (Q - \eta_1)^2 + \eta_2 \right) \underbrace{- m\delta E_1}_{\text{transition to the next class}} \tag{2}$$

$$\frac{dE_j}{dt} = m\delta E_{j-1} - \gamma_1 E_j^{\gamma_2} \left( S + \sum_{j=1}^m E_j \right) \times \left( (Q - \eta_1)^2 + \eta_2 \right) - m\delta E_j$$

for  $j = 2, \dots, m$ ,  
exposed class index

$$\frac{dP}{dt} = m\delta E_j. \tag{4}$$

Here,  $S$  is the density of unparasitized (“susceptible”) budworms, while  $P$  is the parasitoid, presented here as a single group of three identical species. When we fit our models, we found that differentiating between parasitoid species did not improve the fit of the models to the data. The parameter  $\alpha$  is the attack rate of the parasitoid, while the parasitoid functional response term  $\alpha\phi SP/(1 + \rho P)$  depends on  $\rho$ , which modulates the effect of the density of the parasitoid on the parasitoid attack rate. Our data show that attacks by female parasitoids were slightly underdispersed, meaning that the variance in the parasitism rate was lower than the mean and that budworms were almost never parasitized by more than one parasitoid, with only two instances of coinfection out of several thousand observations. It therefore appears that female parasitoids detect and avoid hosts that are already parasitized and thus that parasitoids compete strongly with one another for hosts. To allow for this

biology, we included  $P$  in the denominator of our functional response term, and we did not include coinfection in the models.

As we will describe, in our experiments we manipulated the degree to which parasitoids could access some branches. The parameter  $\phi$  then allows for the possibility that parasitoid attack rates differed across experimental treatments. When we instead fit the models to observational data, we set  $\phi \equiv 1$ .

To allow for a distributed delay between parasitoid attack and budworm death, the model includes multiple exposed classes. The time that hosts spend in each exposed class  $E_j$  follows an exponential distribution with mean  $1/(m\delta)$ , where  $m$  is the number of exposed classes. The total time in the exposed classes, which is the time between parasitoid attack and host death, is then the sum of  $m$  exponentially distributed random variates. This sum is known to follow a gamma distribution with mean  $1/\delta$  and coefficient of variation  $1/(m\delta)^{1/2}$  (Keeling and Rohani 2008). As the number of exposed classes increases, the variance in the length of time an individual spends in the exposed classes decreases, such that for  $m \rightarrow \infty$  the variance is zero, and all individuals spend exactly the same amount of time in the exposed classes. For  $m = 1$ , the time spent in the single exposed class follows an exponential distribution, as in the simplest SEIR models, and in that case the variance in the time between parasitism and death equals the mean. This is a highly restrictive assumption, so we therefore instead included multiple exposed classes, which allowed us to modify the variance in the amount of time that passes before exposed insects progress to the infected class. We then estimated the number of exposed classes  $m$  as part of our fitting routine, to avoid assumptions about the distribution of the delay between parasitoid attack and budworm death.

To explain how the model allows for the effects of tree quality and density-dependent mortality, we note first that  $(S + \sum_{j=1}^m E_j)$  represents the total budworm population, summed across each exposure class  $j$ . The parameters  $\gamma_1$  and  $\gamma_2$  then describe the effects of direct density dependence due to competition for resources. Density-dependent mortality is affected by tree quality through the covariate  $Q$ , which is measured in terms of DBH, a covariate that serves as a proxy for tree age and therefore pollen cone density. McCullough (2000) suggested that mortality is lowest on trees of intermediate size, implying that the effects of quality on mortality are a quadratic function of DBH. In equations (1)–(4), we therefore show a model with quadratic effects of DBH, with parameters  $\eta_1$  and  $\eta_2$ , but we also considered models with linear effects of DBH.

The models that include DBH effects differ only slightly from the models in which direct density dependence is not a function of DBH, but the models with DBH incorporate a specific mechanism. This is important because, as we will show, the models that include DBH explain the data only

modestly better than the models that do not. The models that include DBH, however, provide deeper insights into the mechanisms determining budworm survival.

The terms in our models that represent the parasitoid functional response and the effects of host tree quality are somewhat phenomenological in that the particular model terms that we used to represent these mechanisms are somewhat arbitrary. In referring to our models as “mechanistic,” we are therefore making a distinction from models typically used to analyze data, which in the case of survival data like ours are usually generalized linear models (McCullagh and Nelder 1989). We refer to our models as mechanistic because, unlike generalized linear models, our models distinguish between different mechanisms of mortality and because our models describe how host and parasitoid dynamics are determined by interactions between species and by interactions between individuals within each species.

#### *Behavior of the Short-Term Models*

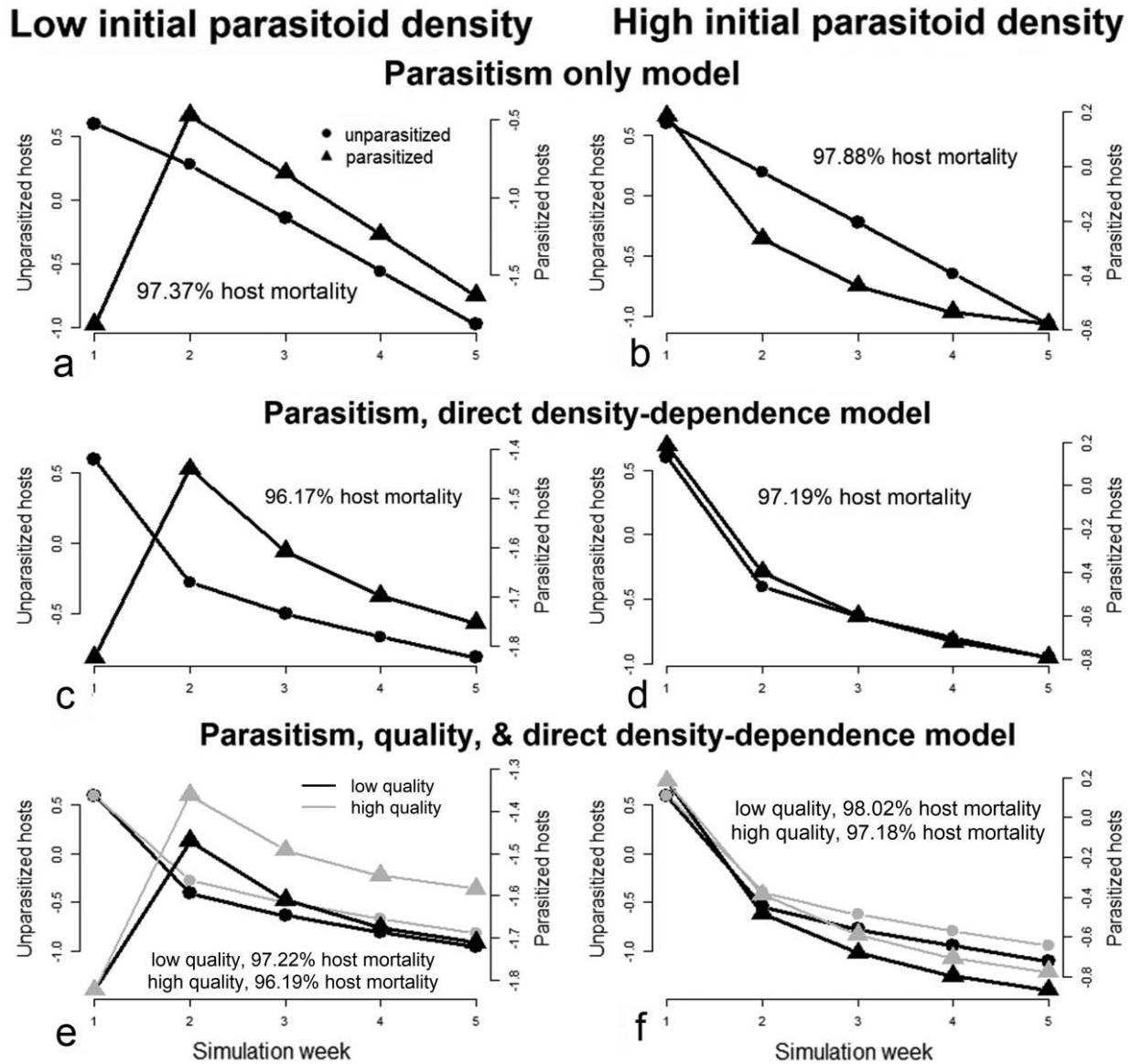
The behavior of our competing models of larval mortality differ mostly in terms of the speed of the decline in larval densities (fig. 1). Overall mortality is very high in outbreaking populations, and the effects of parasitoids and tree quality are both density dependent. The differences between models are then clearest if we simulate the models across a range of initial host and parasitoid densities. When initial parasitoid densities are low, for example, all the models predict that parasitoid densities will increase sharply early in the season (fig. 1). In models with host tree quality effects, however, this effect is modulated by tree quality, so that the initial rise in the parasitoid population is substantially lower on lower-quality hosts. At both low and high initial parasitoid densities, higher-quality trees slow the decline in larval density, leading to lower overall mortality. The effects of these differences on cumulative mortality are often modest, such that the influence of poor tree quality on direct density dependence increases mortality by only about a percentage point. This difference can nevertheless have important effects on outbreak cycles over the long term, as we will show.

#### **Testing the Short-Term Models**

##### *Data Collection*

Data are available in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.tf0s1qg>; Gallagher and Dwyer 2019).

*Observational data.* Budworm populations rise and fall over the course of outbreaks. We collected samples over 4 years, and therefore we have data from populations across a range of densities. Densities also vary over space in a given year, likely because of spatial variability in fire history and thus tree



**Figure 1:** Comparisons of model behavior for three competing models under different parasitoid density conditions and for varying plant quality in the case of the third model. Here we plot total parasitized hosts, a group that is represented in the models by the sum of the exposed classes rather than by the final adult parasitoid class. Unparasitized and parasitized densities are reported in terms of larvae per bud on a  $\log_{10}$  scale. Note that host and parasitoid densities are on different scales.

quality. To take advantage of this spatial variation, we collected budworms from a variety of spatial locations each year. Our sites also included a range of parasitoid densities because parasitoid attacks in this system are density dependent.

In 2012, we sampled budworms from an outbreak in Wisconsin at three sites that spanned a distance of 40 km north to south, including two sites with high budworm densities and one site with an intermediate budworm density. The Wisconsin population collapsed in 2012, so from 2013

to 2015 we sampled seven additional sites in Michigan. Sites in Michigan spanned a distance of 25 km from north to south and were chosen to include a wide range of budworm densities. Initial densities of hosts and parasitoids for each site and each year are given in table A2 (tables A1–A5 are available online).

At each site, we recorded the DBH of each sampled tree, and we measured the density of parasitized and unparasitized larval budworms over the spring feeding period. To do

this, we collected 50 branch tips from each of five trees, recording the number of larvae and the number of larvae parasitized on each branch tip. To quantify the number parasitized, we reared each larva in the laboratory until either a parasitoid emerged or the larva successfully pupated. We repeated this process weekly, from larval emergence in early May until pupation in late June or early July.

*Experimental Data.* To disentangle the effects of parasitism from the effects of tree quality and resource competition, we used mesh bags to experimentally exclude parasitoids on some branches during the spring feeding period. Some larvae in our experimental exclusion treatments had already been parasitized the preceding summer. As we will show, however, excluding parasitoids during the spring feeding period led to a strong reduction in the fraction of budworms that were parasitized by the end of an experiment.

Experiments were conducted at four sites, all in Michigan, in 2013 and 2014. Parasitoid exclusion bags were deployed on branches for 1–6 weeks total, but the experiments began at different times and ran for different lengths of time. These variations improved our ability to quantify changes in larval mortality over time. Table A1 provides a complete list of experiments and when they began and ended.

We then used differences in mortality between control and experimental branches to quantify the effects of mortality due to parasitoids separately from mortality due to competition for resources. To fit our models to data from experiments that ran for different lengths of time, we ran the models only for the number of weeks in each experiment, and we adjusted the initial conditions so that they matched the observed host densities at each experiment's starting time. Sampling budworm larvae is necessarily destructive because it requires breaking apart pollen cones. Accordingly, we could not measure initial budworm density on the branches that we used in the experiments, but budworm densities within each site did not vary much between trees or between branches. The observational data that we collected each week at every experimental site thus provided the initial densities needed to fit the models to the experimental data.

To create controls for our parasitoid exclusion bags, we cut two 10 × 10-mm square holes in some of the bags to allow parasitoids to access the budworm larvae. Full controls, in contrast, had no bags at all. Bags were deployed on branches on two to six trees per site with six branches per tree, such that two branches on each tree were enclosed in uncut bags, two were enclosed in bags with holes, and two were not enclosed in bags at all. At the end of each experiment, we removed the surviving budworms and raised them in the laboratory.

When we fit the models to the experimental data, we set the parasitoid attack rate  $\alpha \equiv 0$  for the bagged treatments because no parasitoid attacks could occur during the ex-

periment. Any parasitism that was observed in the bagged branches was then the result of attacks that had occurred late the previous summer, shortly after budworm hatch. As we will show, survival rates on the bagged branches were lower than can be explained by parasitoid attacks alone, which is consistent with a role of resource competition as an additional source of mortality.

For the bags with holes, we included an additional parameter  $\phi$ , such that  $0 \leq \phi \leq 1$ . This parameter allowed for the possibility that parasitism rates on the branches with partial controls would fall in between the parasitism rates on the branches with uncut bags and the control branches. Rates of parasitism in the bags without holes turned out to be comparable to those in the bags with holes, however, indicating that the holes were too small for parasitoids to easily access the branches inside the bags.

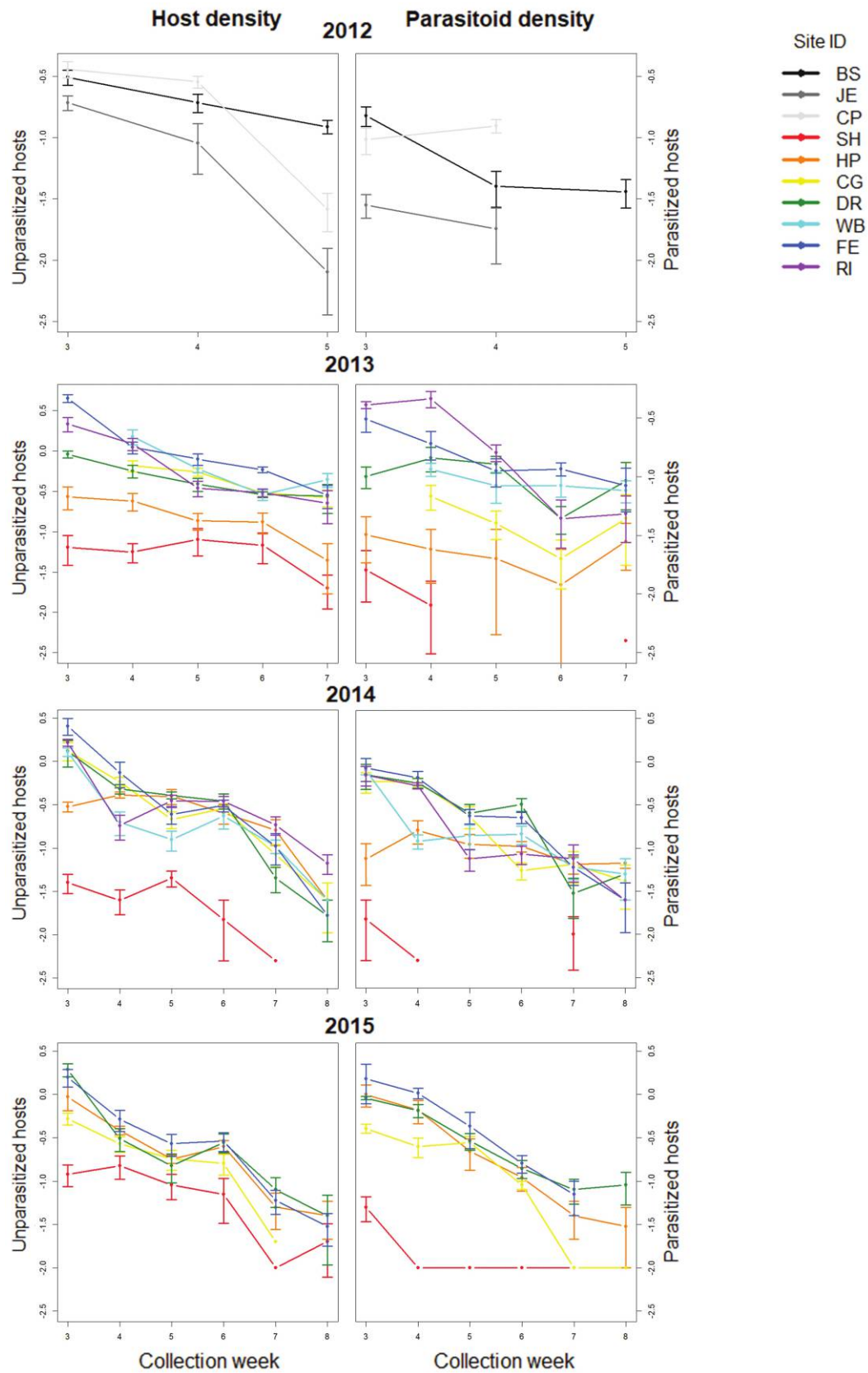
#### *Fitting the Models to Data*

We used our data to first calculate the density of unparasitized hosts over time, symbolized as  $S$  in equations (1)–(4). Measuring the density of adult parasitoids,  $P$  in equations (1)–(4), was logistically impractical, so we measured the density of hosts in the exposed classes,  $E_j$  in equations (1)–(4). We were able to determine if a budworm was parasitized only after the parasitoid emerged, so in practice we measured the total density of exposed hosts  $\sum_j E_j$ . As we will show, the resulting data are sufficient to provide reasonable estimates of all model parameter values.

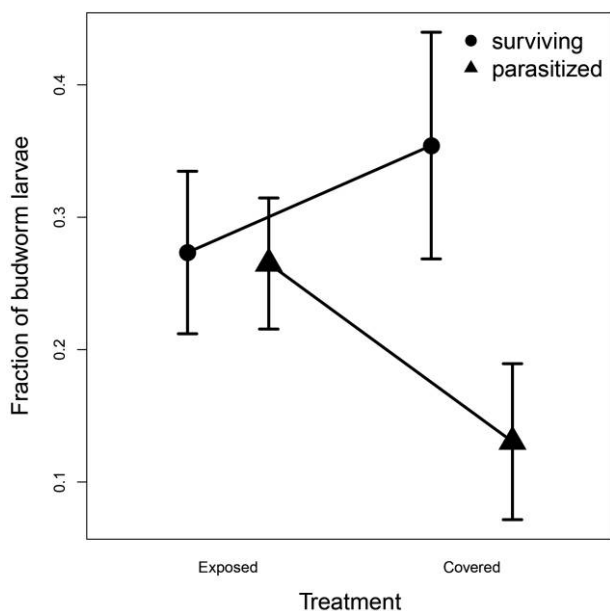
To fit the models to the data, we treated the observed initial densities of parasitized and unparasitized budworms as fixed parameters. We then used the models to make predictions of subsequent densities of parasitized and unparasitized budworms over time, and we compared these predictions to the observed densities. This approach necessitated the use of a nonlinear fitting algorithm to identify parameter values that provided a good fit of the models to the data. We used an algorithm known as line-search MCMC, which is easily adaptable to Bayesian calculations and which takes full advantage of the high degree of parallelization in modern computing environments (Kennedy et al. 2015; see the appendix for more details).

#### *Results*

At our study sites, declines in larval budworm populations were always substantial, but the severity of the decline was much higher in high-density populations (fig. 2). Density-dependent mortality therefore appeared to play a key role in our study populations, as assumed in our models. A second model assumption was confirmed by the lower rates of parasitoid-induced mortality in our bagged experimental branches (fig. 3). As we mentioned, previous studies of jack



**Figure 2:** Changes in the density of unparasitized and parasitized budworms at our study sites in Wisconsin in 2012 and Michigan in 2013, 2014, and 2015. Our data set includes three to seven sites per year, so that each line represents a particular site in a particular year. Insect densities are reported in terms of larvae per bud on a  $\log_{10}$  scale.



**Figure 3:** Summary of the effects of parasitoid exclusion treatments on larval survival and parasitism in our experiments. Here, branches with bags with holes are temporarily included in the covered category because the parasitism rate in the bags with holes was comparable to the rate in bags without holes. Each point is a mean across all experiments, and error bars show 1 SEM.

pine budworm parasitoids indicated that the parasitoids have only one generation per year, with parasitoid attacks occurring in the late summer and new parasitoids emerging in early spring, shortly after the bags were placed on the branches in our experiments. In our experiments, however, the parasitism rate was clearly higher on exposed branches than on bagged branches. This difference could only have occurred if parasitoid attacks continued during the larval period rather than having occurred solely in the previous year, shortly after budworm egg hatch. In addition, we continued to collect infected larvae for 8 weeks, a period that is far longer than the majority of incubation times in Hymenop-

teran and Dipteran parasitoids (Godfray 1994). Increases in parasitism rates over time in our observational data must therefore have been due to additional parasitism that occurred in the spring. The parasitoids thus appear to have multiple generations per year, and previous conclusions that parasitoid attacks only occur in late summer appear to be incorrect. This finding supports our use of the SEIR model, in which parasitoid attacks occur throughout the larval period of the budworm.

Watanabe-Akaike information criterion (WAIC) analysis (Gelman et al. 2013) shows that model 4 is the best model among the suite of competing models that we tested (table 1). This model includes density-dependent mortality that increases linearly with DBH so that it reflects the presumably lower pollen cone density typical of senescent trees. Additional WAIC scores are presented in table A4, with parameter estimates in table A3. In all cases, the best models assume that the different parasitoid species have identical effects on budworm mortality and can therefore be treated as if they are a single parasitoid “species.”

WAIC scores, however, did not allow us to determine conclusively which of the top three models best explains the data. For model 2, which includes direct density dependence but no effect of DBH,  $\Delta\text{WAIC} = 1.08$ . For model 3, which includes a DBH effect that does not affect density-dependent mortality,  $\Delta\text{WAIC} = 1.50$ . A  $\Delta\text{WAIC}$  value  $>3$  is generally considered to be sufficiently large to indicate that two models are meaningfully different (Burnham and Anderson 2004; Watanabe 2010). We reach similar conclusions by comparing models using the weight of the WAIC scores, which gives the probability that a given model is the best option among the models considered (Wagenmakers and Farrell 2004). There is a 39% chance that model 4 is the best model, while models 2 and 3 have 22.7% and 18.4% chances, respectively, of being the best model. Together, these top three models have a combined weight of 70.1%. The other three models, however, can be ruled out more conclusively. The fourth-best model is model 5, which has a nonlinear effect of DBH, with  $\Delta\text{WAIC} = 5.20$ . In this model, very small and very large

**Table 1:** Watanabe-Akaike information criterion (WAIC) scores for a subset of our competing models, with the remaining scores included in the appendix

Model	Description	$k$	Penalty	$L$	$\Delta\text{WAIC}$	wWAIC
1	Parasitoid attacks only	5	8,200	-365.93	16,517.6	.000
2	<i>Direct density dependence</i>	7	1.36	-312.88	1.08	.227
3	<i>DBH effect</i>	7	.892	-313.55	1.50	.184
4	<b>Linear DBH affects direct density dependence</b>	7	<b>.816</b>	<b>-312.88</b>	<b>.0</b>	<b>.390</b>
5	Nonlinear DBH affects direct density dependence	9	2.48	-313.8	5.20	.029
6	Independent DBH/direct density dependence	8	3.32	-314.21	7.70	.008

Note: The column labeled “Penalty” shows the WAIC penalty calculated for each model. The best model is in boldface, and the second- and third-best models are in italics. “Independent DBH/direct density dependence” refers to a model for which the effect of diameter at breast height (DBH) acts as an independent influence on insect mortality rather than as a covariate on the effects of direct density dependence.  $\Delta\text{WAIC}$  = WAIC differences; wWAIC = weight of the WAIC score.



trees are poorer-quality host plants for the insects than trees of intermediate size, but any such nonlinear effects were weak enough in our data that the linear model provides a much better explanation for the data.

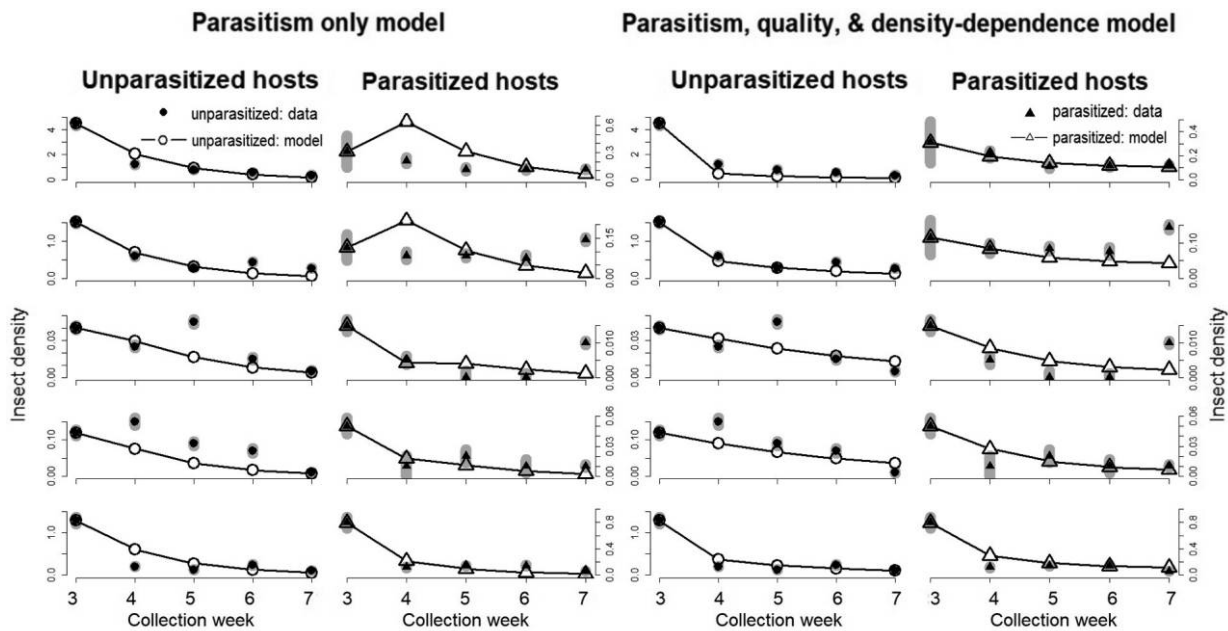
Our WAIC analysis thus confirms that budworm mortality is affected both by density-dependent parasitoid attacks and by competition for resources. The analysis also provides evidence that increasing tree age increases competition for resources, but the support for this argument is more modest, since the WAIC scores for the top 3 models are close enough that no one model is the overall winner. The model in which density-dependent mortality increases with increasing tree age, however, suggests a mechanism underlying resource competition in the form of age-related variation in host tree quality. This is important because forest fires usually reduce the average age of the trees in jack pine forests (McCullough 2000), so the effect of tree age in our results suggests that there may be feedbacks between fire and jack pine budworm outbreaks.

The better fit of the best model is clearly apparent in visual comparisons of the output of model 4, which includes effects of both parasitoids and resource competition, and model 1, a host-parasitoid-only model, when plotted against the observational data. As figure 4 shows, at high densities the host-parasitoid-only model sometimes predicts that the

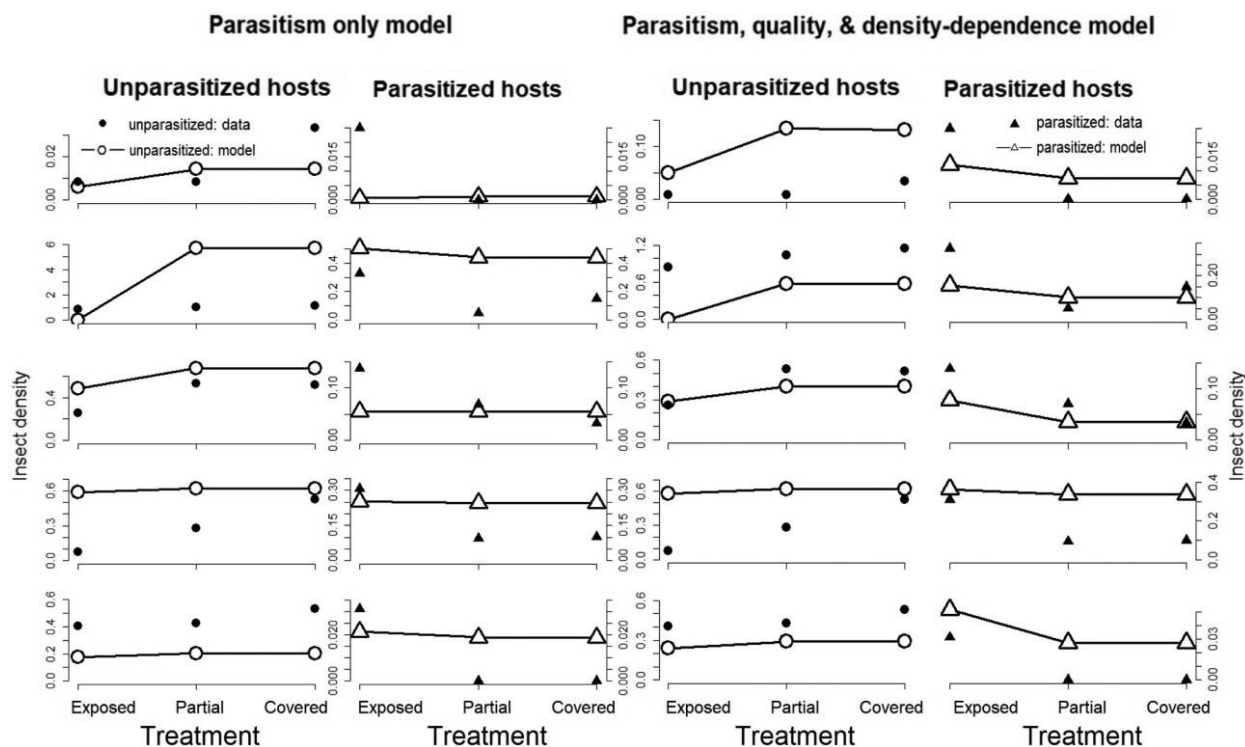
density of parasitized hosts will increase during the larval period, whereas in our data the density of parasitized hosts almost always decreased during the larval period. More generally, the model that allows for resource competition does a better job of describing the decline in the density of either unparasitized or parasitized hosts than the host-parasitoid-only model.

The best model also provides a visually better fit to individual replicates of our experimental data (fig. 5). In the case of these individual replicates, sample sizes were often small enough that binomial variation was substantial (for clarity, we omitted the binomial confidence bounds on the data). The visual fit to the experimental data is therefore always imperfect, but the experimental data were nevertheless extensive enough to substantially strengthen our inferences. The model with resource competition provides a better fit to these data than a model without resource competition, because the effects of resource competition led to greater differences in the density of unparasitized and parasitized hosts between experimental treatments.

To better understand the effects of larval host density on the relative impacts of parasitoid attacks and resource competition, in figure 6 we show predictions of cumulative mortality for our best model and for the host-parasitoid-only model across a range of host densities. As the figure shows,



**Figure 4:** Fit of two of our models (columns) to observed host and parasitoid density data for five of our 22 site-year combinations (rows). These five examples were chosen to show the model fit across a range of insect densities. The panel on the left shows the fit of the simplest model (model 1), which includes only the density-dependent effects of parasitoid attacks, while the panel on the right shows the fit of the best model (model 4), which includes increasing density-dependent mortality with tree age. Insect densities are reported in terms of larvae per bud. Gray bars on the data show 1 SEM, calculated across replicate samples from each site.



**Figure 5:** Fit of two of our models to final host and parasitoid densities for each of three treatments, for five of 38 experimental data sets. As in figure 4, these five examples were chosen to show the model fit across a range of insect densities. “Exposed” indicates branches with no bags, “Covered” indicates branches with bags, and “Partial” indicates branches with control bags that have holes in them. Each row indicates a different experiment. Also as in figure 4, the panel on the left shows the fit of the simplest model (model 1), which allows only for density-dependent parasitoid attacks, while the panel on the right shows the fit of the best model (model 4), which also includes effects of increasing density-dependent mortality with diameter at breast height. Note that both models show a modest but general trend of increased survival and decreased parasitism on bag-covered branches, which were protected from ongoing parasitoid attacks. Insect densities are reported in terms of larvae per bud. Error bars have been removed for clarity.

mortality increases sharply with increasing host density in both models, consistent with previous studies (McCullough 2000). For the best model, however, direct density-dependent mortality dominates at the highest densities, with parasitoid-induced mortality having only minor impacts at these densities. Resource competition and tree quality therefore appear to play key roles in terminating budworm outbreaks. Although previous work has identified effects of resource limitation on other outbreaking insects (Abbott and Dwyer 2007; Elder et al. 2013), the importance of density dependence in our best model provides some of the strongest evidence that resource limitation and host plant quality can affect outbreaking insects.

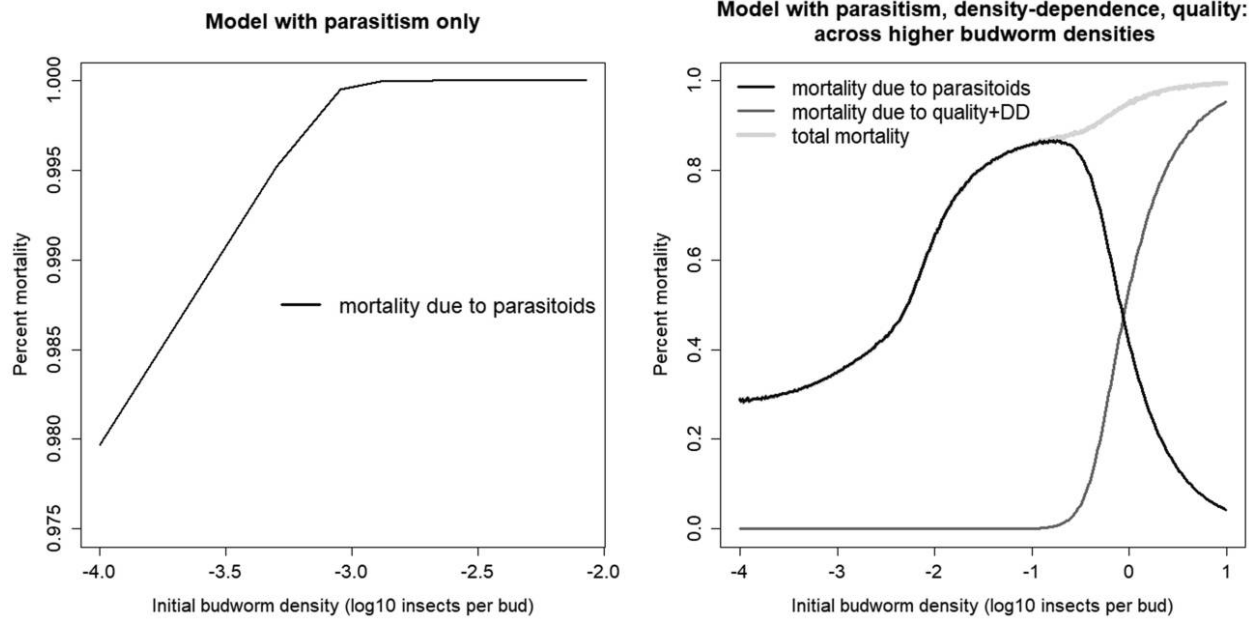
### The Long-Term Models

#### *Long-Term Model Construction and Fitting Routine*

To understand the implications of our model-fitting results for budworm outbreaks, we extended our short-term mod-

els to allow for jack pine budworm reproduction and for the parasitoid attacks that occur shortly thereafter. Jack pine budworm reproduce once a year, in late summer, laying eggs that hatch after 1–2 weeks. Newly hatched larvae do not feed but spin silk hibernacula and overwinter on the tree trunk. At around the time of budworm hatch, adult parasitoids attack the newly hatched larvae, and parasitoid larvae then overwinter within these hosts.

In what follows, we present results for simulations of long-term models based on three of our short-term SEIR models: the model with mortality due to parasitoids alone (model 1), the model that also includes direct density-dependent effects (model 2), and the best model, which includes quality effects on direct density dependence (model 4). Our long-term models then consist of a differential equation model of larval mortality linked to a set of difference equations that describe host reproduction and parasitoid overwintering. To make this link, we first express the initial conditions for the differential equations (1)–(4) in terms of the host density  $N_n$  and the parasitoid density  $Z_n$  in generation  $n$ :



**Figure 6:** Effects of density on cumulative mortality in a parasitoid-only model (*left*) and in the best model (*right*) across a wide range of densities. Densities generally span the range that we observed in our study plots, as evidenced by densities at time zero in figure 2, except that for the parasitoid-only model we restricted the upper range, for which parasitoid-induced mortality is very close to 1. Initial budworm densities are in terms of larvae per bud on a  $\log_{10}$  scale.

$$S(0) = N_n, \tag{5}$$

$$E_1(0) = Z_n. \tag{6}$$

Here,  $S(0)$  is the unparasitized host population at the beginning of the larval period, and  $E_1(0)$  is the initial density of parasitized hosts.

We then construct difference equations for host density  $N_{n+1}$  and parasitoid density  $Z_{n+1}$ , which account for budworm reproduction and overwintering survival, along with parasitoid attacks at time  $T$ , the end of the larval period:

$$N_{n+1} = \lambda e^{\epsilon_n} S(T), \tag{7}$$

$$Z_{n+1} = \beta P(T) \lambda S(T). \tag{8}$$

Here,  $S(T)$  and  $P(T)$  correspond to the density of susceptible budworms and adult parasitoids at time  $T$ , the end of the larval period. Values for  $S(T)$  and  $P(T)$  are calculated by the larval SEIR models. The parameter  $\epsilon_n$  is a Gaussian random variate, exponentiated to avoid negative values;  $\epsilon_n$  thus allows for weather-driven variation in the dynamics across years.

The symbol  $S(T)$  represents the insects that have survived to adulthood and will therefore reproduce, with net fecundity  $\lambda$ , leading to host density  $N_{n+1}$  the following spring. Here,  $\lambda$  accounts for both reproduction and density-independent

overwinter mortality. The parasitoid population in the following spring  $Z_{n+1}$  consists of the offspring of the parasitoids at the end of the previous generation  $P(T)$ . These parasitoid offspring result from attacks on the offspring of the surviving hosts,  $\lambda e^{\epsilon_n} S(T)$ . Here, late-summer parasitoid attacks follow a type I functional response, equivalent to the functional response in a Lotka-Volterra predator-prey model (Gotelli 2008), with attack rate  $\beta$ . We used a type I functional response because all newly hatched budworms are in the susceptible class at the end of the summer, as opposed to the mix of exposed and susceptible larvae at the beginning of the spring. Parasitoid interference is therefore less likely to be an important factor shortly after budworm hatch. Moreover, including a more complex functional response would have made it necessary to estimate an additional parameter, and our overwinter data are more limited than our larval mortality data. The addition of further parameters might therefore have resulted in overfitting.

During the larval periods in 2013 and 2014, we collected data from seven field sites in Michigan, and in 2015 we collected data from five of these seven sites. We therefore had 12 transitions with which to estimate the budworm reproductive rate  $\lambda$  and the parasitoid attack rate  $\beta$  (table A5). We only needed to estimate two parameters, so we used a simpler approach to estimate  $\lambda$  and  $\beta$  than was previously used to estimate parameters for the larval mortality model.

We then used the variation in  $\lambda$  across years and sites to estimate, on a log scale, the variance in the stochasticity term  $\epsilon_n$ .

To allow for variation in tree quality, we simulated each model on a forest of 2,500 jack pine trees. Initial simulations of a forest with simple tree growth and death terms but without fire showed that within 100 years the forest becomes dominated by a few very large jack pines. The effects of forest fires on jack pine forests are sufficiently complex that they are beyond the scope of this work, and so in the interest of simplicity we assumed that trees neither grow nor die but instead have fixed size. For the purposes of our model, this means only that the trees have a fixed quality. We further assumed that the trees were all relatively large (40 cm DBH) and therefore of low quality. It is not unusual that jack pine forests mostly consist of large trees (Kenkel et al. 1997), and the low-quality case provides the strongest distinction between the models with and without quality effects. In the appendix, we also show simulations from a case with young, high-quality trees. As expected, under high tree quality conditions, simulating the model with quality effects results in cycling behavior that is more similar to the model without quality effects.

The long-term model first simulates the SEIR model to calculate the density of surviving hosts,  $S(T)$ , and emerging parasitoids,  $P(T)$ . The SEIR model uses the initial density on each tree to determine larval survival on that tree. The densities of surviving hosts  $S(T)$  and parasitoids  $P(T)$  are then summed across all trees and used in the difference equations (7) and (8). The distribution of insects within sites was underdispersed and thus highly regular, and both the budworm and its parasitoids have high dispersal rates (Nealis and Lysyk 1988; McCullough 2000). We thus assumed that parasitized and unparasitized hosts are distributed evenly across trees at the beginning of the larval feeding period in each generation. The model therefore does not include effects of spatial structure.

#### *Long-Term Model Behavior*

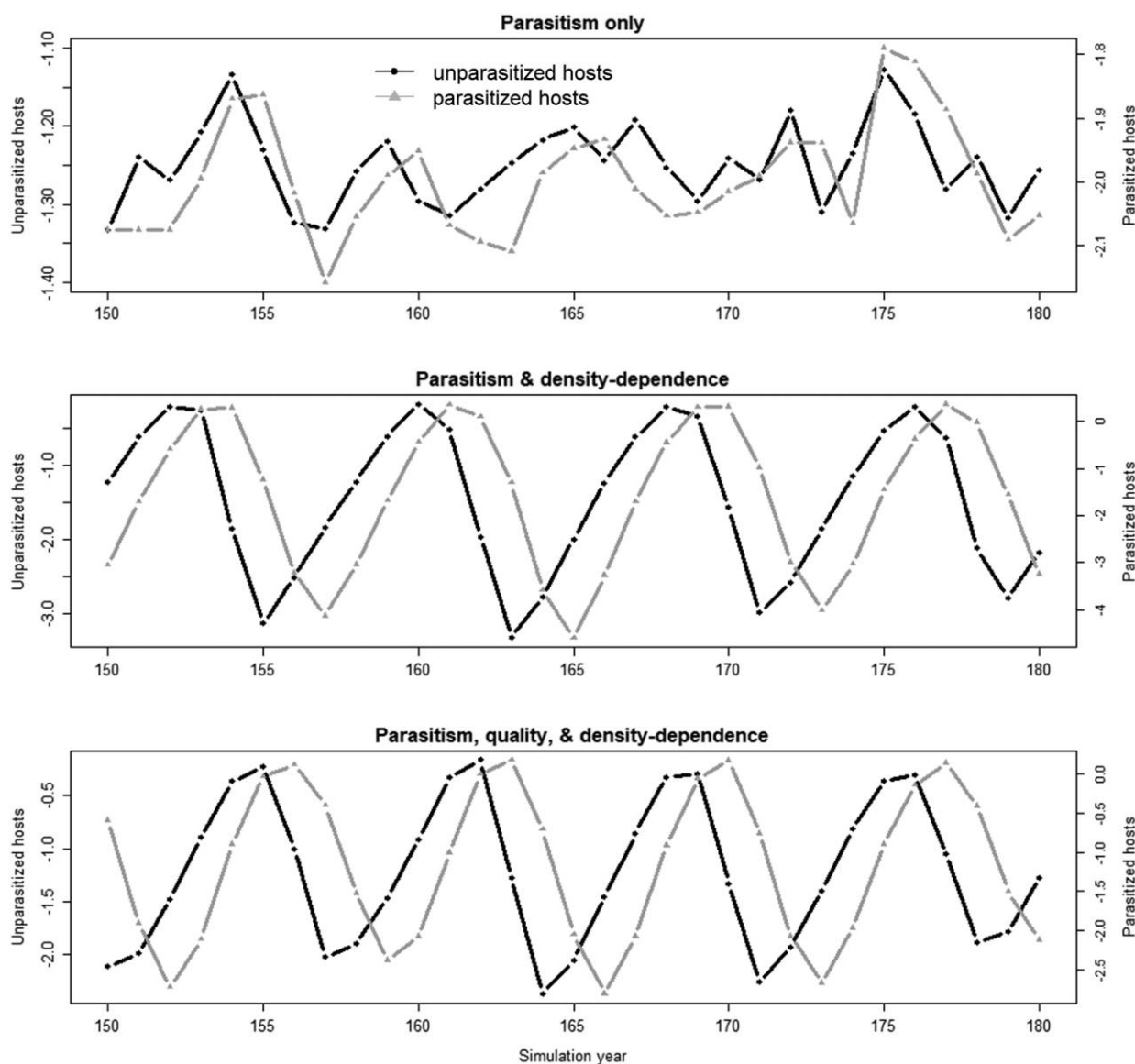
In figure 7 we show simulations of the long-term models. The first model includes only the host and the parasitoid; the second includes the host, the parasitoid, and resource competition; and the third includes the host, the parasitoid, and quality-dependent resource competition. Although the SEIR models with resource competition provide by far the best fit to the larval survival data, the model with only the host and the parasitoid is useful for purposes of comparison. All three models produce outbreak cycles, but the severity of these cycles, as measured by the amplitude of the fluctuations, differs strongly between models (fig. 7). The model with only the host and the parasitoid has cycles with the shortest period (4.80 years; all periods are averages across 25 realizations)

and the smallest amplitude (0.115; all amplitudes are again averages across 25 realizations). The model with the host, the parasitoid, and resource competition has the longest period (7.55 years) and largest amplitude (2.66), and the model with quality-dependent competition has an intermediate period (6.90 years) and amplitude (1.88).

The result that the host-parasitoid model shows the shortest-period, smallest-amplitude cycles is at least moderately surprising, given that many host-parasitoid models show long-period, large-amplitude cycles (Varley et al. 1974; Cobbold et al. 2009; Nenzén et al. 2018). In our case, however, parasitoid competition for hosts, as determined by the parasitoid functional response in the model, strongly dampens the outbreak cycles. Indeed, in the absence of stochasticity, the host-parasitoid-only model approaches a stable equilibrium (long-term dynamics for all three models without stochasticity are presented in the appendix). Given the extent to which parasitoids compete for hosts, this high level of stability is perhaps unsurprising (Turchin 2003), but the stability of the host-parasitoid-only model stands in stark contrast to the pronounced cycles typical of host-parasitoid dynamics in other forest defoliators (Turchin et al. 2003).

Adding resource competition then leads to more severe cycles because the resulting direct density dependence becomes a strong driver of dynamics late in the outbreak cycle. The further addition of quality dependence to resource competition dampens the cycles slightly because here we assume that the trees are of low quality, which leads to more severe density-dependent mortality. As we show in the appendix, allowing for higher quality leads to less damping of the outbreak cycles and thus longer periods and larger amplitudes. Consistent with this unstable behavior, in a model with no parasitoids at all, hosts rapidly become extinct (not shown).

Long-term outbreak data for Wisconsin show a period of roughly 6–12 years (Volney and McCullough 1994). According to our data, natural outbreaks show a range of initial budworm densities that spans nearly two orders of magnitude (fig. 2). Simulations from the models with resource competition are thus most similar to the dynamics of budworm outbreaks in nature. It is of course true, however, that our assumption of fixed, low-quality trees is a significant simplification because fire would result in fluctuations in tree quality (Stocks 1987*b*). In a model with fire effects, tree quality would therefore be higher at least some of the time, likely increasing the period and amplitude of cycles in the model with quality effects. Given that the period and amplitude of the outbreaks in the quality-dependent model are shorter and less severe, respectively, than in outbreaks seen in nature, it may be that incorporating fire into the model will improve the fit of the model to outbreak data. For now, however, we argue simply that our models show that the combination of a host-parasitoid interaction and



**Figure 7:** Dynamics of the long-term models, using best-fit parameters estimated from our data. The Y-axes show the densities of unparasitized and parasitized hosts at the beginning of the larval period. Densities are in units of larvae per bud on a  $\log_{10}$  scale. Note that unparasitized and parasitized hosts are plotted on different scales and that each panel has its own scale, so that the dynamics are clearly apparent. The top panel is model 1 (see table 1), which includes only effects of the parasitoid. The middle panel is model 2, which includes both parasitoids and direct density dependence. The bottom panel is model 4, which includes parasitoid attacks, quality effects, and direct density dependence.

quality-dependent resource competition can lead to dynamics that cannot be easily intuited from classical theory.

### Discussion

Early studies argued that populations of herbivores are kept in check by natural enemies (Hairston et al. 1960). Classical models of insect outbreaks similarly include only natural

enemies, typically parasitoids (May and Hassell 1981; Godfray 1994) or pathogens (Anderson and May 1980). As early as 1979, however, Lawton and McNeill (1979) convincingly argued that data show that herbivorous insect populations are influenced by trophic levels both above and below them. Further empirical research has confirmed that insect mortality is often determined by both natural enemies and host plant foliage quality (Moreau et al. 2018), but few studies of

herbivorous insects have quantified the relative importance of these drivers (Hunter 2001; Walker and Jones 2001). More recent research has begun to fill this gap (Siemann et al. 1998; Larsson et al. 2000; Lingbeek et al. 2017; Mendes and Cornelissen 2017), in particular showing that natural enemies are more important for some insect species (Asimwe et al. 2016), while resource effects dominate in others (Denno et al. 2002). In some species interaction effects occur (Ochua-Hueso 2016), including in outbreaking forest defoliators (Klemola et al. 2007; Myers et al. 2011; Elder et al. 2013; Moreau et al. 2018). Theory is only beginning to catch up to data, however (Abbott and Dwyer 2007; Stieha et al. 2016; Nenzén et al. 2018), and so model fitting has played a minor role in most empirical studies.

In previous work on the jack pine budworm system, high levels of parasitism have been well documented (Nealis 1991; McCullough 2000). Multiple studies have also documented impacts of host plant quality on larval survival (Nealis and Lomic 1994; Regniere and Nealis 2007; Moreau et al. 2018). Combining data collection with model fitting allowed us to quantify the relative importance of different mortality sources across a range of insect densities. Moreover, our parameterized models show that a combination of a host-parasitoid interaction and quality-driven resource competition can together lead to results that cannot be easily predicted from classical theory. Indeed, traditional Lotka-Volterra models suggest that natural enemy interactions will tend to lead to unstable dynamics, while competitive interactions will tend to lead to stable dynamics (Gotelli 2008). In our models, in contrast, a natural enemy model yields less severe outbreaks and thus more stable dynamics, whereas a model that also includes resource competition yields more severe outbreaks and thus less stable dynamics.

As we described, the less severe cycles of the host-parasitoid model likely result from parasitoid interference, while the more severe cycles of the models with resource competition result from high direct density-dependent mortality at high budworm densities. Understanding these effects was greatly facilitated by using nonlinear fitting routines to analyze a combination of observational and experimental data. We therefore argue that high-performance computing has a key role to play in experimental field ecology. It is important to repeat, however, that a more realistic model would include the effects of fire, which may alter our results.

Historically, forest fires have played a crucial role in maintaining the health of jack pine forests (McCullough and Kulman 1991; McCullough et al. 1998). Forest fire frequency is currently increasing in western North America as a result of anthropogenic climate change (Abatzoglou and Williams 2016), and it may well increase in eastern North America as well (Wang et al. 2017). Our results suggest that increased fire frequency could increase the severity of jack pine budworm outbreaks because the younger forests that result from

fires are of higher quality and therefore may result in larger-amplitude cycles. Additionally, outbreaks of the closely related spruce budworm increase the chance of fire in mixed spruce/jack pine forests (James et al. 2017), likely because insect defoliation kills branches and trees, leading to a buildup of fuel. A similar increase in fire risk could occur in jack pine forests as a result of jack pine budworm defoliation (McCullough 2000).

Climate change may therefore interact with budworm outbreaks to increase fire frequency beyond what jack pine forests can tolerate. Predicting this type of ecological effect of climate change is difficult due to the complexity of both natural ecosystems and the climate system (Bergeron and Flannigan 1995; Carcaillet et al. 2001; Dale et al. 2001; Tweiten et al. 2009; Knorr et al. 2016), but our models have allowed us to quantify some of the factors involved in the jack pine budworm system. In future work, we will therefore consider in greater detail how climate change is likely to alter the interaction between jack pine budworm outbreaks and forest fires and thus how climate change will affect jack pine forests.

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