THE UNIVERSITY OF CHICAGO

COMBINING HIGH-PERFORMANCE COMPUTING AND ECOLOGICAL FIELD EXPERIMENTS TO UNDERSTAND INSECT OUTBREAKS

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DEPARTMENT OF ECOLOGY AND EVOLUTION

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ABSTRACT

Effectively managing outbreaks of defoliating insects requires an understanding of the factors regulating outbreaks, which in turn requires mechanistic models. Classical models of insect defoliators include only density-dependent attacks by natural insect enemies, but variation in host plant quality can also strongly affect defoliator survival. I have combined model fitting with field experiments and observational data collection to identify the mechanisms driving the complex dynamics of the forest defoliator jack pine budworm (Choristoneura pinus). I collected data in outbreaking budworm populations from 2012-2015, recording budworm density, rates of parasitism, tree quality, and climate measurements, as well as conducting parasitoid exclusion experiments. Then I fit mechanistic models to my observational and experimental data on jack pine budworm outbreaks, using non-linear differential equations. The results show that drivers of budworm population dynamics include direct density-dependence, density-dependent parasitoid attacks, and the effects of plant quality. I then embedded my model of larval mortality into an annual model of insect population dynamics and their interactions with jack pine trees and forest fires. This model shows that the influence of plant quality directly affects the period of insect outbreaks, which in turn changes the interval between forest fire events. My results indicate that before we can make predictions about the effects of climate change on fire frequency and forest health, we must understand the effects of defoliating insects.

CHAPTER 1

INTRODUCTION

Outbreaks of defoliating insects play a major role in deforestation. Insect pest control is therefore a key issue in protecting forest health (Liebhold and Kamata, 2000). Mitigation efforts require a quantitative understanding of the mechanisms driving outbreaks, but such an understanding remains elusive. Variation in plant quality and natural enemy attack rates influence larval survival, and are known to play key roles in determining outbreak periodicity and severity (Elderd et al., 2013; Hunter, 2001), but the relative importance of plant quality and natural enemies remains unclear. The literature on forest defoliators in particular has long been dominated by studies of natural enemies (Hairston et al., 1960), in part because simple models of host-parasitoid and host-pathogen interactions can quantitatively reproduce outbreak data, and because high levels of parasitoids and pathogens have often been observed in defoliator populations (Varley et al., 1974). The relative importance of plant quality and natural enemies in driving insect outbreaks is thus poorly understood. More broadly, interactions among defoliating insects, their host plants, and their natural enemies provide useful test cases for general theories about the joint effects of predators and resources on prey population dynamics.

Here I have quantified the relative impact of parasitoids and host plant foliage quality on the survival of a forest defoliating insect, the jack pine budworm (*Choristoneura pinus*). Interactions between the jack pine budworm, its food source, its parasitoids, and forest fires drive long-period cycles in budworm abundance. At intervals of 6-12 years, budworm outbreaks cause extensive defoliation and tree death (Nealis et al., 1997; Dixon and Benjamin, 1963; McCullough and Kulman, 1991a; Volney, 1988). Tree death and canopy defoliation, or “topkill” (McCullough, 2000), in turn leads to increased severity of wildfires (Flower et al., 2014; McCullough, 2000). Parasitoid mortality shows the density-dependent behavior that drives outbreaks in models, while larval mortality is known to be higher on very young jack pines (McCullough, 2000; Nealis, 1991), showing that tree quality also plays an important role. The relative importance of parasitoids and tree quality in this system, however, has not been previously quantified.

In principle, ecological models provide a means of understanding the relative importance of different mechanisms in population dynamics, but using models to make inferences requires substantial data sets (Bolker, 2008). In particular, a reliance on observational data alone increases the risk of incorrect inferences (King et al., 2008). Accordingly, to understand the relative importance of natural enemies and plant quality in determining jack pine budworm larval survival, I collected both observational and experimental data. I then implemented nonlinear fitting algorithms so that I could use mechanistic models to make inferences about the mechanisms operating in my study populations.

My observational data consist of density measurements of jack pine budworm larvae and their associated parasitoids over the course of the larval period. Data were collected from outbreaking jack pine budworm populations over the course of four years in the states of Wisconsin and Michigan, USA. These data allowed me to directly quantify the effects of parasitoids, but they do not distinguish between the effects of parasitoids and the effects of tree quality. To disentangle the effects of enemies and quality, I also carried out experiments in which I quantified mortality due to tree quality in the absence of parasitoid attacks.

In Chapter 2, to construct a model of larval mortality, I used a nonlinear fitting algorithm to fit a set of competing models to the observational and experimental data, such that some models included the effects of both parasitoids and tree quality, while other models included the effects of parasitoids alone. Next, I used WAIC model selection to choose between models, to show that the best model includes the effects of both parasitoids and tree quality on larval survival (Hooten and Hobbs, 2015; Gelman et al., 2014; Watanabe, 2010).

My models show that the effects of tree quality manifest as a modification of direct density dependence, so that quality modulates resource competition. In addition to having important implications for the management of jack pine forests, this result significantly broadens our understanding of the ways in which plant quality can affect insect population ecology, and more broadly adds to the growing consensus that quality may interact in complex ways with natural enemy attacks (Elderd et al., 2013; Hunter, 2001).

In Chapter 3, I then explored the long-term dynamics of the jack pine system. To construct a long-term model, I embedded the model of larval mortality into an annual model of the jack pine and jack pine budworm life cycle, with reproduction and discrete time steps. I included realistic fire behavior in the model and then varied parameters to understand how insect outbreaks, forest fires, and jack pine forests interact and affect one another. I showed that fires are a critical component of the system, as expected. Fires act to increase the period and amplitude of insect outbreaks, and maintain a high level of tree survival over time. The fire interval at which tree survival is maximized depends on the severity of insect outbreaks. My model also shows that insect outbreaks greatly increase variation in tree sizes, and that outbreaks help to drive the fire interval. From these results, it is clear that we cannot expect to understand and make predictions about the effects of climate change with incorporating the biology of forest defoliators.

CHAPTER 2

MODELING LARVAL MORTALITY

2.1 Introduction

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WAIC model selection to choose between models, to show that the best model includes the effects of both parasitoids and tree quality on larval survival (Hooten and Hobbs, 2015; Gelman et al., 2014; Watanabe, 2010). Our models show that the effects of tree quality manifest as a modification of direct density dependence, so that quality modulates resource competition. In addition to having important implications for the management of jack pine forests, this result significantly broadens our understanding of the ways in which plant quality can affect insect population ecology, and more broadly adds to the growing consensus that quality may interact in complex ways with natural enemy attacks (Elderd et al., 2013; Hunter, 2001).

2.2 Model construction

2.2.1 Biology

The first step in our research was to construct a set of competing models of larval budworm survival, based on budworm biology. Jack pine budworm is a defoliating insect native to Canada and the northern United States that feeds almost exclusively on jack pine (*Pinus banksiana*), a major component of North American forests (Hall et al., 1993; Mallett and Volney, 1990; McCullough, 2000). Outbreaks last 2-4 years and often result in heavy defoliation of jack pine trees, particularly in older or "overmature" trees, sometimes causing topkill or even tree death on a large scale (McCullough, 2000). Because jack pine is economically important to the logging industry, and young jack pine stands provide breeding grounds for the endangered Kirtland's Warbler (*Setophaga kirtlandii*), management of jack pine forests has significant conservation implications (Probst, 1986). Forest fires play an important role in the ecosystem, acting to release jack pine seeds from their serotinous cones and allow for regeneration of jack pine forests (Volney et al., 1995).

The budworm has a single generation per year, with the nonfeeding adults reproducing in late summer. Larvae hatch in the the fall and overwinter without feeding, before re-emerging in the spring to feed on pollen cones and eventually needles. Our models therefore track larval survival over the course of the feeding period, but not budworm reproduction. Because previous work has demonstrated the importance of the role of parasitoids in the system, all of our models include mortality due to parasitoid attacks. In our study populations, parasitoid mortality was largely (>99%) due to two Hymenopterans, the Braconid *Apanteles fumiferana* and the Ichneumonid *Glypta fumiferana*, as well as several species of hard-to-distinguish Dipterans in the family Tachinidae, which in the interests of simplicity we have grouped together. Parasitoids attack newly hatched budworm larvae and then overwinter within their host and emerge the following spring (Nealis and Lysyk, 1988). Previous work based on parasitoid infection rates at single time points indicated that the relevant parasitoid species have only a single generation per year (Nealis and Lysyk, 1988). Because we collected parasitoid data each week during the larval feeding period, our data instead show that additional parasitoid attacks on the same host generation occur during the larval feeding period. This is an important finding, because in order to model the larval population dynamics within the spring feeding period, we designed an SEIR epidemiological model that allows for multiple parasitoid generations within a single host generation. The SEIR model structure also allows for a time lag between parasitoid attack and death of the host, which in the budworm is roughly 14 days.

Because budworm densities are very high during outbreaks, larvae compete intensely for resources, so some versions of our models also include direct density-dependent mortality.

The main larval food source is pollen cones or male strobili (Nealis et al., 1997; McCullough, 2000), and pollen cone production, and thus larval survival, is very low on young trees (McCullough, 2000). Therefore in some versions of our model we included an explicit quality term, in the form of diameter at breast height ("DBH"), a measure of tree age. To ensure that DBH is a reasonable proxy for age, we took cores from a subset of trees and confirmed that counts of tree rings correlate well with DBH measurements in these trees ($r^2 = 0.75$, $p < 0.01$, $F(1, 14) = 41.23$; see Appendix 1).

In summary, all of our models include density-dependent parasitoid attacks, while a subset additionally include the effects of direct density-dependent mortality, and mortality due to low tree quality. We also allowed for different attack rates and behavior of the three parasitoid species, but designed the models so that if the effects of two or all three species are sufficiently similar, they can be grouped together. Our most complex model is then:

$$\begin{aligned}
\frac{dS}{dt} &= -\frac{\alpha_i \phi S P_i}{1+\rho_i P_i} - \gamma_1 S^{\gamma_2}((Q-\eta_1)^2+\eta_2)(S+\sum_{i=1}^{3}\sum_{j=1}^{m_i} E_{i,j}) && (2.1)\\
\frac{dE_{i,1}}{dt} &= \frac{\alpha_i \phi S P_i}{1+\rho_i P_i} - \gamma_1 E_{i,1}{}^{\gamma_2}((Q-\eta_1)^2+\eta_2)(S+\sum_{i=1}^{3}\sum_{j=1}^{m_i} E_{i,j}) && (2.2)\\
&\quad - m_i \delta_i E_{i,1}, \quad \text{for } i = 1,2,3 && (2.3)\\
\frac{dE_{i,j}}{dt} &= m_i \delta_i E_{i,j-1} - \gamma_1 E_{i,j}{}^{\gamma_2}((Q-\eta_1)^2+\eta_2)(S+\sum_{i=1}^{3}\sum_{j=1}^{m_i} E_{i,j}) \\
&\quad - m_i \delta_i E_{i,j}, \quad \text{for } j = 2, ..., m_i && (2.4)\\
\frac{dP_i}{dt} &= m_i \delta_i E_{i,j} && (2.5)
\end{aligned}$$

Here, S represents the density of unparasitized ("susceptible") budworms, while P_1, P_2, and P_3 represent the three parasitoids in our data, *A. fumiferana*, *G. fumiferana*, and Tachinid spp., respectively. The symbol α_i is then the attack rate of parasitoid i, while the parasitoid functional response terms $-\frac{\alpha_i \phi S P_i}{1+\rho_i P_i}$ depend on ρ_i, which scales the effect of each parasitoid species i on its own attacks. Because the parasitoids appear to have different biology, we assume that the density of each species affects only its own functional response. To allow for the possibility that parasitoid attack rates were different in experiments, we include the parameter ϕ, which adjust attack rates in experiments only. We do not allow for the possibility of co-infection by multiple parasitoids, as we saw only a single instance of coinfection over the course of our data collection. For parasitoid species i, the time in the jth parasitized-but-not-yet-dead or "exposed" class follows an exponential distribution with mean $1/m_i\delta_i$, where m_i is the number of exposure classes for that species. The total time that a budworm spends in the exposed classes is then the sum of m_i exponential random variates, which is known to follow a gamma distribution with mean $1/\delta_i$ and coefficient of variation ("C.V.") $1/\sqrt{m_i}$.

To explain the effects of tree quality and density dependence, we note first that $(S + \sum_{i=1}^{3}\sum_{j=1}^{m_i} E_{i,j})$ represents the total budworm population, allowing for each parasitoid species i and exposure class j. The parameters γ_1 and γ_2 then describe the influence of direct density dependence, due to competition for resources. The effects of tree quality affect density-dependent mortality through the covariate Q, measured in terms of DBH. Initial analyses suggested that the effects of quality on mortality may be a quadratic function of age, such that mortality is lowest on trees of intermediate size, and the strength of these effects is determined by the parameters η_1 and η_2. We also considered a model with linear effects of quality, which performed slightly worse.

From a statistical perspective, an important point is that, by allowing for effects of quality on direct density-dependent mortality, we introduce a covariate in the form of DBH to represent tree age. Tree age is one of several different ways in which variation between jack pines may affect budworm survival. Tree quality likely also influences budworm survival through other mechanisms such as differences in the number of pollen cones produced (Mc-

Cullough, 2000) and differences in the concentration of plant secondary compounds known as terpenoids (Raffa et al., 2005). In the models that include DBH effect, the underlying model structure differs only slightly from the models that allow for simpler forms of direct density dependence, but the models with DBH are much more mechanistic. This is important because, as we will show, the WAIC scores for models with DBH are only modestly better than for models that do not include covariates, but we argue that the models that include DBH nevertheless provide substantially stronger insight into the mechanisms determining budworm survival.

2.2.2 Model behavior

Our suite of competing models are very different in structure, but because larval densities can only decline with time, the models differ show only slight differences in behavior, mostly in terms of the speed of the decline in larval densities (fig. 2.1). As 2.1 shows, direct density dependence can increase mortality by as much as a percentage point, a difference that may have important effects for outbreak cycles over the long-term. When initial parasitoid densities are low, parasitoid densities increase sharply early in the season. Tree quality can strongly modulate these effects, such that when initial parasitoid densities are low, the initial rise in the parasitoid population is noticeably lower on low-quality hosts. At both low and high initial parasitoid densities, higher quality trees lead to slower declines and in budworm densities, and overall lower mortality.

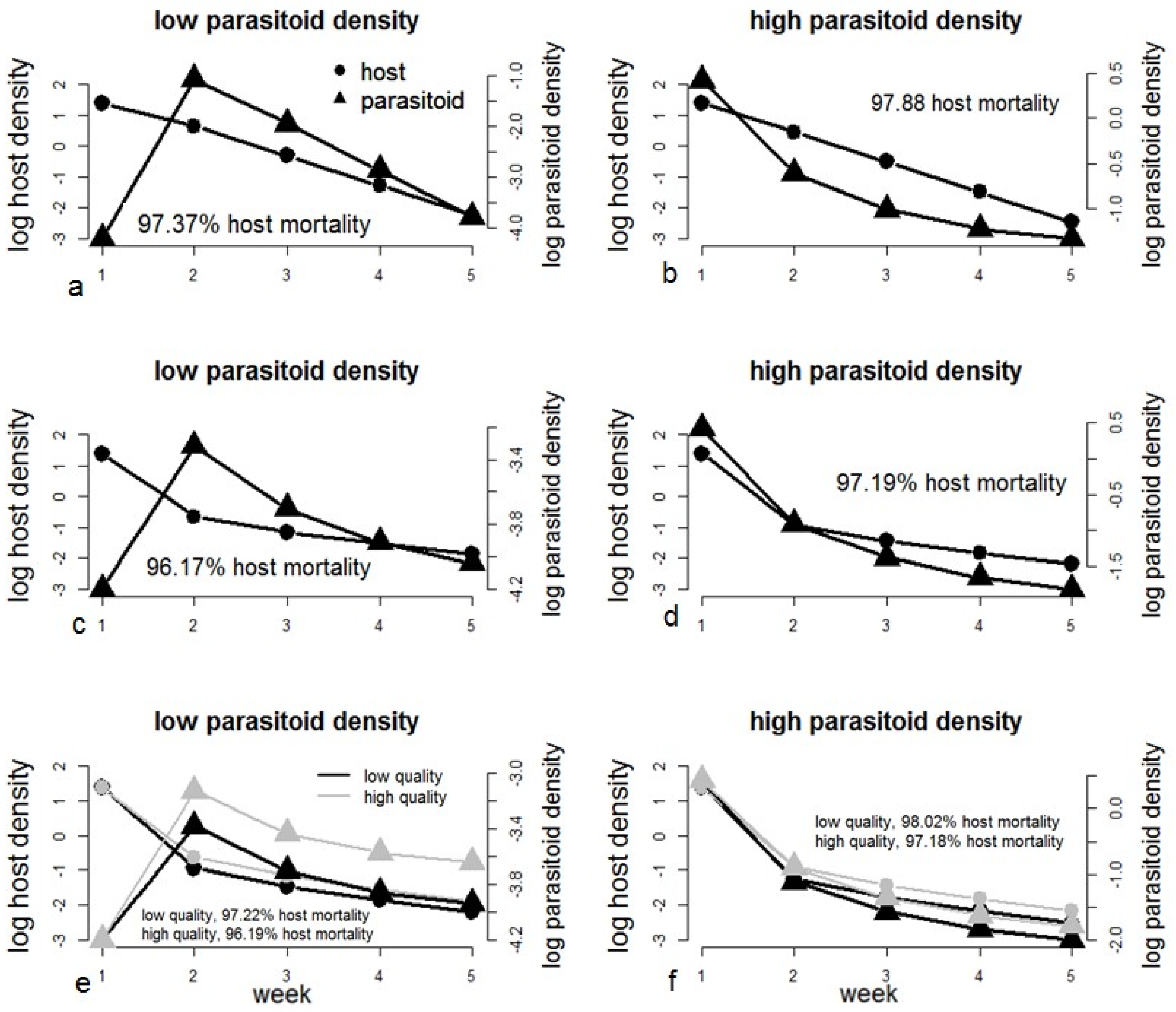

Figure 2.1: Larval mortality is reduced on high quality trees

Figure 2.1 shows comparisons of the model output for three competing models, under different parasitoid density conditions. The third model also shows model behavior under varying plant quality conditions. Shown here are parasitoid insects that emerged from hosts collected in the field, meaning that they are represented in the model by the sum of the exposed classes, rather than the final adult parasitoid class. Note also that host and parasitoid density are shown on different scales.

2.3 Testing the models

2.3.1 Methods and data collection

Observational data

In 2012, we sampled budworms from an outbreak in Wisconsin, at three sites that spanned a distance of 40 km north to south, and at included two high density sites and one intermediate density site. Because the budworm populations in Wisconsin collapsed in 2012, from 2013-2015, we sampled budworms from seven Michigan sites that spanned a distance of 25 km north to south, and that include a wide range of jack pine budworm densities.

At each site, we recorded the DBH of each sampled tree, and we measured larval budworm density and parasitism over the spring feeding period by collecting fifty branch tips from each of five trees. We repeated this process weekly, beginning with larval emergence in May and continuing until pupation in June or July, for a total period of eight weeks annually. To determine the fraction of sampled larvae that had been attacked by each parasitoid species, we reared the collected larvae in the laboratory.

Experimental data

To disentangle the effects of parasitism from the effects of tree quality and resource competition, we experimentally excluded parasitoids on branches at three sites in Michigan that included a range of budworm densities. To eliminate parasitoid access to budworm larvae, we covered branches with mesh bags. As partial controls, we covered some branches with bags from which two 10 × 10 mm squares of fabric had been cut, allowing parasitoids to access the larvae. Bags stayed on branches for 1-6 weeks, and tree quality was measured in terms of DBH, which our initial samples showed had strong effects on larval survival. This allowed us to account directly for mortality due to ongoing parasitoid attacks. Additional differences in mortality between control and experimental branches were then indicative of the effects of tree quality.

Experiments included between two and six trees per site, and six branches per tree, such that two branches on each tree were enclosed in uncut bags, two were enclosed in cut bags, and two were not enclosed in bags at all. At the end of each experiment, we removed surviving budworms and raised them in the laboratory. As we will show, survival rates were lower than can be explained by parasitoid mortality alone.

2.3.2 Fitting the models to the data

To fit models to our data, we used a computationally intensive nonlinear fitting algorithm. In this algorithm, we calculated likelihood scores using a Poisson probability distribution. The

Poisson distribution is appropriate for count data (Pawitan, 2001), but it assumes that the mean and variance of the data are roughly equal. Although in ecological data the variance is frequently higher than the mean, our data are not overdispersed. The average variance to mean ratio for host density across sites was 0.67, with 95% confidence bounds of 0.30 to 1.04. The average variance to mean ratio for parasitoid density was 0.24, with 95% confidence bounds of 0.13 to 0.35. We then used Bayes's theorem to calculate the posterior distribution of the model parameters. To do this, we used a modification of Metropolis-Hastings Markov chain Monte Carlo (MCMC) known as line search MCMC (Kennedy et al., 2015). Line search MCMC takes advantage of modern highly parallel computing environments by using a large number of line searches to automate proposal construction.

In the first step in this algorithm, we mapped out the likelihood surface using a simple version of an algorithm known as "line search", in which one parameter is systematically varied while the others are kept constant, and each parameter is allowed to vary in turn (Press et al., 1992). The results of this algorithm are sensitive to the starting values of the parameters, but by running the algorithm many times in parallel, it is possible to locate regions of parameter space that produce high likelihoods. In the second step in the algorithm, we used the top 5 to 10% of the parameter combinations from the line searches in principal components analysis (PCA) to generate proposal distributions for MCMC. In the MCMC step in the algorithm, we therefore drew from normal distributions with means and variances from the PCA analysis before back-transforming to the original coordinate system of the model parameters. The resulting proposed parameter values are almost entirely uncorrelated, which greatly improves the mixing of MCMC chains (Kennedy et al., 2015).

Although line search is generally less efficient than MCMC, a large enough number of line searches should give effectively identical results to MCMC. This is important because it means that, by comparing the results of the MCMC algorithm to the results of the line search algorithm, we could test whether MCMC did indeed provide better results than line search, and more generally whether the two algorithms were able to locate similar areas of high likelihood. Therefore we calculated AIC scores for each model (Burnham and Anderson, 2004) using the maximum likelihood from the line searches, and WAIC scores (Gelman et al., 2014) from the thinned posterior distribution of the MCMC chains for each model. Because AIC is an approximation to WAIC that is in general overly optimistic, the AIC values should be modestly higher, and in every case but one, this proved to be the case (see Appendix 3). The one exception was the simplest model, for which the WAIC score was vastly higher than the AIC score. This likely occurred because that model violated the assumption of AIC that the model in question is a reasonable approximation of the unknowable true model (Konishi and Kitagawa, 2008).

To further test for the convergence of our MCMC chains we first inspected trace plots for all parameters to verify mixing. We then calculated Gelman-Rubin statistics, which are effectively equal to the variance across chains divided by the average variance within chains. Because we drew the initial parameter set for each chain with an inflated variance for each parameter, the variance across chains will always be larger than the variance within chains, but in our case, all Gelman-Rubin values were below 1.1, strongly indicating convergence (Gelman et al., 2014).

2.3.3 Results

At our study sites, declines in larval budworm populations were always large, but the severity of the decline was much higher in higher-density populations (fig. 2.2).

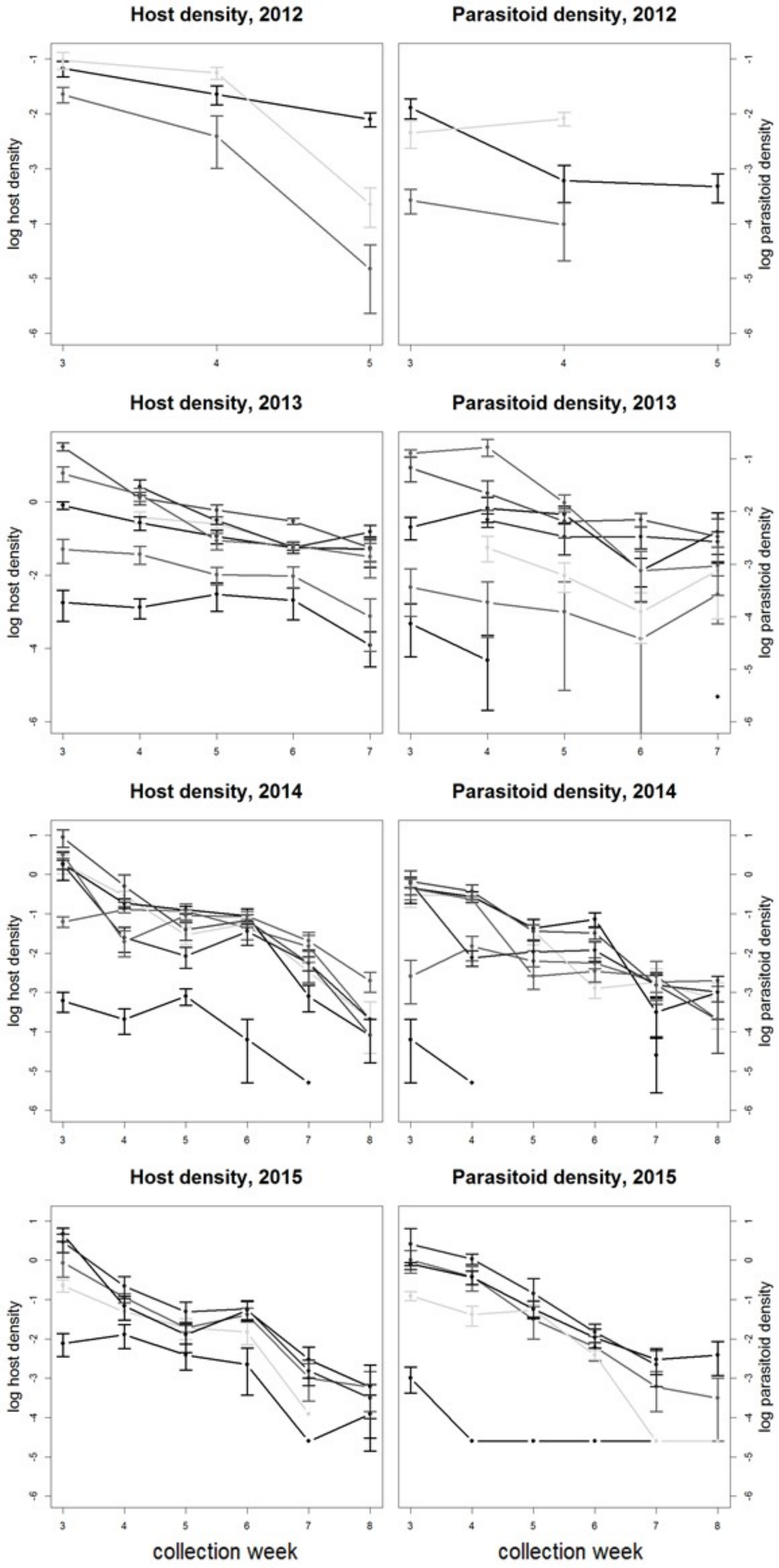

Figure 2.2: Larval budworm populations exhibit density-dependent declines

Changes in the density of unparasitized and parasitized budworms in our study sites in Wisconsin and Michigan, between 2012 and 2015. Each line indicates the population density at a given site over time. Our data include between 3 and 7 sites per year.

Parasitoid densities in our experiments were much lower on branches inside bags, confirming our model assumption that parasitoid densities increase during the larval period, and contradicting the conclusion of previous work arguing that parasitoids attacks only occur in the fall (Nealis, 1987). It might be possible to make inferences about these experimental data by using a generalized linear statistical model, but by fitting a more mechanistic model we can take into account a wide range of factors, thereby improving our statistical power in detecting effects of plant quality.

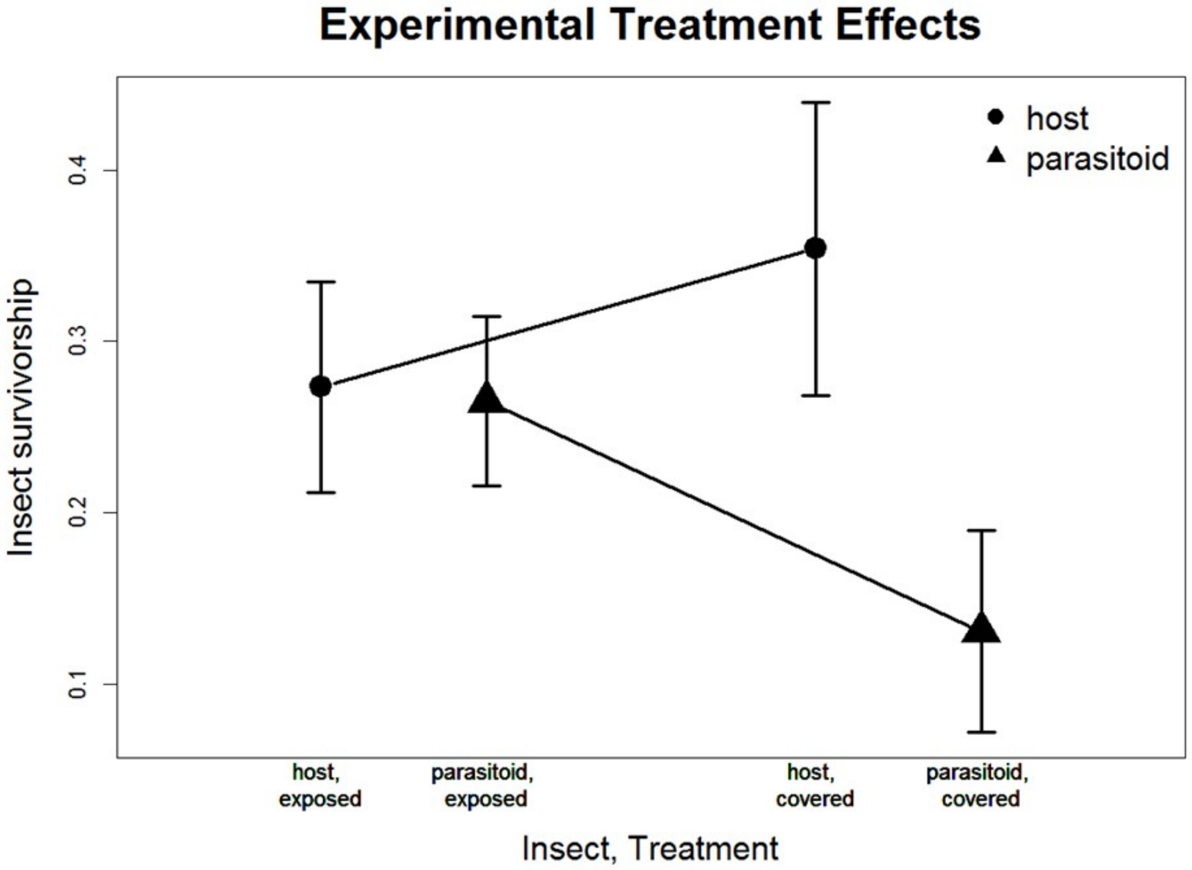

Figure 2.3: Experiments show the effects of ongoing parasitoid attacks

Figure 2.3 presents the effects of parasitoid-exclusion treatments on densities of parasitized and unparasitized budworms in our experiments. Each point is a mean across all experiments, and error bars show 1 standard error of the mean. Because of the strong effects of parasitoids, a model that includes only density-dependent parasitoid attacks explains most of the variation in the observational data (fig. 2.4). In addition, however, our experiments provided some evidence that DBH affects larval mortality, and including quality improves the fit of our models both to observational data (fig. 2.4), and to experimental data (fig. 2.3).

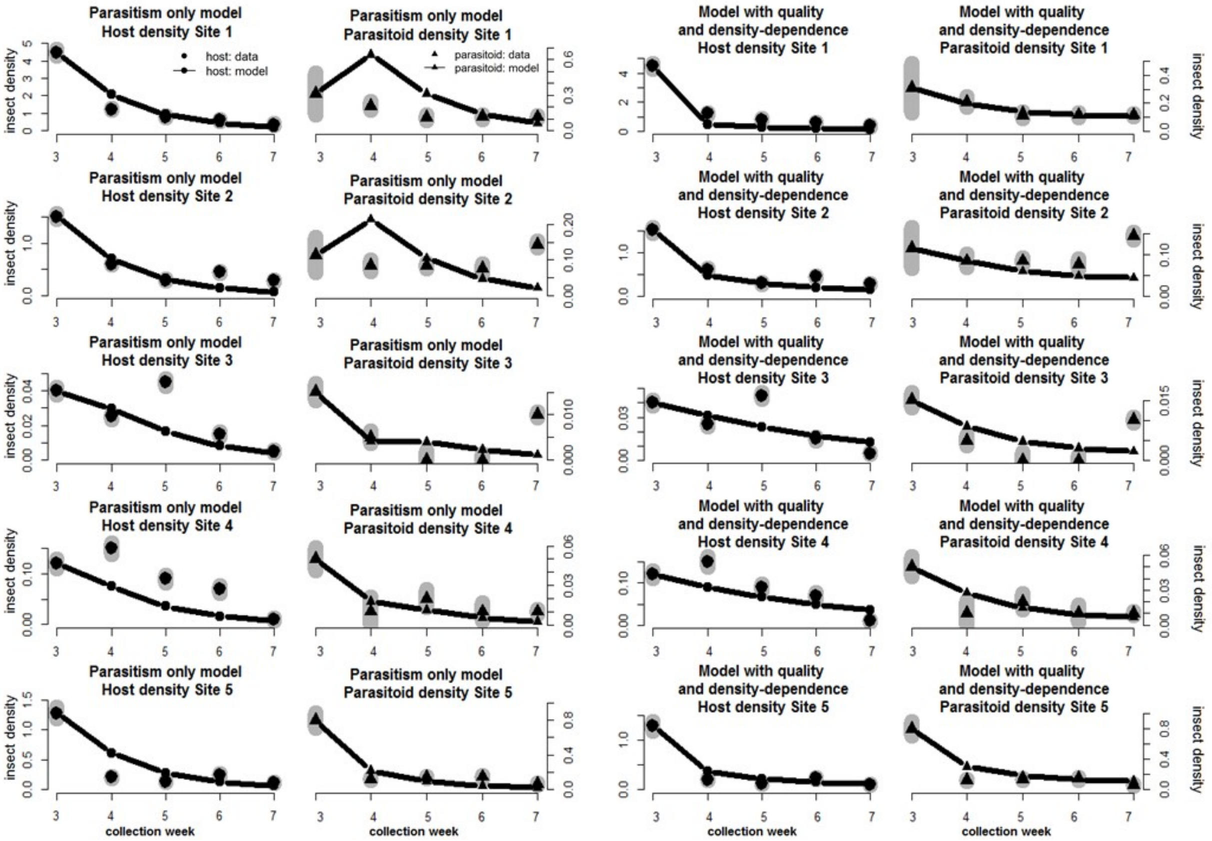

Figure 2.4: Fitting models to observational data

The fit of two of our models to observed host and parasitoid density data for 5 of 22 total sites. The panel on the left of figure 2.4 shows the fit of a model that includes the effects of a single parasitoid species, while the panel on the right shows the fit of a model that includes three different parasitoids, as well as the effects of tree quality, in terms of DBH. Gray bars on the data show one standard error of the mean, calculated across replicate samples from each site.

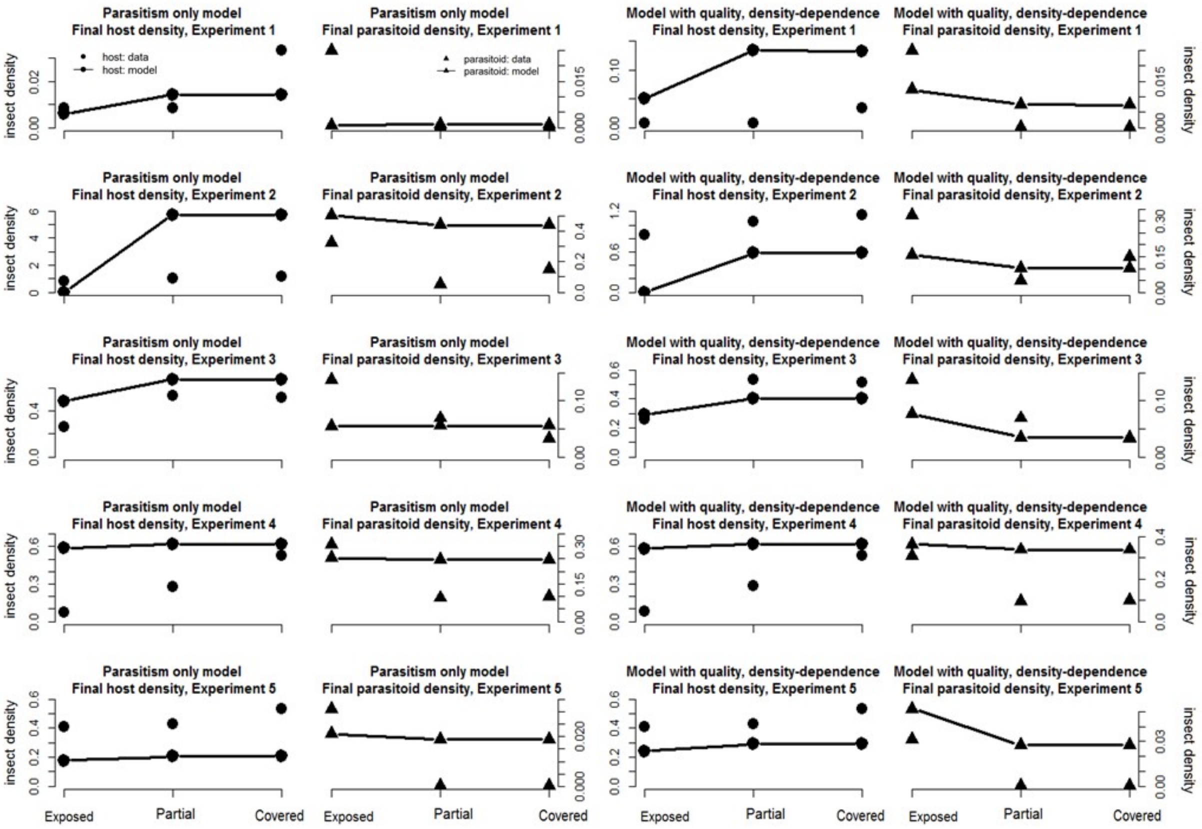

Figure 2.5: Fitting models to experimental data

The fit of two of our models to final host and parasitoid densities for each of three treatments, for 5 of 38 experimental datasets. The panel on the left shows the fit of the simplest model, which allows only for density-dependent parasitoid attacks. The panel on the right shows the fit of the best model, which also includes effects of direct density dependence that are modulated by tree quality. In addition to capturing the trend of increased survival and decreased parasitism on covered treatments in the data, this model also tracks the empirical data points more closely than the simpler model. Note that both models show the general trend of increased survival and decreased parasitism for covered treatments, which were protected from ongoing parasitoid attacks.

These qualitative results are confirmed by WAIC scores (Table 2.1), which show that the two best models both include three parasitoid species, and effects of DBH on direct density dependence. We could not use WAIC scores to determine which of the two most competitive models is a better fit to the data, as $\Delta\text{WAIC} = 0.20$ for the model with linear effects of DBH (Burnham and Anderson, 2004; Watanabe, 2010). In the model with a nonlinear effect of DBH, very small and very large trees are poorer quality host plants for the insects than are trees of intermediate size, but these nonlinear effects are weak enough that the linear model explains the data nearly as well.

We also calculated the weight of the WAIC score for each model. Models numbered 4.3 and 5.3 in 2.1 have a combined weight of 0.748, meaning there is a 74.8% chance that one of these two models is the best candidate out of the 18 competing models (Wagenmakers and Farrell, 2004). We therefore have strong evidence that including the effects of host plant quality significantly improves the ability of our model to predict larval mortality. Nevertheless, the third-best model, which includes direct density dependence without including effects of DBH, also explains the data well, suggesting that the effects of DBH are arguably not necessary. We nevertheless argue that the models that include DBH effects provide the deepest insight into the mechanisms determining budworm survival, especially given that forest fires have strong effects on jack pine forest health and budworm population cycles(McCullough, 2000). Taking into account DBH, and thus tree age, thereby provides better understanding, but the model without DBH effects has the advantage of requiring less data.

Table 2.1: WAIC scores confirm a significant nonlinear effect of quality

Model	# P'toid spp.	Description	k	L	ΔWAIC	wWAIC
1	1	Parasitoid attacks only	5	-398.49	16440.27	0.000
1	2	Parasitoid attacks only	9	-365.31	51.15	0.000
1	3	Parasitoid attacks only	13	-365.05	52.20	0.000
2	1	Direct density dependence	7	-348.79	11.61	0.001
2	2	Direct density dependence	11	-343.28	6.20	0.018
2	*3*	*Direct density dependence*	*15*	*-340.74*	*2.30*	*0.124*
3	1	DBH effect	7	-349.20	14.20	0.000
3	2	DBH effect	11	-343.25	17.61	0.000
3	3	DBH effect	15	-343.25	11.44	0.001
4	1	Lin. DBH affects direct d-d	7	-349.30	21.51	0.000
4	2	Lin. DBH affects direct d-d	11	-343.28	5.79	0.022
4	*3*	*Lin. DBH affects direct d-d*	*15*	*-341.07*	*0.20*	*0.355*
5	1	Nonl. DBH affects direct d-d	9	-349.11	24.11	0.000
5	2	Nonl. DBH affects direct d-d	13	-345.46	11.96	0.001
5	**3**	**Nonl. DBH affects direct d-d**	**17**	**-340.32**	**0.00**	**0.393**
6	1	Independent DBH/direct d-d	8	-350.23	19.98	0.000
6	2	Independent DBH/direct d-d	12	-345.10	9.14	0.004
6	3	Independent DBH/direct d-d	16	-345.51	15.04	0.000

WAIC scores for our competing models shown in table 2.1 confirm a significant nonlinear effect of quality. Note that "d-d" = "direct density dependence", ΔWAIC = WAIC differences, wWAIC = WAIC weights, "Lin." = linear, "Nonl." = Nonlinear. The best model is in bold-face, and the second- and third-best models are in italics.

2.4 Discussion

Classical models of complex population dynamics in insects include only natural enemies, such as the parasitoids that we studied here (Godfray, 1994; May and Hassell, 1981). Empirical research has long since shown host plant foliage quality can also affect insect survival and reproduction (Hunter, 2001), but theory has only begun to catch up to the data (Abbott and Dwyer, 2007; Elderd et al., 2013). In particular, a key issue is that it is not obvious how quality and natural enemies interact to determine larval survival. By fitting models to data, we have provided an initial solution to this problem, because our approach allows us to estimate the effects of multiple sources of mortality acting on the same population at the same time. Our work thus provides important support for the growing consensus that host plant quality can affect defoliator population dynamics.

Our study allows for the effects of multiple interacting mortality factors on larval budworm survival, but as is the case with all ecological models, we could not account for every possible variable. For instance, we did not account for differences in insect density in different parts of the crown, which can vary in low-level outbreaks (Volney, 1988), or the location of the trees within a stand, which can affect pollen cone production (Radeloff et al., 2000); nor did we quantify the number of male pollen cones produced by each tree or each site. Pollen cones are the preferred food source of early instar budworm larvae, and their production is frequently suppressed by individual trees in the year following severe defoliation, resulting in decreased larval budworm survival (Kulman et al., 1963; Nealis, 1991). However, we measured and incorporated into the model the effects of tree age as approximated by DBH, which is also correlated with pollen cone production. And since tree growth is also known to be suppressed following heavy budworm defoliation (Gross, 1992; Kulman et al., 1963), our study also allows budworm defoliation to affect tree quality in subsequent years.

We also chose not to quantify the effects of generalist arthropod predators directly (Jennings, 1971), but instead accounted for this additional mortality implicitly through fitted parameters in the model. It is possible that a more complex model incorporating these variables could improve the fit, but we considered many different competing models in the course of our study, and we found that the most complex model formulation was not the best fit to the data. Furthermore, increasingly complex models would require additional data, and are often unnecessary to capture the the dynamics of a population, and can result in overfitting (Dwyer and Elkinton, 1993; Johnson and Omland, 2004).

This study makes use of many recent advances in high-performance computing, particularly the increases in computing speed and power that make the line search MCMC method possible (Kennedy et al., 2014). Overall, our method has many advantages over standard analyses of insect ecology data. We are able to directly estimate the contributions of multiple types of mortality at once, and also to incorporate experimental data, which previous uses of high-performance computing in ecology have not done (King et al., 2008; Streicker et al., 2012). We have therefore shown that high-performance computing is an extremely useful tool in experimental ecology, and demonstrated some of the methods that researchers can employ when fitting models to observational and experimental data.

In the future, the interactions between jack pine forests, jack pine budworm, parasitoid insects, and forest fires will be strongly affected by climate change. Predicting the effects of climate change is a difficult task due to the complexity of climate variables and natural ecosystems (Bergeron and Flannigan, 1995; Carcaillet et al., 2001; Dale et al., 2001; Knorr et al., 2016; Tweiten et al., 2009), but our models have allowed us to quantify much of the complexity in the jack pine system. Historically, forest fires are a critical component of the jack pine forest life cycle, and play an important role in maintaining long-term forest health (McCullough and Kulman, 1991a; McCullough et al., 1998). In future work, we will therefore consider the long-term dynamics of the jack pine system, and incorporate different climate scenarios into our models, in order to gain insight into the potential effects of climate change.

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CHAPTER 3

LONG-TERM POPULATION DYNAMICS

3.1 Introduction

Many forest insects undergo boom-bust population cycles, in which peak densities heavily defoliate forests, in some cases leading to widespread tree mortality. A longstanding explanation for these cycles is that they are driven by natural enemies such as parasitoids and pathogens, on the grounds that natural enemy mortality is high during insect outbreaks, and natural enemy models can explain outbreak data from nature. More recent empirical research has shown that plant quality can also affect insect mortality (Nealis and Lomic, 1994; Hunter, 2001), and theoretical research has shown that allowing for plant quality effects can improve the ability of natural enemy models to explain outbreak data (Elderd et al., 2013). In some cases, however, increased tree mortality may increase the frequency and severity of forest fires. A key unanswered question, then, is how does fire alter the interactive effects of host plant quality and natural enemies on long term forest health? This is a question of pressing importance, given that the changes in temperature and precipitation are predicted to drive increases in fire frequency and severity in much of North America (Heon et al., 2014).

Here we attempt to understand how natural enemies, host plant quality, and fire frequency and severity together drive outbreaks of the jack pine budworm, and alter the health and structure of jack pine forests. Jack pine forests are a strongly fire dominated ecosystem, with fires generally occurring at 28-56 year intervals. Jack pine budworm outbreaks often kill jack pine trees, and the resulting accumulation of dead branches and trees likely increases the frequency and severity of fires. Jack pine trees grow quickly. Mature jack pines are somewhat fire resistant, and fires allow the serotinous jack pine cones to release their seeds, encouraging forest regeneration following a fire. Sufficiently severe fires can kill even large trees, however, and given the expected increase in fire frequency, climate change may threaten the future survival of jack pine forests. Since tree mortality due to jack pine budworm also affect fire frequency and severity, budworm outbreaks may strongly exacerbate the effects of climate change.

A basic difficulty in understanding how the interaction between climate change, fire, and insect outbreaks affects forests is that the spatial and temporal scales involved are large enough that experiments are logistically impractical. Our approach is therefore to first construct a mathematical model of fire and insect outbreaks, in which model parameters were estimated from a combination of experimental and observational data on jack pine budworm and jack pine. Second, we altered conditions in the model to understand how natural enemies, tree quality, and fires affect jack pine budworm outbreaks and forest health. Finally, we increased fire frequency and severity in the model, as predicted by climate change models, to understand how climate change will determine the fate of jack pine forests.

Our results show that insect outbreaks and forest fires have a complex relationship. Forest fire events increase the period and amplitude of insect outbreaks, and that the period and amplitude of outbreaks influence fire interval. This interaction also determines tree survival and overall forest health. Insect outbreaks greatly increase variation in tree sizes. Tree survival is maximized at intermediate fire intervals, which reflect those seen in nature. Because insect outbreaks help drive fire interval, we cannot expect to understand the effects of climate change on future forest fires without understanding the biology of forest defoliators.

3.2 Model construction

3.2.1 Overview

Like many outbreaking insects (Hunter, 1991), the jack pine budworm has a single generation per year, with the nonfeeding adults reproducing in late summer. Larvae hatch in the the fall and overwinter without feeding, before re-emerging in the spring. The two most important mechanisms driving larval mortality are parasitoid attacks and competition for food, either pollen cones in spring or needles in early summer (McCullough, 2000). In previous work (Gallagher and Dwyer, prep), we showed that most parasitoid attacks are due to two Hymenopteran species, the Braconid *Apanteles fumiferana* and the Ichneumonid *Glypta fumiferana*, and a group of hard to distinguish Dipterans in the family Tachinidae, which are treated as a single species.

The jack pine budworm literature suggested that these parasitoids have only a single generation per year, with all attacks occuring in the fall (Nealis and Lysyk, 1988), but by collecting more detailed data we were able to show that additional attacks and generations occur during the larval feeding period. We therefore describe parasitoid attacks using a modification of an SEIR model from mathematical epidemiology (Keeling and Rohani, 2007). In this model, host larvae that have been parasitized are classified as “exposed”, while multiple exposed classes allow for a time lag between the parasitoid attack and the emergence of the adult parasitoid, which kills the host. In addition to parasitoid attacks, we allow for direct density dependent budworm mortality due to competition for resources.

In our previous work (Gallagher and Dwyer, prep), we used advanced nonlinear fitting algorithms to compare the ability of different versions of our SEIR model to explain an extensive data set on the mortality of jack pine budworm larvae during the spring feeding period. This work showed that the data are best explained by a model that includes multiple parasitoid species and generations during the spring, as well as direct density dependence that is modulated by tree size, a measure of host tree quality. The effects of tree size likely reflect variation across trees in the number of pollen cones, a key resource for larval bud worms (McCullough, 2000).

Given this model of spring mortality, an important next step is to quantify reproduction and mortality during the fall. To do this, we constructed a model that describes adult reproduction, fall parasitoid attacks, and overwintering survival, and we fit this model to measurements of budworm density over this time period. We then have estimates of all parameters describing budworm survival and reproduction, allowing us to predict long-term budworm outbreak cycles.

Our model also incorporates forest fires, which strongly affect jack pine forests. Jack pine forests are a fire dependent system, relying on regular fires to revitalize the forest by opening serotinous cones, and burning dead trees and branches to clear space for new seedlings (McCullough et al., 1998; Lecomte et al., 2006b). Regular fire events also provide some level of protection from budworm damage, as budworm larvae are less likely to survive when feeding on trees growing on previously burned areas (McCullough and Kulman, 1991a,b). Multiple factors interact to determine fire frequency, including temperature, precipitation, and the availability of fuel, particularly highly flammable dead biomass (McCullough et al., 1998; Heon et al., 2014). This is important because climate change is projected to increase the severity and frequency of insect outbreaks (Whitman et al., 2015), and tree death due to insect outbreaks is a significant contributor to forest fire risk (Stocks, 1987b; McCullough et al., 1998; Fleming et al., 2002; Taylor and MacLean, 2009). After severe fires, little biomass is left behind, and there is often a relatively longer interval before the next fire event compared to the delay following less severe fires (Lecomte et al., 2006b).

3.2.2 Multiple generation model

Our model consists of a set of difference equations that describe long-term population dynamics of the budworm, its parasitoids, and the jack pine forest. The model tracks the population density of the jack pine budworm and three parasitoid species over time, as well as the size and health of the forest. To calculate larval survival and parasitoid attacks on each tree in the forest during the spring and summer, we use a modification of a standard SEIR model from epidemiology. We also calculate the growth and survival of each tree over the spring and summer, such that growth and survival depend on the tree's size, overall insect densities, and whether a fire occurs (McCullough et al., 1998). We then calculate budworm reproduction, fall parasitoid attacks, and overwintering survival using a second set of differential equations. This latter model generates the initial population sizes for the SEIR model in the following spring.

The difference equations that describe changes in the host, H, and the parasitoids, Z_1, Z_2, and Z_3, on each tree j are then:

$$
\begin{aligned}
H_{j,n+1} &= \lambda H_{j,n} \underbrace{i_H(H_{j,n}, Z_{j,1,n}, Z_{j,2,n}, Z_{j,3,n}, Q_{j,n})}_{\text{Spring \& summer survival}} \underbrace{\hat{i}_H(\lambda H_{j,n} i_H, H_{j,n} i_{Z_1}, H_{j,n} i_{Z_2})}_{\text{overwinter survival}} && (3.1)\\
Z_{j,1,n+1} &= \lambda H_{j,n} \hat{i}_{Z_1}(\lambda H_{j,n} i_H, H_{j,n} i_{Z_1}, H_{j,n} i_{Z_2}) && (3.2)\\
Z_{j,2,n+1} &= \lambda H_{j,n} \hat{i}_{Z_2}(\lambda H_{j,n} i_H, H_{j,n} i_{Z_1}, H_{j,n} i_{Z_2}) && (3.3)\\
Z_{j,3,n+1} &= Z_{j,3,0} && (3.4)
\end{aligned}
$$

In the equation for the host density $H_{j,n+1}$ i_H is the fraction of hosts that survive parasitoid attacks and competition for resources during the spring and summer larval period, where i_H is calculated using our SEIR model (see equations 7-10). The symbol $\hat{i}_H$ is larval survival from hatch in the fall until the beginning of larval feeding the following spring. $\hat{i}_H$ depends on the number of newly hatched larvae $\lambda H_{j,n} i_H$, which are the offspring of $H_n i_H$ survivors of the summer larval period. $\hat{i}_H$ also depends on the number of parasitoids of species 1 and 2 produced during the summer $H_{j,n} i_{Z_1}$, and $H_{j,n} i_{Z_2}$. Parasitoid species 3 does not use jack pine budworm larvae as an overwintering host, so it does not affect $\hat{i}_H$.

In the equation for parasitoid species 1, $\hat{i}_{Z_1}$ is the fraction of budworms that are attacked by the parasitoid, which in turn depends on the summer dynamics, much as in the host equation. The equation for parasitoid species 2 is fundamentally similar, but because parasitoid species 3 is a generalist, we make the simple assumption that its density only changes during the budworm larval period.

To complete the model, we first describe the equations for the forest. In generation n, tree j has quality $Q_{j,n}$, as measured by its diameter at breast height (DBH), and it may be dead, as determined by its death status, where $D_{j,n} = 1$ means that tree j is dead. Bare space is equivalent to zero DBH, so that for bare space, $Q_{j,n} = D_{j,n} = 0$. The forest model is then:

$$
\begin{aligned}
Q_{j,n+1} &= r(Q_{j,n}, H_n, H_{n-1})Q_{j,n}\psi_j\theta_j + \omega_j I(Q_{j,n} = 0) & (3.5)\\
D_{j,n+1} &= Q_{j,n}(1-\psi_j)\theta_j I(Q_{j,n} \neq 0) + D_{j,n}\psi_j I(D_{j,n} \neq 0) & (3.6)
\end{aligned}
$$

Here, if the tree in location j is living at time n, its DBH at generation $n+1$ is calculated by the equation for $Q_{j,n+1}$. If the tree is dead ($D_{j,n} \neq 0$), equation $D_{j,n+1}$ determines what becomes of the biomass of the dead tree in generation $n+1$.

The function $r(Q_{j,n}, H_n, H_{n-1})$, then, is the growth rate in generation n, which depends on the herbivore density in the two preceding generations. The functions $I()$ are indicator variables, such that $I(Q_{j,n} = 0) \equiv 1$ if tree j's biomass is reduced to zero by fire, and zero otherwise, and $I(D_{j,n} = 0) \equiv 1$ if the tree is alive, and is zero otherwise. The symbols θ_j, ψ_j and ω_j are Bernoulli random variates that describe whether particular events occur.

First, $\theta_j = 1$ means that the tree's biomass has not been reduced to zero by fire, and $\psi_j = 1$ means that the tree has survived insect defoliation. If the tree has zero biomass and $\omega_j = 1$, then a germination event occurs, creating a tree with DBH = 1 (in units of centimeters). The probability that biomass is reduced to zero in a fire depends on the DBH of the tree and the total dead biomass $\sum_j D_{j,n}$ (see equations 16-18), while the probability of dying due to defoliation depends on the insect density $H_{j,n}$.

3.2.3 Larval mortality model

Larval mortality is described by an SEIR model that allows for budworm losses to the three parasitoids and to competition for resources. In practice, these equations are specific to each tree j, but in the interest of simplifying the notation, here we include indices only for exposure classes and parasitoid species.

$$
\begin{aligned}
\frac{dS}{dt} &= -\frac{\alpha_1 S P_1}{1+\rho_1 P_1} - \frac{\alpha_2 S P_2}{1+\rho_2 P_2} - \frac{\alpha_3 S P_3}{1+\rho_3 P_3} \\
&\quad -\gamma_1 S^{\gamma_2}((Q-\eta_1)^2+\eta_2)(S+\sum_{k=1}^{3}\sum_{x=1}^{m_k} E_{k,x}) \qquad (3.7) \\
\frac{dE_{k,1}}{dt} &= \frac{\alpha_k S P_k}{1+\rho_k P_k} - \gamma_1 E_{k,1}{}^{\gamma_2}((Q-\eta_1)^2+\eta_2)(S+\sum_{k=1}^{3}\sum_{x=1}^{m_k} E_{k,x}) \\
&\quad -m_k \delta_k E_{k,1}, \quad \text{for } k = 1,2,3 \qquad (3.8) \\
\frac{dE_{k,x}}{dt} &= m_k \delta_k E_{k,x-1} - \gamma_1 E_{k,x}{}^{\gamma_2}((Q-\eta_1)^2+\eta_2)(S+\sum_{k=1}^{3}\sum_{x=1}^{m_k} E_{k,x}) \\
&\quad -m_k \delta_k E_{k,x}, \quad \text{for } x = 2, ..., m_k \qquad (3.9) \\
\frac{dP_k}{dt} &= m_k \delta_k E_{k,x} \qquad (3.10)
\end{aligned}
$$

Here S is the density of unparasitized ("susceptible") budworms, while P_1, P_2, and P_3 represent the three parasitoid species. In generation n, $S(0) = H_n$, $P_1(0) = Z_{1,n}$, $P_2(0) = Z_{2,n}$, while $P_3(0) = Z_{3,0}$ because of the assumed lack of dynamics for species 3. The symbol α_k is the attack rate of parasitoid species k, while the parasitoid functional response terms $-\frac{\alpha_k S P_k}{1+\rho_k P_k}$ depend on ρ_k, which scales the effect of each parasitoid species k on its own attacks. Parameter m_k is the number of exposed classes for parasitoid species k, and δ_k is the rate of progression through the exposed classes. Quality Q and parameters γ_1, γ_2, η_1, and η_2 describe how direct density dependence is mediated by plant quality $Q = Q_{j,n}$. Specifically, γ_1 determines the severity of the quality effects, while η_1 determines the rate at which these effects change with changing quality. Because both budworms and parasitoids are highly mobile, we assume that the initial density of insects is the same on every tree. The effect is that, at the end of the larval period, budworms and parasitoids redistribute themselves evenly throughout the forest.

3.2.4 Forest model

Neither fire nor defoliation is likely to eliminate all living trees, and so we assume that there are always at least two live trees. At the beginning of each model realization, we assume that the probability of each tree in the forest being alive is 0.8, while the probability of the tree having zero DBH, representing bare space, is 0.1, leaving a probability of 0.1 that the tree is standing dead timber. Initial DBH values for both live and dead trees were drawn from a uniform distribution ranging from 1 to 60 cm.

Living trees

Tree growth declines gradually with increasing tree size, while high budworm densities have a strong negative effect on jack pine growth rate, and increase the chance of tree death (Gross, 1992; Kulman et al., 1963; McCullough, 2000). Fire events also kill trees, especially when the fire intensity is high, which is more likely when the biomass of dead trees is high.

To allow for these effects, we first describe tree growth as follows:

$$g0 = 0.18 \tag{3.11}$$

$$g = g0 - 10^{-5}(Q_{t,n})^2 \tag{3.12}$$

$$Q_{t,n+1} = (g+1)Q_{t,n} \tag{3.13}$$

$$if \quad H_{n-1} > 0.25, \qquad g = (4/5)g \tag{3.14}$$

$$if \quad H_n > 0.25, \qquad g = (1/4)g \tag{3.15}$$

Equations for normal growth rates were determined by fitting a nonlinear regression to data from Gross (1992), Laidly (1981), and Rudolf (1965). Suppressed growth rates at high budworm densities are also based on work by Gross (1992).

Here $g0$ is the baseline growth rate and $Q_{t,n}$ is the DBH of the tree. Because growth is suppressed by heavy defoliation, we assume that, above a threshold density of 0.25 insects per branch tip, growth is reduced by a factor of 4. Defoliation can affect growth in the following year as well, and therefore if the insect density in the previous year was greater than the threshold value of 0.25, growth is reduced by a smaller factor of 1.25. In all cases, the minimum value of g is $1e^{-3}$, and the maximum value is $g0$.

High budworm densities also increase the probability of tree death. Independent of insect attacks, each tree also has a constant 1% chance of death each year, to account for deaths due to disturbance or disease unrelated to insects and forest fires. Above a threshold density of 0.95 larvae per branch tip, the chance of death for each living tree increases to 8%. (For more information about jack pine growth and the effects of defoliation, see Gross (1992) and Kulman et al. (1963)).

Fire behavior and effects

In our model, the probability of a fire event is driven by the quantity of dead biomass within a jack pine stand, according to the function:

$$P_{\text{fire}} = \nu Q_d \sum D_{j,n-1} \tag{3.16}$$

Where P_{fire} is the probability of a fire occurring, ν is a scaling constant equal to $2e^{-5}$, Q_d is the average DBH of all dead trees in the stand, and $\sum_j D_{j,n-1}$ is the total number of dead trees in the stand. We then adjust the parameter ν to vary the risk of fire at any given level of dead biomass. Since fire intensity can be severe in stands of any age (Stocks, 1987a, 1989), in our model, fire intensity is deterministic and simply depends on the number of dead trees in the stand. If less than 40% of trees in the stand are dead at the beginning of the year, the fire will not be severe.

When a fire does occur, both living and dead trees may be destroyed, which in our model leaves behind an empty location in the forest. In our model, the probability of destruction by burning is based on linear regressions from the literature (Agee, 1998), as follows. First, if less than 40% of trees are already dead prior to the fire, fire severity is low in generation n, and the probability that tree j will be burned is:

$$P_{\text{burning}} = 0.86 - 0.0053 Q_{j,n} \tag{3.17}$$

If the initial number of dead trees is greater than 40% of the total trees in the stand, then fire severity is high, with:

$$P_{\text{burning}} = 1.1 - 0.0079 Q_{j,n} \tag{3.18}$$

Fire events also allow empty cells to germinate at much higher rates. In our model, we again follow the literature in assuming that, in the first five years after a severe fire, there is a 0.5 probability of germination per year, while for five years after a mild fire, annual germination probability is 0.2. In all other years, the probability of germination is 0.05 (Agee, 1998; Lecomte et al., 2006a,b)).

3.2.5 Reproduction and overwintering model

In our model, budworms that survive the summer reproduce with reproductive rate λ. We then use a second set of ordinary differential equations to calculate the fraction of newly hatched budworm larvae that are attacked by adult parasitoids, in the time before the larvae retreat into their hibernaculae to overwinter. Because we have only 12 fall to spring transitions, we kept this part of the model as simple as possible.

$$\begin{aligned}
\frac{d\hat{S}}{dt} &= -\beta_1 \hat{S}\hat{Z}_1 - \beta_2 \hat{S}\hat{Z}_2 \quad (3.19)\\
\frac{d\hat{P}_1}{dt} &= \beta_1 \hat{S}\hat{Z}_1 \quad (3.20)\\
\frac{d\hat{P}_2}{dt} &= \beta_2 \hat{S}\hat{Z}_2 \quad (3.21)
\end{aligned}$$

Here $\hat{S}$ is the density of newly hatched budworms, $\hat{P}_1$ and $\hat{P}_2$ are the densities of parasitoid species 1 and 2, and β_1 and β_2 are their attack rates. Here $\hat{Z}_1$ and $\hat{Z}_2$ are the densities of adults in parasitoid species 1 and 2 at the end of the summer period. As a generalist, parasitoid species 3 does not overwinter within jack pine budworm larvae, and is therefore not included in this part of the model.

For initial conditions, this model makes use of the changes calculated by the SEIR model. The initial budworm density $\hat{S}(0) = \lambda H_n i_H$, where H_n is the initial budworm population in the spring, and i_H is the fraction surviving the summer. Likewise, $\hat{P}_k(0) = H_n i_{Z_k}$, where i_{Z_k} is the fraction of budworms successfully attacked by parasitoid species k during the summer. The model for fall parasitoid attacks is then used to calculate budworm and parasitoid densities in the spring of the following year, according to:

$$H_{n+1} = \hat{S}(\hat{T}) \tag{3.22}$$

$$P_{1,n+1} = \hat{P}_1(\hat{T}) \tag{3.23}$$

$$P_{2,n+1} = \hat{P}_2(\hat{T}) \tag{3.24}$$

Where T is the length of time during which the parasitoids attack first and second instar larvae immediately after hatching in the fall.

Our model for the fall larval period includes only four additional insect specific parameters: reproductive rate λ, and end season parasitoid attack rates β_1 and β_2. Attack period T cannot be distinguished from the values of β_k, and therefore we do not include T in what follows. To estimate these parameters, we measured budworm densities and parasitoid infection rates in jack pine forests from the end of the summer to the beginning of the following spring at multiple sites in the lower peninsula of Michigan, for a total of 12 transitions. We fit the data to these transitions using maximum likelihood, specifically using the `optim()` function in the R programming language, and we bootstrapped the data to determine 95% confidence intervals for each parameter, using 100 random restarts for each synthetic data set to ensure convergence. The resulting parameter values are $\lambda = 10.8$ (95% C.I. 5.6-12.0), $\beta_1 = 3.5$ (95% C.I. 2.7-6.2), $\beta_2 = 0.9$ (95% C.I. 0.5-1.5).

These parameters give cycles with an outbreak period of roughly 6-8 years, matching the outbreak cycle of jack pine budworm in Wisconsin and Michigan, where we collected these data. In more northerly locations, however, notably in Saskatchewan and Manitoba, outbreaks historically have a period of 10 years, and a larger amplitude. In some cases, we will therefore allow for 10 year cycles, with a concomitant increase in the outbreak amplitude.

3.3 Results

Figure 3.1 shows a time series of the model output in the absence of fire. As the figure shows, the model produces budworm outbreaks with an outbreak period of 6-8 years, matching outbreak periods observed in nature (McCullough, 2000). These cycles are driven by a combination of density dependent parasitoid attacks, as in classical host-parasitoid models, but are also strongly affected by mortality due to competition for resources. In fact, between outbreaks, mortality due to competition for resources can be as high as 40%. In the absence of fire, however, average tree DBH is remarkably stable, and tree size is essentially uniform. However, as we will show, in the absence of fires, most trees are dead due of a lack of fire driven regeneration.

Figure 3.2 then shows that these dynamics are qualitatively similar in the presence of fire, in that parasitoids and quality dependent competition for resources drive insect outbreak cycles. The addition of fire, however, greatly increases the fraction of trees surviving, as forest fires allow for much higher rates of regeneration. This effect reduces average DBH and produces realistically variable tree sizes, which can be seen in Fig. 3.4.

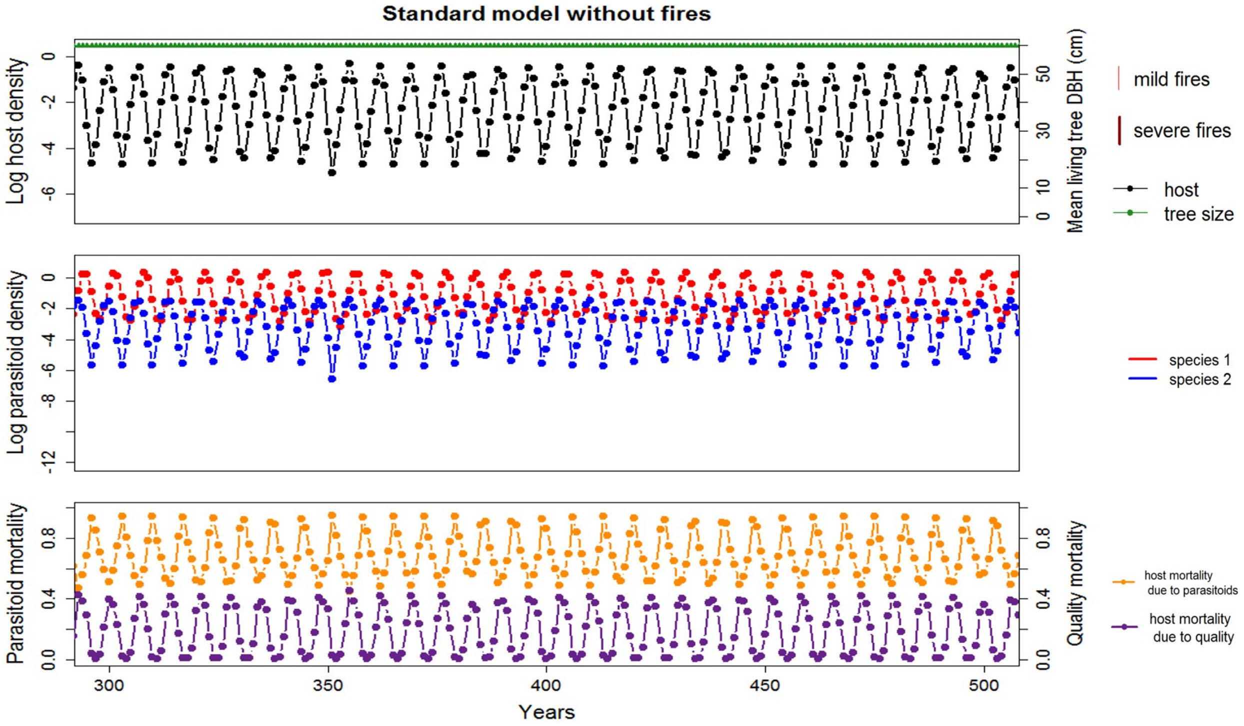

Figure 3.1: Long-term model behavior in the absence of fires

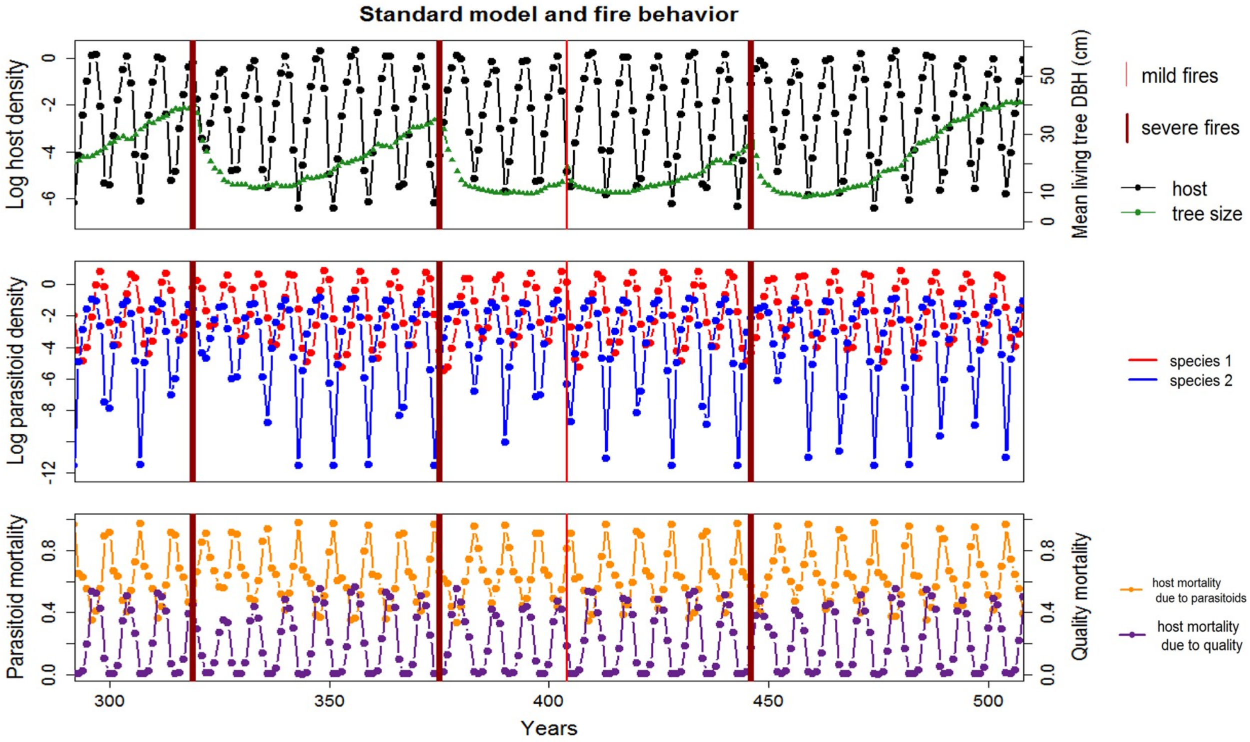

Figure 3.2: Long-term model behavior with realistic fire frequency

Figures 3.3 and 3.4 present model predictions for a range of values of the quality parameters γ_1 and η_1, confirming the qualitative results of figures 3.1 and 3.2. Figure 3.3 shows that increasing the magnitude of the quality effect, by increasing γ_1, has a stabilizing effect on insect outbreaks, such that larger values of γ_1 lead to lower outbreak amplitudes and shorter periods. The figure also confirms that fire is destabilizing for a range of parameter values, leading to more severe outbreaks at longer intervals.

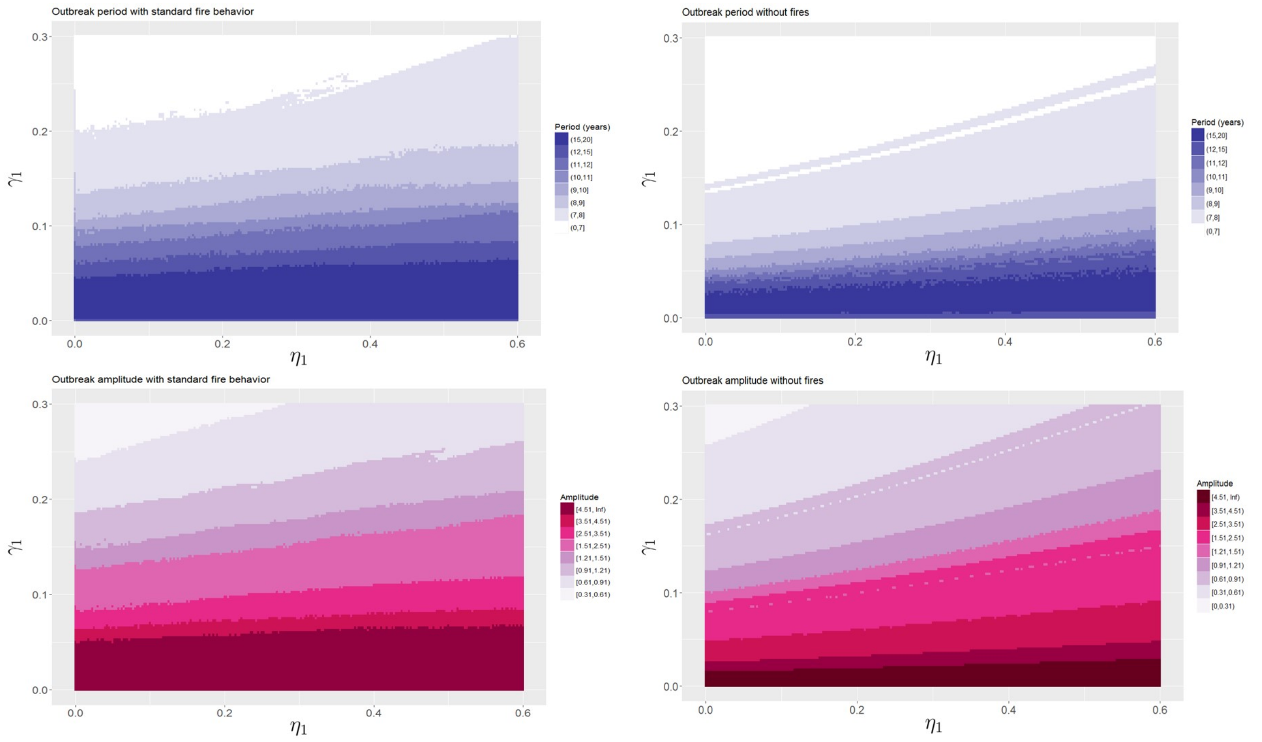

Figure 3.3: The period and amplitude of insect outbreaks under different quality and fire conditions

In Figure 3.4 we can see that in the absence of fire, almost all the trees in the forest are the same large size. Insects alone thus have a very minimal effect on size structure. In the absence of fire, however, the vast majority of trees are dead, and the average fraction surviving is close to zero. This is a well-known effect in fire dependent systems: without fires, trees are killed by periodic insect outbreaks, and fire dependent species like jack pine are not able to persist.

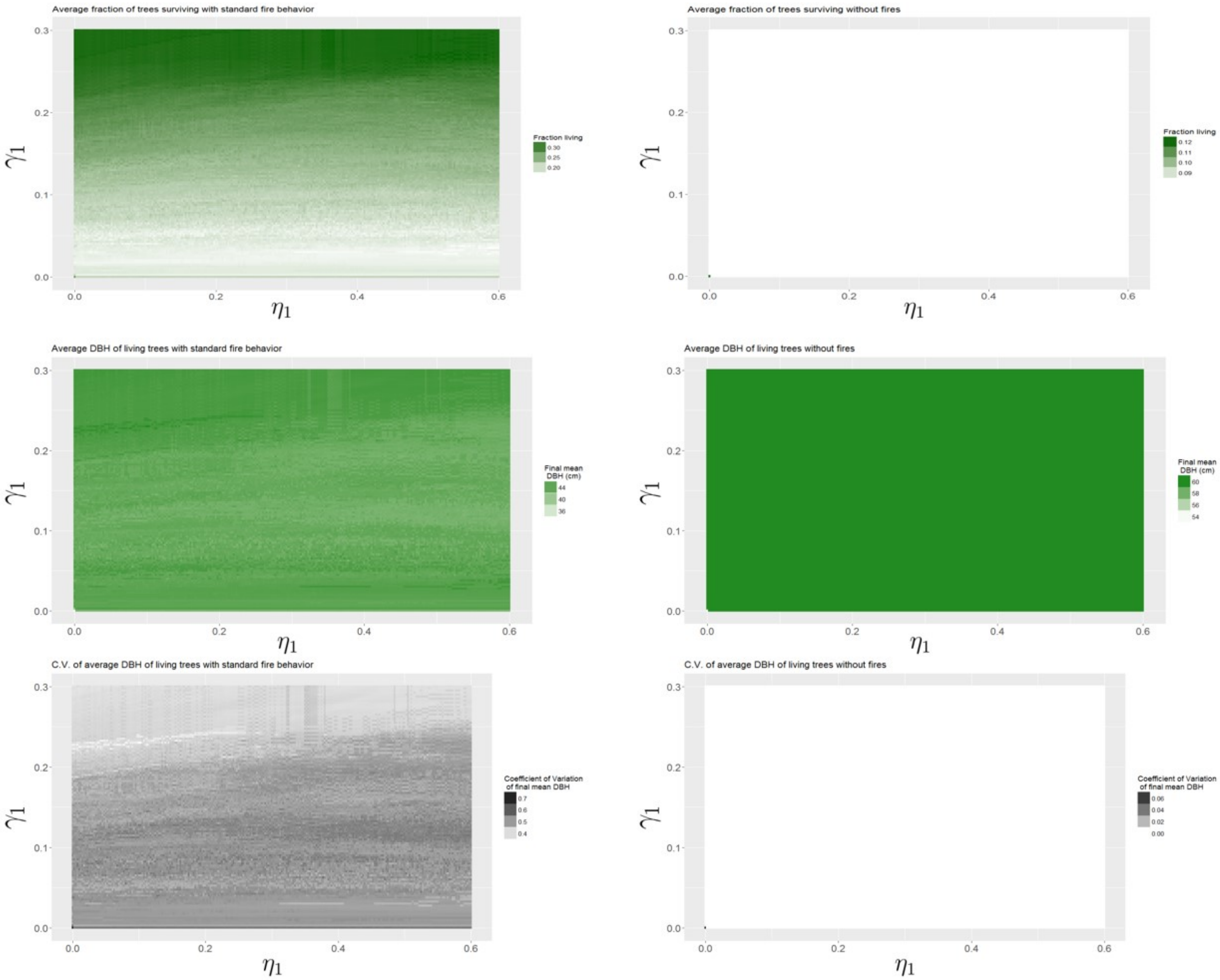

Figure 3.4: Few trees survive in the absence of fires

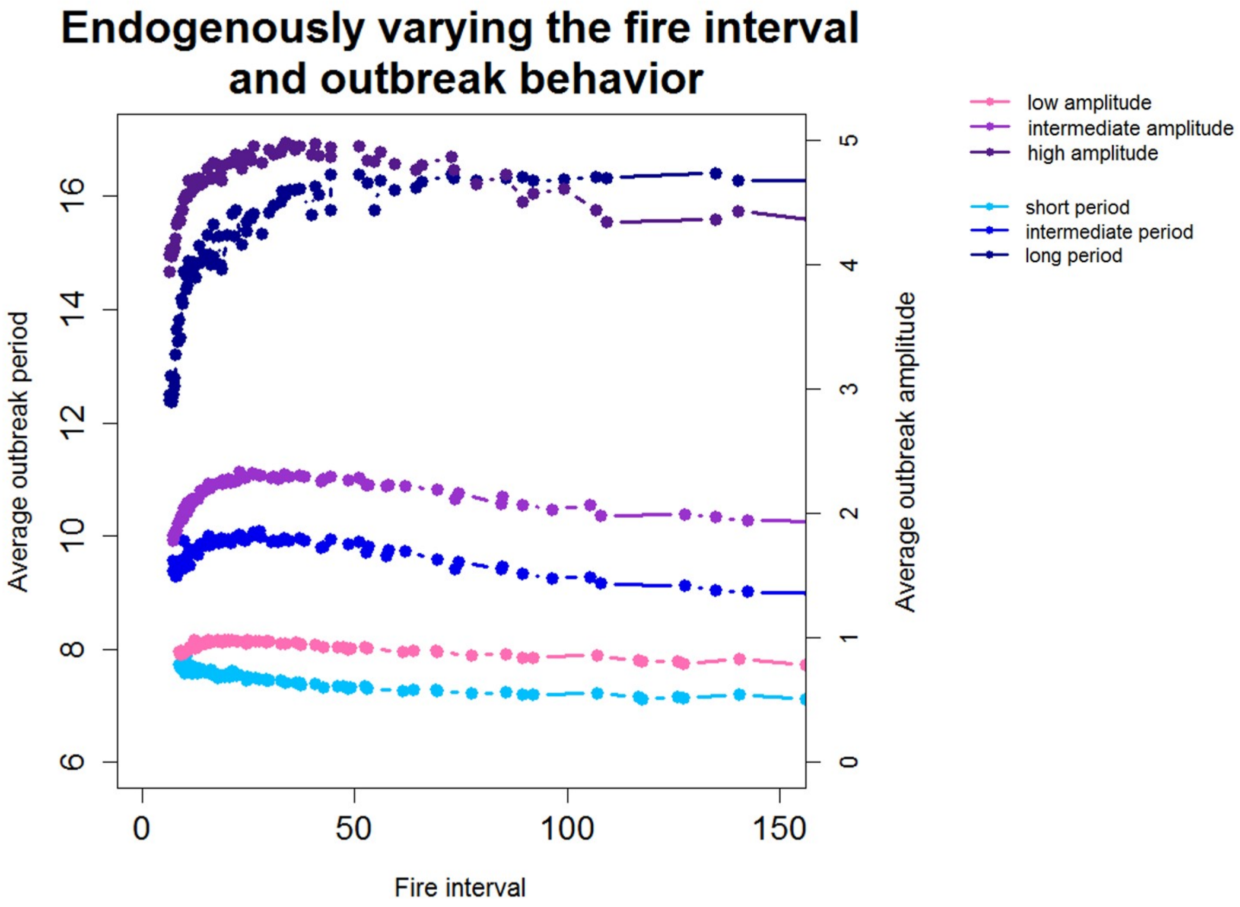

Figure 3.5: Fire interval and plant quality both influence insect outbreaks

To understand how fire interval influences outbreak behavior, we adjusted the parameter ν that controls the probability of a fire occurring for a given amount of dead biomass, thereby varying the fire interval in the model. We also varied the quality parameter γ_1, which has a strong effect on the period of insect outbreaks, as figure 3.3 shows. Figure 3.5 then demonstrates the change in the period and amplitude of budworm outbreaks over a range of fire intervals, for three different values of the quality parameter γ_1. The low amplitude, short period outbreaks match our observed data from the lower peninsula of Michigan ($\gamma_1 = 0.21$), while the intermediate case ($\gamma_1 = 0.10$) has a period of roughly 10 years, similar to what has been seen in the Canadian provinces Manitoba and Saskatchewan (Volney, 1992). For comparison, we also show an example of outbreak behavior with an extremely long period and high amplitude ($\gamma_1 = 0.03$).

As figure 3.5 shows, the period of outbreaks increases rapidly at low values of the fire interval, leading to a peak at intermediate values, before slowly declining at high fire intervals. A deep understanding of this effect is beyond what we can accomplish here, given the complexity of our model. We suspect that peaks may occur at intermediate fire intervals due to some resonance phenomenon, such that fire intervals that are close to the period of the outbreak cycles drive more severe cycles. Irrespective of these complexities, however, our model clearly shows that varying the fire interval alters the population cycles in the budworm.

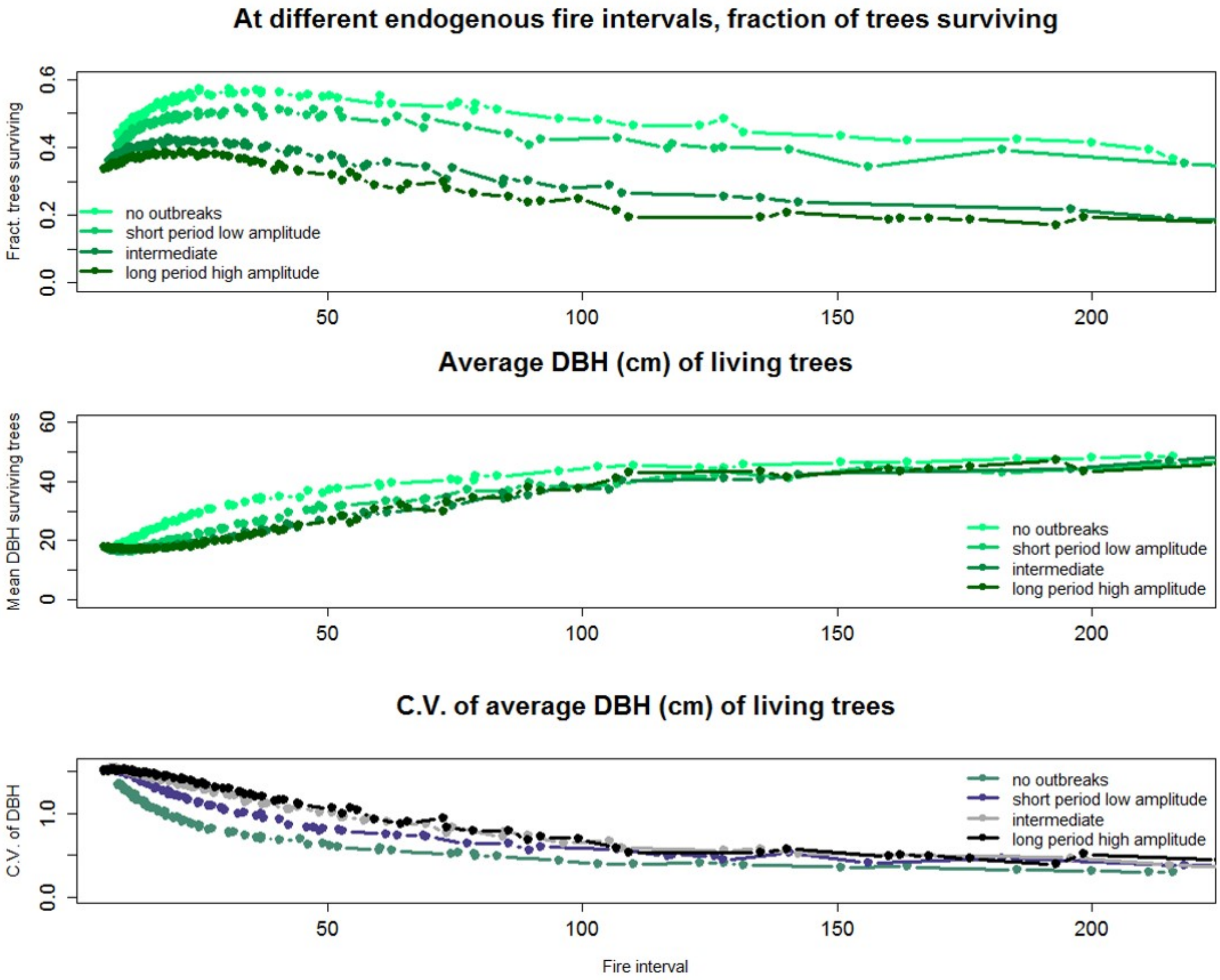

Figure 3.6: Few trees survive under extreme fire or insect outbreak regimes

Adjusting the fire interval and the strength of the quality effect also provides interesting insights into the factors determining the health of jack pine forests. First, as fig. 3.6 shows, the fraction of trees that are alive in the absence of insects is maximized at intermediate fire intervals, because short fire intervals kill the trees before they can begin to grow, while long fire intervals leads to a forest full of trees that have died due to natural (non-insect) causes. Allowing for insects then leads to a substantial reduction in the fraction of trees that are alive, irrespective of fire interval, but the effect is much stronger when the outbreak cycles have longer periods and larger amplitudes. The intensity of insect outbreaks thus strongly modulates the effects of fire on the forest.

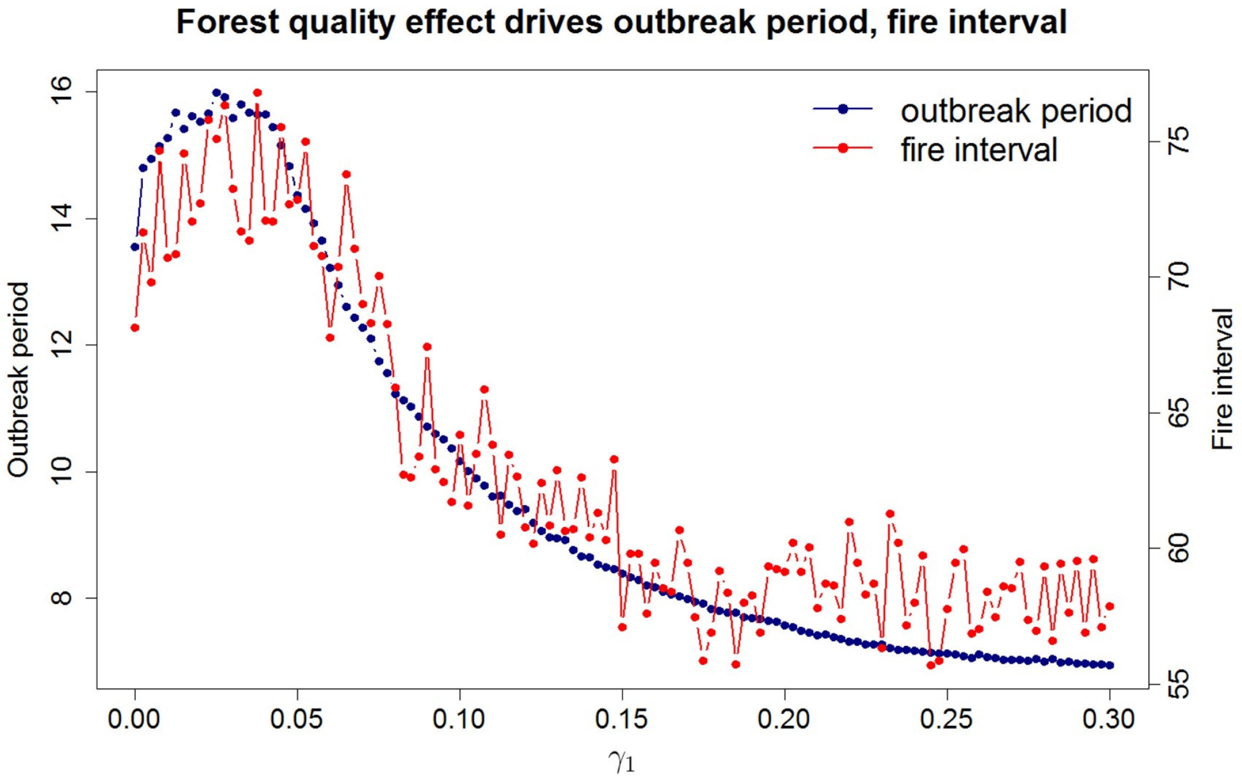

Figure 3.7: Plant quality directly alters the period of insect outbreaks, which affects the fire interval

The strong effect of outbreaks on tree survival in fig. 3.6 suggests that changes in the severity of insect outbreaks may produce changes in the fire interval. To test for such effects, we again allowed the value of the quality effect parameter γ_1 to vary, except that in this case we kept the fire probability parameter ν constant. As fig. 3.7 then shows, changes in the period of insect outbreaks can lead to substantial changes in the fire interval. A regression of fire interval on outbreak period, in fact, yields $r^2 = 0.9$. Because γ_1 only has direct effects on the insect, this strongly indicates that tree quality is an important driver of both insect outbreak period and forest fire interval. This is a critical result, because it suggests that we cannot understand or predict the effects of climate change on forest fires without considering the biology of pest insects.

3.4 Discussion

Many classical models of forest defoliator outbreaks include only a host and its specialist parasitoid. Classical models can produce population cycles that qualitatively match cycles in defoliator populations in nature (Hassell, 1978; May and Hassell, 1981), but the lack of consideration of the effects of host plant quality is a major handicap. By incorporating the effects of host plant quality, and including the biologically critical impact of forest fires, we have expanded these classical models in a way that allows us to answer key questions about the future of jack pine forests.

First, our models show that the effects of host tree quality strongly modulate insect outbreak cycles, a result that has been seen in previous theoretical research (Underwood, 1999). A study of the larch budmoth by Turchin et al. (2003) also found quality to have a stabilizing effect, although the effect of quality was weak. These stabilizing effects are in contrast to models by Abbott and Dwyer (2007) and Elderd et al. (2013), in which the effects of host plant quality were destabilizing. The difference is in the mechanism of the quality effect. For instance, Elderd et al. (2013) showed that increased tannins in defoliated oaks reduces heterogeneity in disease risk in gypsy moths, thereby acting to destabilize gypsy moth outbreaks.

Although our model was constructed to describe jack pine budworm outbreaks, the model structure is is infact sufficiently general that it could be used to develop insight into the future of other fire dependent forest systems. For example, while current research suggests that fire frequency can be expected to increase in much of North America (Heon et al., 2014), this increase may not be true for all fire dependent forests in North America. By adjusting model parameters, such as those that determine fire frequency or the strength of the effect of quality, our model can make predictions about future forest health for a range of geographic locations and tree species.

Jack pine forests are known to be a fire dependent system, which is reflected in the behavior of our model. We found that tree survival is highest at intermediate fire intervals, similar to those seen in nature. Few trees survive under extreme fire regimes, whether fires are extremely rare or extremely frequent. Previous work has similarly shown that forest fires affect plant quality in dramatic and measurable ways (McCullough and Kulman, 1991a,b), but our results show that plant quality in turn has an effect on fires that is mediated by defoliator insects. Adjusting the effect of plant quality in the model changes the outbreak period of the insects, which in turn directly affects the fire interval. This result is in contrast to previous models of defoliator dynamics and plant quality, which have not included the effects of forest fires or disturbances on a large scale. Our work thus provides a clear example of how fires, plant quality, and defoliator insects may interact to determine the fate of forests.

Finally, our model makes it clear that we cannot expect to predict future fire frequency and the effects of climate change without considering the biology of forest defoliators. Severe insect outbreaks, in combination with a shortened fire interval, greatly reduce both the fraction of jack pine trees that survive and the average tree size. Our work thus demonstrates the biological complexities that must be considered when making predictions about the effects of climate change.

3.5 Acknowledgments

For assistance in the field, many thanks to Jenny Uehling, Benjamin Hazelton, and Dr. Alison Hunter. Our data collection benefited greatly from helpful conversations with staff at the Great Lakes Forestry Research Center in Sault Ste. Marie, Michigan, especially Dr. John Dedes. Staff at the GLFRC also provided insect diet for rearing jack pine budworm larvae in the lab. Thanks also to members of the Wisconsin and Michigan Departments of Natural Resources, especially Patrick Potter and Doug Heym.

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Appendices

APPENDIX A

APPROXIMATING TREE AGE

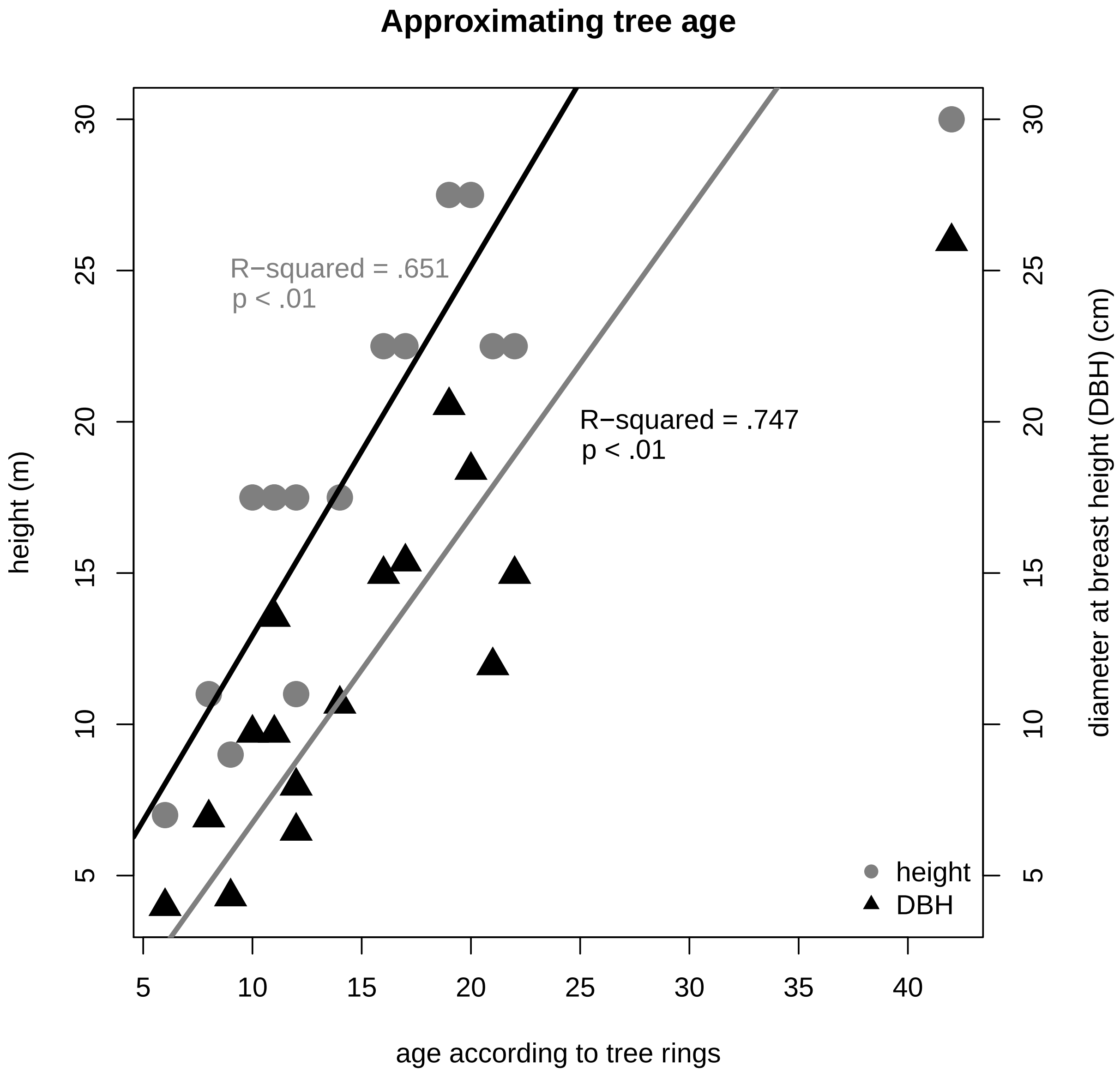

Figure A.1: DBH and tree height can reasonably approximate tree age

Results from coring a subset of trees show that both tree height and DBH are reasonable proxies for tree age. Since the relationship between DBH and age is slightly stronger, and DBH measurements in our study are more precise than height measurements, we chose to use DBH as a proxy for tree age in our models.

APPENDIX B

SAMPLING PROTOCOLS

Our sampling protocol was based on methods described in the literature (Volney and McCullough, 1993) and the results of our own preliminary samples, in which we sampled ten trees per site. These samples showed that budworm counts per pollen cone had low variance to mean ratios between trees at a site, likely because the majority of trees within a site are of similar age, and because larval budworms will disperse to other trees if the pollen cones of the tree on which they emerge are already occupied. Under high-density outbreak conditions, this behavior can result in a relatively even distribution of budworms across a given site. In our later data collection efforts, we therefore reduced the number of trees sampled per site to five and increased the number of sites sampled to seven. Variance to mean ratios remained low, confirming that our sampling scheme was effective.

APPENDIX C

AIC AND WAIC SCORES

Table C.1: Full table of AIC and WAIC scores

Model	Spp.	k	L (line search)	AIC	ΔAIC	wAIC	L (MCMC)	WAIC	ΔWAIC	wWAIC
1	1	5	-381.65	773.3	69.64	0.000	-398.49	17128.07	16440.27	0.000
1	2	9	-365.61	749.23	45.57	0.000	-365.31	738.95	51.15	0.000
1	3	13	-364.24	754.47	50.81	0.000	-365.05	740	52.2	0.000
2	1	7	-347.35	708.7	5.04	0.024	-348.79	699.41	11.61	0.001
2	2	11	-341.33	704.67	1.01	0.182	-343.28	694	6.2	0.018
2	3	15	-340.66	711.31	7.65	0.007	-340.74	690.1	2.3	0.124
3	1	7	-348.22	710.43	6.77	0.010	-349.2	702	14.2	0.000
3	2	11	-342.68	707.36	3.70	0.047	-343.25	705.41	17.61	0.000
3	3	15	-340.57	711.14	7.48	0.007	-343.25	699.24	11.44	0.001
4	1	7	-347.71	709.43	5.77	0.017	-349.3	709.31	21.51	0.000
4	2	11	-341.88	705.76	2.10	0.105	-343.28	693.59	5.79	0.022
4	3	15	-339.51	709.03	5.37	0.021	-341.07	688	0.2	0.355
5	1	9	-347.52	713.03	9.37	0.003	-349.11	711.91	24.11	0.000
5	2	13	-341.13	708.26	4.60	0.030	-345.46	699.76	11.96	0.001
5	3	17	-338.76	711.51	7.85	0.006	-340.32	687.8	0	0.393
6	1	8	-348.16	712.33	8.67	0.004	-350.23	707.78	19.98	0.000
6	2	12	-340.62	705.23	1.57	0.137	-345.1	696.94	9.14	0.004
6	3	16	-338.65	709.29	5.63	0.018	-345.51	702.84	15.04	0.000

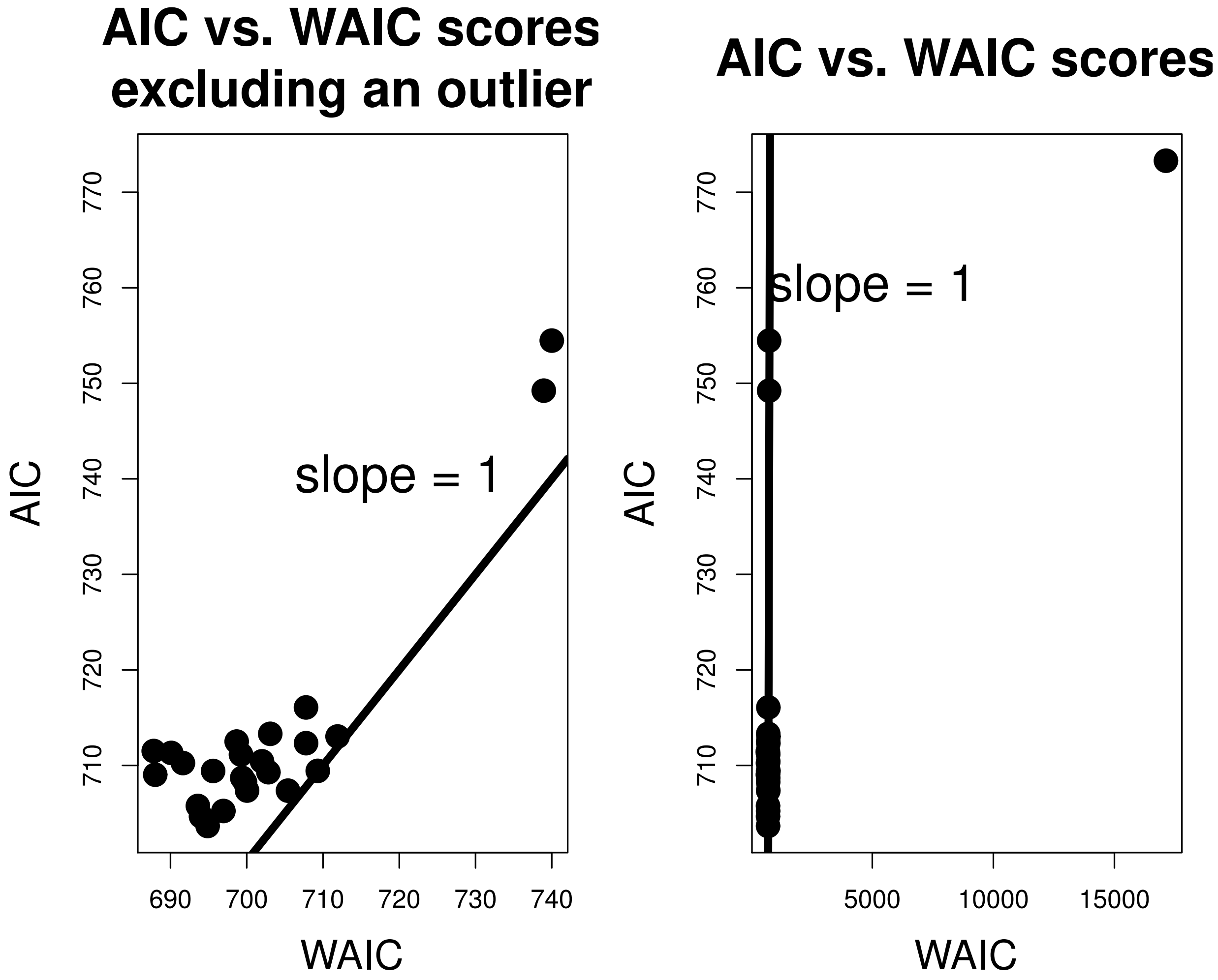

Figure C.1: AIC vs. WAIC scores of competing larval mortality models

This outlying point represents the high WAIC score of the simplest model, accounting only for attacks by a single parasitoid species. See Konishi and Kitagawa (2008) for more information about assumptions underlying the model selection process.

APPENDIX D

DIFFERENTIAL EQUATIONS FOR COMPETING MODELS

Full system of equations for models 1 through 6. Note that Q is not a variable but a covariate describing the DBH of the tree.

Model 1:

$$\frac{dS}{dt} = -\frac{\alpha_1 \phi S P_1}{1+\rho_1 P_1} - \frac{\alpha_2 \phi S P_2}{1+\rho_2 P_2} - \frac{\alpha_3 \phi S P_3}{1+\rho_3 P_3} \tag{D.1}$$

$$\frac{dE_{i,1}}{dt} = \frac{\alpha_i \phi S P_i}{1+\rho_i P_i} - m_i \delta_i E_{i,1}, \quad \text{for } i = 1,2,3 \tag{D.2}$$

$$\frac{dE_{i,j}}{dt} = m_i \delta_i E_{i,j-1} - m_i \delta_i E_{i,j}, \quad \text{for } j = 2,...,m_i \tag{D.3}$$

$$\frac{dP_i}{dt} = m_i \delta_i E_{i,j} \tag{D.4}$$

Model 2:

$$\frac{dS}{dt} = -\frac{\alpha_1 \phi S P_1}{1+\rho_1 P_1} - \frac{\alpha_2 \phi S P_2}{1+\rho_2 P_2} - \frac{\alpha_3 \phi S P_3}{1+\rho_3 P_3}$$

$$-\gamma_1 S^{\gamma_2}(S + \sum_{i=1}^{3}\sum_{j=1}^{m_i} E_{i,j}) \tag{D.5}$$

$$\frac{dE_{i,1}}{dt} = \frac{\alpha_i \phi S P_i}{1+\rho_i P_i} - \gamma_1 {E_{i,1}}^{\gamma_2}(S + \sum_{i=1}^{3}\sum_{j=1}^{m_i} E_{i,j}) \tag{D.6}$$

$$-m_i \delta_i E_{i,1}, \quad \text{for } i = 1,2,3 \tag{D.7}$$

$$\frac{dE_{i,j}}{dt} = m_i \delta_i E_{i,j-1} - \gamma_1 {E_{i,j}}^{\gamma_2}(S + \sum_{i=1}^{3}\sum_{j=1}^{m_i} E_{i,j})$$

$$-m_i \delta_i E_{i,j}, \quad \text{for } j = 2,...,m_i \tag{D.8}$$

$$\frac{dP_i}{dt} = m_i \delta_i E_{i,j} \tag{D.9}$$

Model 3:

$$\begin{aligned}
\frac{dS}{dt} &= -\frac{\alpha_1 \phi S P_1}{1+\rho_1 P_1} - \frac{\alpha_2 \phi S P_2}{1+\rho_2 P_2} - \frac{\alpha_3 \phi S P_3}{1+\rho_3 P_3} \\
&\quad -\gamma_1 S^{\gamma_2} Q && \text{(D.10)} \\
\frac{dE_{i,1}}{dt} &= \frac{\alpha_i \phi S P_i}{1+\rho_i P_i} - \gamma_1 {E_{i,1}}^{\gamma_2} Q && \text{(D.11)} \\
&\quad -m_i \delta_i E_{i,1}, \quad \text{for } i = 1, 2, 3 && \text{(D.12)} \\
\frac{dE_{i,j}}{dt} &= m_i \delta_i E_{i,j-1} - \gamma_1 {E_{i,j}}^{\gamma_2} Q \\
&\quad -m_i \delta_i E_{i,j}, \quad \text{for } j = 2, ..., m_i && \text{(D.13)} \\
\frac{dP_i}{dt} &= m_i \delta_i E_{i,j} && \text{(D.14)}
\end{aligned}$$

Model 4:

$$
\begin{aligned}
\frac{dS}{dt} &= -\frac{\alpha_1 \phi S P_1}{1+\rho_1 P_1} - \frac{\alpha_2 \phi S P_2}{1+\rho_2 P_2} - \frac{\alpha_3 \phi S P_3}{1+\rho_3 P_3} \\
&\quad -\gamma_1 S^{\gamma_2} Q (S + \sum_{i=1}^{3}\sum_{j=1}^{m_i} E_{i,j}) \qquad \text{(D.15)} \\
\frac{dE_{i,1}}{dt} &= \frac{\alpha_i \phi S P_i}{1+\rho_i P_i} - \gamma_1 {E_{i,1}}^{\gamma_2} Q (S + \sum_{i=1}^{3}\sum_{j=1}^{m_i} E_{i,j}) \qquad \text{(D.16)} \\
&\quad -m_i \delta_i E_{i,1}, \quad \text{for } i = 1,2,3 \qquad \text{(D.17)} \\
\frac{dE_{i,j}}{dt} &= m_i \delta_i E_{i,j-1} - \gamma_1 {E_{i,j}}^{\gamma_2} Q (S + \sum_{i=1}^{3}\sum_{j=1}^{m_i} E_{i,j}) \\
&\quad -m_i \delta_i E_{i,j}, \quad \text{for } j = 2,...,m_i \qquad \text{(D.18)} \\
\frac{dP_i}{dt} &= m_i \delta_i E_{i,j} \qquad \text{(D.19)}
\end{aligned}
$$

Model 5:

$$
\begin{aligned}
\frac{dS}{dt} &= -\frac{\alpha_1 \phi S P_1}{1+\rho_1 P_1} - \frac{\alpha_2 \phi S P_2}{1+\rho_2 P_2} - \frac{\alpha_3 \phi S P_3}{1+\rho_3 P_3} \\
&\quad -\gamma_1 S^{\gamma_2} ((Q-\eta_1)^2 + \eta_2)(S + \sum_{i=1}^{3}\sum_{j=1}^{m_i} E_{i,j}) \qquad \text{(D.20)} \\
\frac{dE_{i,1}}{dt} &= \frac{\alpha_i \phi S P_i}{1+\rho_i P_i} - \gamma_1 {E_{i,1}}^{\gamma_2} ((Q-\eta_1)^2 + \eta_2)(S + \sum_{i=1}^{3}\sum_{j=1}^{m_i} E_{i,j}) \qquad \text{(D.21)} \\
&\quad -m_i \delta_i E_{i,1}, \quad \text{for } i = 1,2,3 \qquad \text{(D.22)} \\
\frac{dE_{i,j}}{dt} &= m_i \delta_i E_{i,j-1} - \gamma_1 {E_{i,j}}^{\gamma_2} ((Q-\eta_1)^2 + \eta_2)(S + \sum_{i=1}^{3}\sum_{j=1}^{m_i} E_{i,j}) \\
&\quad -m_i \delta_i E_{i,j}, \quad \text{for } j = 2,...,m_i \qquad \text{(D.23)} \\
\frac{dP_i}{dt} &= m_i \delta_i E_{i,j} \qquad \text{(D.24)}
\end{aligned}
$$

Model 6:

$$\begin{aligned}
\frac{dS}{dt} &= -\frac{\alpha_1\phi S P_1}{1+\rho_1 P_1} - \frac{\alpha_2\phi S P_2}{1+\rho_2 P_2} - \frac{\alpha_3\phi S P_3}{1+\rho_3 P_3} \\
&\quad -\gamma_1 S^{\gamma_2}(S + \sum_{i=1}^{3}\sum_{j=1}^{m_i} E_{i,j}) - \gamma_3 Q S^{\gamma_4} && \text{(D.25)} \\
\frac{dE_{i,1}}{dt} &= \frac{\alpha_i\phi S P_i}{1+\rho_i P_i} - \gamma_1 {E_{i,1}}^{\gamma_2}(S + \sum_{i=1}^{3}\sum_{j=1}^{m_i} E_{i,j}) - \gamma_3 Q {E_{i,1}}^{\gamma_4} && \text{(D.26)} \\
&\quad -m_i\delta_i E_{i,1}, \quad \text{for } i = 1,2,3 && \text{(D.27)} \\
\frac{dE_{i,j}}{dt} &= m_i\delta_i E_{i,j-1} - \gamma_1 {E_{i,j}}^{\gamma_2}(S + \sum_{i=1}^{3}\sum_{j=1}^{m_i} E_{i,j}) - \gamma_3 Q {E_{i,j}}^{\gamma_4} \\
&\quad -m_i\delta_i E_{i,j}, \quad \text{for } j = 2,...,m_i && \text{(D.28)} \\
\frac{dP_i}{dt} &= m_i\delta_i E_{i,j} && \text{(D.29)}
\end{aligned}$$

APPENDIX E

PARAMETER VALUES

Table E.1: Parameter values from the posterior distribution of the larval mortality model

Parameter	Mean value	Lower 25% C.I.	Upper 75% C.I.
α_1	0.200	0.011	3.203
α_2	64.6	35.6	126
α_3	118	76	191
ϕ	0.259	0.196	0.350
ρ_1	7819	6660	10002
ρ_2	152	51.2	487
ρ_3	5887	5076	6972
γ_1	0.343	0.196	0.672
γ_2	2.000	2.000	2.000
η_1	0.098	0.055	0.179
η_2	0.518	0.262	0.975
m_1	1	fixed	fixed
m_2	3.66	2.00	6.00
m_3	1.06	1.00	1.15
δ_1	0.113	0.103	0.124
δ_2	$2.96e^{-4}$	$1.21e - 4$	$5.66e^{-4}$
δ_3	0.476	0.297	1.000

APPENDIX F

REPRODUCTION AND OVERWINTERING MODEL FIT TO DATA

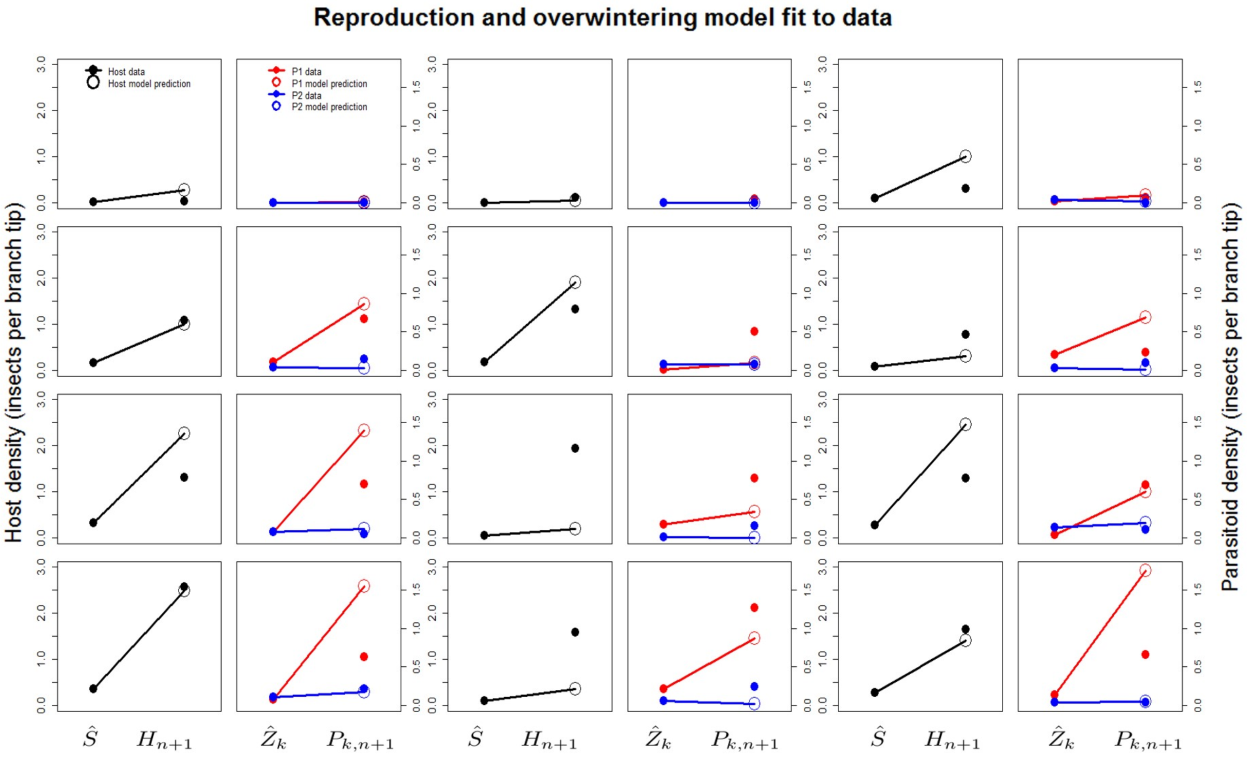

Figure F.1: The reproduction and overwintering model fit to data

APPENDIX G

EFFECT OF PLANT QUALITY FOR DIFFERENT VALUES OF ν

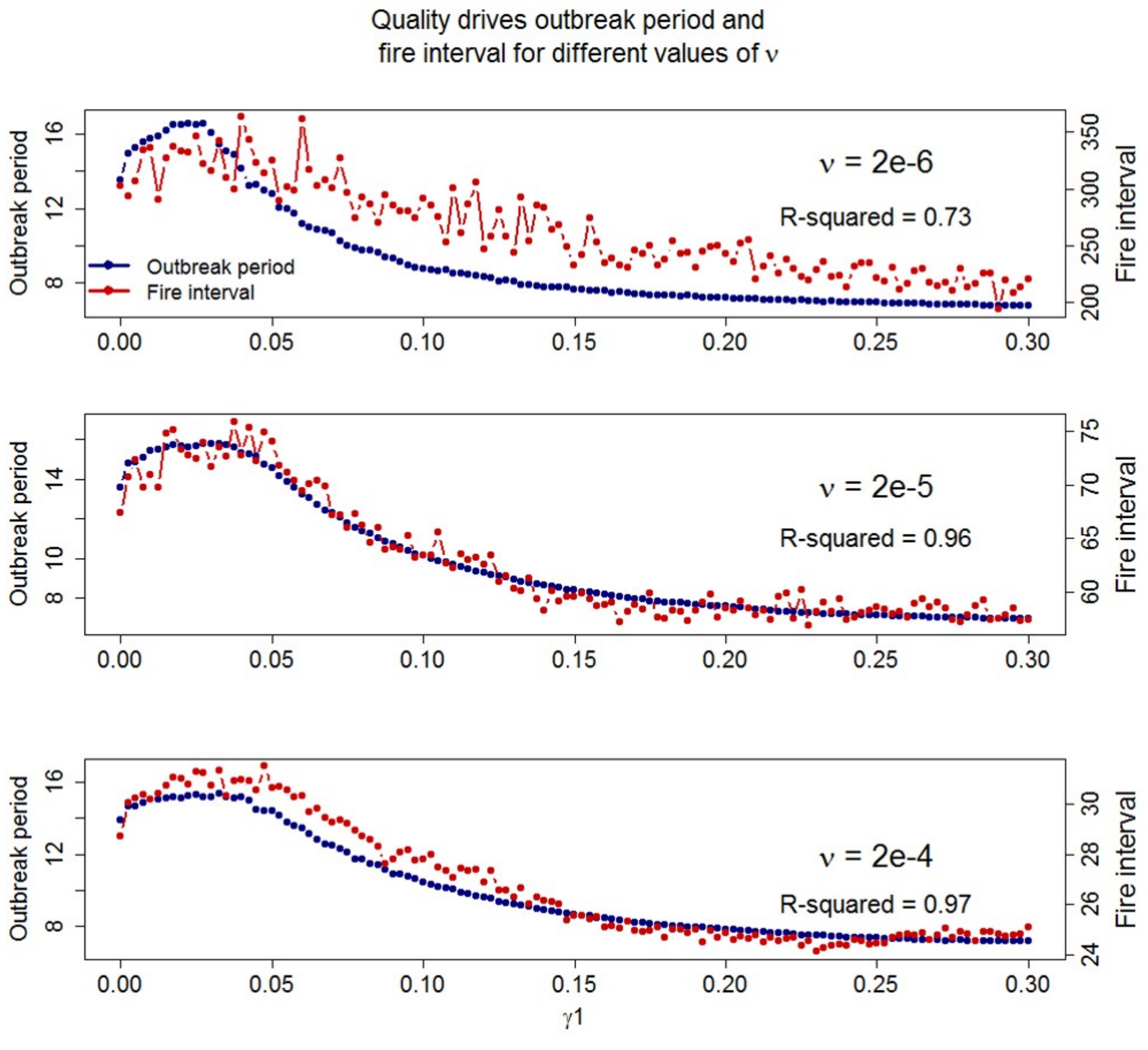

Figure G.1: Outbreak period and fire interval change with the plant quality parameter $\gamma_1$for different values of the endogenous fire frequency parameter ν

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