Data Driven Models of Hemlock Woolly Adelgid Impacts and Biological Control

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Abstract

We present two models of the *Adelges tsugae*, the hemlock woolly adelgid, an invasive insect pest of *Tsuga canadensis*, eastern hemlock, in the eastern United States. An *A. tsugae* infestation often results in the death of *T. canadensis* within years, and has caused significant changes to hemlock forests. We construct two models composed of systems of ordinary differential equations with time dependent parameters to represent seasonality. The first model captures the coupled cycles in *T. canadensis* health and *A. tsugae* density. We use field data from Virginia to develop the model and to perform parameter estimation. The mechanisms we represent in the model, including an *A. tsugae* density dependent *T. canadensis* growth rate, a *T. canadensis* health dependent *A. tsugae* mortality rate and a density dependent *A. tsugae* mortality rate, produce the cycles in *T. canadensis* health and *A. tsugae* density commonly seen with the *A. tsugae* system in the eastern United States. We test sets of initial conditions to determine scenarios that will likely lead to *T. canadensis* mortality.

The second model represents the population dynamics of *A. tsugae* and two introduced biological control organisms, *Laricobius nigrinus* and *Sasajiscymnus tsugae*, released to attempt to control *A. tsugae* populations and allow *T. canadensis* survival. We use field data from the Great Smoky Mountains National Park to develop the model and to perform parameter estimation. The model is stage structured, with two classes per species. To represent the seasonality of the system, in addition to time dependent parameters, the model is composed of multiple systems of ordinary differential equations that control the system at different times of the year.

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Chapter 1

Introduction

1.1 Modeling Tools

Mathematical modeling has been used in various ways to contribute to our understanding, prediction, and management of invasive species [31]. Aspects of biological control have also been studied through modeling [54]. Murdoch et al. state that a key question in the use of biological control organisms, which has not been answered by theory, is "'what kind(s) of species, and how many, should we release given the modes of competition and co-existence among them?'" [54]. We present two data driven models of the invasive *Adelges tsugae*, hemlock woolly adelgid, to address this question. The first model represents the coupled cycles between *A. tsugae* and its hemlock tree host, *Tsuga canadensis*. The second model represents the population dynamics of *A. tsugae* and introduced biological control beetle predators, *Laricobius nigrinus* and *Sasajiscymnus tsugae*. We develop the Hemlock-Adelgid model based on field data of *T. canadensis* health and *A. tsugae* densities observed over 13 years in Virginia [42, 40]. We use field data of *A. tsugae*, *L. nigrinus* and *S. tsugae* densities observed over 3 years in the Great Smoky Mountains National Park to develop the Adelgid-Predator model [68, 67].

Both models are systems of ordinary differential equations with time dependent parameters. We implement and study these models as multiple systems with constant parameters that apply at different times of the year, with initial conditions of each system taken from the state variable values of a previous system. In the Hemlock-Adelgid model,

both species are explicitly modeled throughout the year and all initial conditions of the systems are the state variable values at the final time of the previous system. Thus in the Hemlock-Adelgid model, solutions are continuous functions of time. The Adelgid-Predator model is stage structured, with two classes for each of the three species. As not all life stages are active in the system throughout the year due to the seasonality of the three species, the model solutions include discontinuities and some initial conditions depend on the density of other classes, as biologically appropriate. We determine the seasonality of the models through the literature and the field data we use in developing the models.

We perform parameter estimation on each of the models using the field data, the numerical ordinary differential equations solver ode45, and fmincon and MultiStart in MATLAB. For each model, we construct a constrained optimization problem with the sum of the squares of the relative error between the data and model output as the objective function value, which we minimize over the parameter values. We provide upper and lower bounds for each of the parameter values we are estimating and specify one of the n starting points, a vector of values for each of the parameters we estimate. MultiStart generates the remaining $n-1$ starting points with pseudorandom number generation within the bounds for the parameters [35, 36]. As all but one of the starting points for each run of MultiStart are found by pseudorandom number generation, they are likely to be unique, even across different runs of MultiStart. Once starting points are found through MultiStart, fmincon attempts to find a minimizer of the objective function starting at each starting point. The objective function value is minimized by the set of parameter values that produce model simulation results closest to the data, as measured by the relative error. We use the fmincon Interior Point algorithm, which uses direct steps, or, as necessary, conjugate gradient steps to locate a local minimum [34, 33]. Due to the time required to complete optimization for the Hemlock-Adelgid model, we use parallel computing through the Parallel Computing Toolbox in MATLAB and compiled results across multiple runs of MultiStart and fmincon.

Using the parameter values found through parameter estimation for the Hemlock-Adelgid model, we vary *T. canadensis* and *A. tsugae* initial conditions to determine which initial conditions are likely to lead to *T. canadensis* mortality. We also simulate the model results over longer times to study longer term behavior of the Hemlock-Adelgid model. We study

the behavior of the Adelgid-Predator model by varying the value of the parameter that represents the *T. canadensis* proportion tips alive and by considering the dynamics of the different combinations of species to begin to answer the question posed by Murdoch et al. about the impact of multiple biological control organisms [54].

1.2 Biological System

There are two species of hemlock trees native to eastern North America, *Tsuga canadensis*, the Eastern hemlock and *Tsuga caroliniana*, the Carolina hemlock. *Tsuga canadensis* is an extremely shade tolerant, slow growing species with lifespans of 800 years or more [21]. *Tsuga caroliniana* is a closely related species. Both species are impacted by *Adelges tsugae*, and have experienced mortality in forest and ornamental settings due to *A. tsugae* infestations [26]. *Tsuga caroliniana* has a much more restricted range in Georgia, Tennessee, South Carolina, North Carolina and Virginia, while the range of *T. canadensis* extends from northern Georgia and Alabama, into Canada and west to the Great Lakes. The data we use in developing our models were collected from *T. canadensis*. *Tsuga canadensis* are ecologically important, causing year-round shading, increased soil acidity, and decreased stream temperatures for fish and other aquatic species [58, 16]. *Tsuga canadensis* provide food, cover and habitat for deer, rabbit, and bird species and several bird species are hemlock obligates. *Tsuga canadensis* can die within 4 to 15 years of the initial *A. tsugae* infestation, although some trees can survive for longer [26, 56, 51]. *Tsuga canadensis* that die as a result of *A. tsugae* infestation are often replaced with other species as increased light availability and changes in nutrient cycling allow other species to establish [16, 26].

The first record of *Adelges tsugae* in the eastern United States is from a museum specimen from 1951 [26]. *Adelges tsugae* is now found in half of the native range of *T. canadensis* in eastern North America. The genotype of *A. tsugae* found in the eastern United States is from Japan where *Picae torano*, a spruce, is its primary host, where sexual reproduction occurs, and *Tsuga sieboldii*, a native hemlock, is the secondary host [26]. In the eastern United States, no spruce species support the sexual reproduction of *A. tsugae*, so all reproduction of *A. tsugae* is asexual and occurs on *T. canadensis* [47]. There are two generations of *A. tsugae*

each year in the eastern United States [26, 24, 45]. The two generations, the sistens and progrediens generations, have different lengths. The eggs that become the sistens generation are laid in the early summer, and once hatched, the first instar, also called crawlers, disperse on the *T. canadensis*, as the only mobile life stage. After they settle at the base of needles, they enter dormancy over the summer. In the fall they continue developing and mature to adults in early spring when they lay eggs. The white woolly ovisacs that both generations of *A. tsugae* produce are the most recognizable life stage. The second generation does not have a dormancy period, but matures during the spring. The offspring of the sistens generation develop into two types of adults, the progrediens generation whose offspring are the sistens generation, and a winged adult morph, the sexuparae. The sexuparae disperse from *T. canadensis* in search of the primary host spruce where the sexual part of *A. tsugae* life cycle can occur. As no primary hosts occur in the eastern United States, these adults do not successfully reproduce and their dispersal acts as a source of morality in the *A. tsugae* population. *Adelges tsugae* spread between *T. canadensis* as eggs or crawlers through wind dispersal or via other organisms, such as birds, deer and humans [46].

In the native range of *A. tsugae*, *Tsuga* species are not often impacted by *A. tsugae* infestations. This is due to resistance by *Tsuga* species and to natural enemies that control *A. tsugae* populations [50]. *Tsuga canadensis* is susceptible to *A. tsugae*, and no native predators successfully control *A. tsugae* populations in the eastern United States [26]. *Adelges tsugae* impact *T. canadensis* by removing nutrients, through feeding on the nutrients stored and transferred by the parenchyma cells in the xylem, and by causing a hypersensitive response in infested branches that impacts water transport in *T. canadensis* [26]. Infested *T. canadensis* branches become discolored, desiccate, lose needles, and experience dieback which can lead to severe dieback and eventual mortality of the tree [47, 26]. Several strategies have been used to manage *Tsuga* populations in the eastern United States. *Tsuga caroliniana* have been crossed with Chinese *Tsuga* to produce hybrids with increased *A. tsugae* resistance [52]. Silvicultural management such as forest thinning to increase light levels have been shown to reduce *A. tsugae* densities and maintain *T. canadensis* health [1]. The use of insecticides for chemical control of *A. tsugae* has also been well studied. Systemic insecticides, including imidacloprid, applied through soil drench, soil injection and trunk injection methods have

shown to be effective at controlling *A. tsugae* densities and protecting *T. canadensis* health [26]. Biological control organism have also been studied, reared and released including predators native to Japan, China and western North America, such as *Sasajiscymnus tsugae* and *Laricobius*, *Scymnus*, and *Leucopis* species [55]. Procedures and guidance for integrated pest management, including chemical control while biological control organisms establish and grow to effective densities have been released by the U. S. Forest Service [39].

Chapter 2

Hemlock-Adelgid Model

2.1 Introduction

The hemlock woolly adelgid, *Adelges tsugae*, is an invasive insect affecting hemlock trees, *Tsuga canadensis* in the eastern United States. Geographic variation in *T. canadensis* mortality due to *A. tsugae* has been observed in the invaded range [26]. In southern areas or where trees experience water or other stress, more rapid or widespread *T. canadensis* mortality has been observed. In northern areas where winter temperatures may control *A. tsugae* densities, *T. canadensis* survive *A. tsugae* infestations longer. In a study of *T. canadensis* growth and survival and *A. tsugae* density conducted at three Connecticut forests sites by McClure, all trees died within four years of *A. tsugae* introduction [47]. In this study, cycles in *A. tsugae* density, with peaks in the first and third year of *A. tsugae* infestation, and corresponding cycles of *T. canadensis* new growth were documented. After *T. canadensis* were observed to survive *A. tsugae* infestation for longer at some sites in Massachusetts, Paradis conducted a study at six sites in Massachusetts and Connecticut meant in part to compare to the McClure study [56]. *Adelges tsugae* population dynamics and *T. canadensis* health, measured as the percent viable buds, were recorded over several years. All trees in this study survived the seven years they were observed, but similar cycles in *A. tsugae* density and *T. canadensis* health as documented by McClure were recorded.

These coupled cycles in *T. canadensis* health and *A. tsugae* densities seem to be an important feature in *A. tsugae* population dynamics in the eastern US. Our goal is to

investigate mechanisms leading to cycles in *T. canadensis* health and *A. tsugae* density by formulating a mathematical model of these two species. This is joint work with Suzanne Lenhart and Gregory Wiggins and in collaboration with Thomas McAvoy. We formulate the model based on field data from a study led by McAvoy, which recorded *T. canadensis* canopy characteristics and *A. tsugae* densities at a field site in Mountain Lake, Virginia from 2001 to 2015 [40]. A preliminary report of the study was presented in 2005 [42]. We use field data from McAvoy to perform parameter estimation on the model.

2.2 Data

As a part of a study on the impact of chemical control on *A. tsugae* densities and the health of *T. canadensis* conducted by McAvoy et al. between 2001 and 2015, *T. canadensis* characteristics were observed annually and *A. tsugae* densities were recorded twice annually on four groups of trees at Mountain Lake Resort in Giles County, Virginia [42, 40]. *Adelges tsugae* infestation was first observed in the area in 1999. Some trees in each group were treated with various insecticide treatments, while others were left untreated. We use data from the untreated trees in performing parameter estimation on our model, which represents the interacting dynamics of *T. canadensis* health and *A. tsugae* density. We exclude chemically treated trees from the data for the parameter estimation as chemical treatment is intended to impact the *A. tsugae* density, and thus treated and untreated *T. canadensis* with equal canopy health are expected to support different *A. tsugae* densities [39]. *Tsuga canadensis* treated with imidacloprid, a systemic insecticide, have been found to have reduced *A. tsugae* densities following chemical treatment, which allows improvements in *T. canadensis* health over time [65]. Chemical treatment may lead to declines in photosynthetic potential and other impacts on *T. canadensis* [20]. However, chemical treatment methods do not appear to impact *T. canadensis* tolerance of an *A. tsugae* infestation at a particular density [41].

Five canopy characteristics, percent live crown ratio, live branches, tips alive, new foliage, and crown density, were observed during the growing season as measures of *T. canadensis* health, each recorded as a percentage to the nearest five percent. The canopy

characteristics were observed and recorded using methods described and recommended by the Forest Inventory and Analysis Program of the US Forest Service [60]. Densities of live *A. tsugae* adults were recorded once per generation, with *A. tsugae* counted on 30 centimeters of four terminal branches of the cardinal points in the early spring to record sistens density and in the early summer to record progrediens density. *A. tsugae* densities are in units of *A. tsugae* per centimeter of twig. The lengths of the newest growth on each twig within the 30 centimeters of branch observed were also recorded. *Adelges tsugae* density can then be calculated as the total number of *A. tsugae* individuals divided by the sum of the lengths of the newest growth of all twigs on the 30 centimeters of branch. Alternatively, *A. tsugae* density can be calculated as the total number of *A. tsugae* individuals divided by 30, as a representation of *A. tsugae* per centimeter of branch, instead of *A. tsugae* per centimeter of newest growth on individual twigs. As the field study that provides data for the Adelgid-Predator model in Chapter 3, uses the latter method, resulting in *A. tsugae* per centimeter of branch, we calculate *A. tsugae* density in the same way here so that we can use parameter values from the Hemlock-Adelgid model in the Adelgid-Predator model. The mean of the densities of the four branches was taken to determine the *A. tsugae* density per tree.

Trees with missing data were excluded from each group, and the means of *T. canadensis* canopy measures and *A. tsugae* density were determined for each observation date. Over the course of the study, individual *T. canadensis* died, which is a common fate of *T. canadensis* that are infested with *A. tsugae* but go untreated. As *T. canadensis* will not recover after losing their canopies, a tree with 0 percent live crown ratio, live branches, tips alive, new foliage, and crown density is permanently dead. In determining the mean proportion of tips alive and *A. tsugae* density on each date, we exclude dead *T. canadensis* individuals. Thus in our work, the proportion tips alive and *A. tsugae* density can be interpreted as a representation of the state of the average living *T. canadensis* in the stand, rather than the average *T. canadensis* in the stand, which may have a much smaller proportion tips alive if many *T. canadensis* have died.

Each observation date was assigned a week in the calendar year. We have no biological reason to believe that conditions are different between the four groups of *T. canadensis*, but as initial data was recorded for the different groups in different years, and we are interested in

the coupled cycles of *T. canadensis* health and *A. tsugae* density over time, we use the data for the groups separately to use the longest time series possible in the data. We use the data from two of the four groups of *T. canadensis* in parameter estimation, group I, the Indian Trail group, and group II, the Lower Jungle Trail group. We exclude the other groups due to chemical treatment during the study or *A. tsugae* densities too low to be expected to impact *T. canadensis* health, as shown in Figure 2.1. The data we use in parameter estimation is shown in Table 2.1 and Figure 2.2 for the group I trees and Table 2.2 and Figure 2.3 for the group II trees.

In addition, we use the data to determine a *T. canadensis* proportion tips alive value that is likely to result in tree mortality. We assume that at some low proportion tips alive, *T. canadensis* are unlikely to recover, regardless of the history of the *A. tsugae* infestation or the previous changes in *T. canadensis* proportion tips alive. To determine this value, we use both chemically treated and untreated trees, from all four groups of trees. We exclude trees with only one proportion tips alive observation, trees with inconsistencies in data collection, such as two observations on the same date with different values, and trees that are dead at all observations. As we did in preparing the data for parameter estimation, we assume that a tree is dead when all canopy characteristics are observed to be 0. Thus it is possible for a tree to have zero proportion tips alive, but not be considered dead. The goal of this analysis is to determine a proportion tips alive value to use in interpreting model results. After excluding trees for the reasons above, we have a time series of proportion tips alive data with at least two observations for 433 trees. We consider proportion tips alive measurements from 0 to 0.4 in increments of 0.05. For each proportion tips alive value, we find the number of trees ever recorded at a proportion tips alive less than or equal to our value of interest, and the number of those trees that eventually died. We then calculate the proportion of trees that died after being recorded below our value of interest. The results are show in Table 2.3. Based on the calculated proportion of trees that eventually died, we choose the value 0.10 as the proportion tips alive value at which *T. canadensis* mortality is likely as 75.45% of trees recorded reaching a proportion tips alive of 0.10 or below were recorded as dead over the course of the study. We choose a proportion tips alive corresponding to a lower mortality rate since additional trees from this group may have died after the conclusion of the study

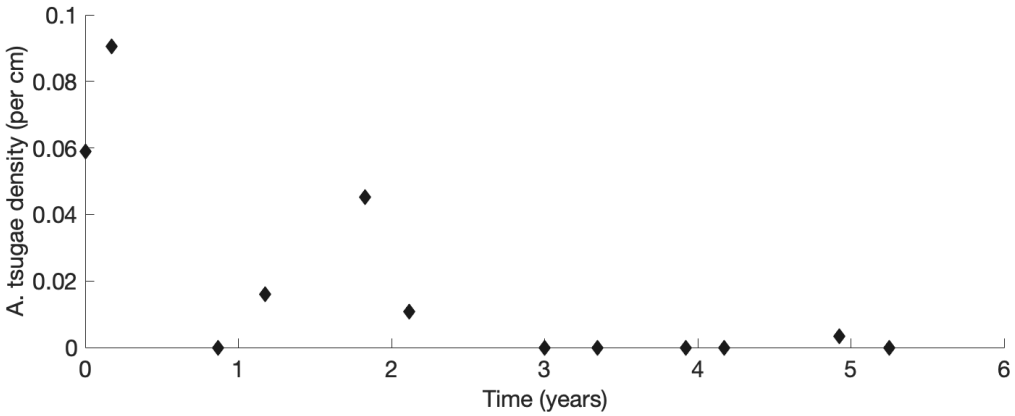


Figure 2.1: Blueberry Hill group *A. tsugae* density data plotted over the 6 years of *A. tsugae* data collection. The first observation (time 0) was recorded April 24, 2003. *A. tsugae* densities seen in this plot, which are all less than 0.1 *A. tsugae* per centimeter are not expected to impact *T. canadensis* health, and thus we do not use these data in parameter estimation for the model.

Table 2.1: Mean *T. canadensis* proportion tips alive and *A. tsugae* density data for group I trees, including the number of living trees at each time point. The first observation (time 0) was recorded April 11, 2001.

Time (years)	Proportion tips alive	*A. tsugae* density (per cm)	Number of living trees
0	0.7750	2.8442	10
0.8462	0.5400	1.9125	10
1.1923	0.5700	3.8467	10
2.0192	0.1170	0.0508	10
2.1923		0.0050	10
2.7885	0.2020	0.0203	10
3.1923	0.1200	0.0111	6
3.8654		0.2583	4
4.2115	0.5250	0.0167	2
5.0385		0	2
5.1923	0.5500	0.0417	2
5.9231		0.0792	2
6.2115	0.5250	0.4292	2
6.9231		0.0838	2
7.1923	0.5500	2.0708	2
12.6923	0.5750		2

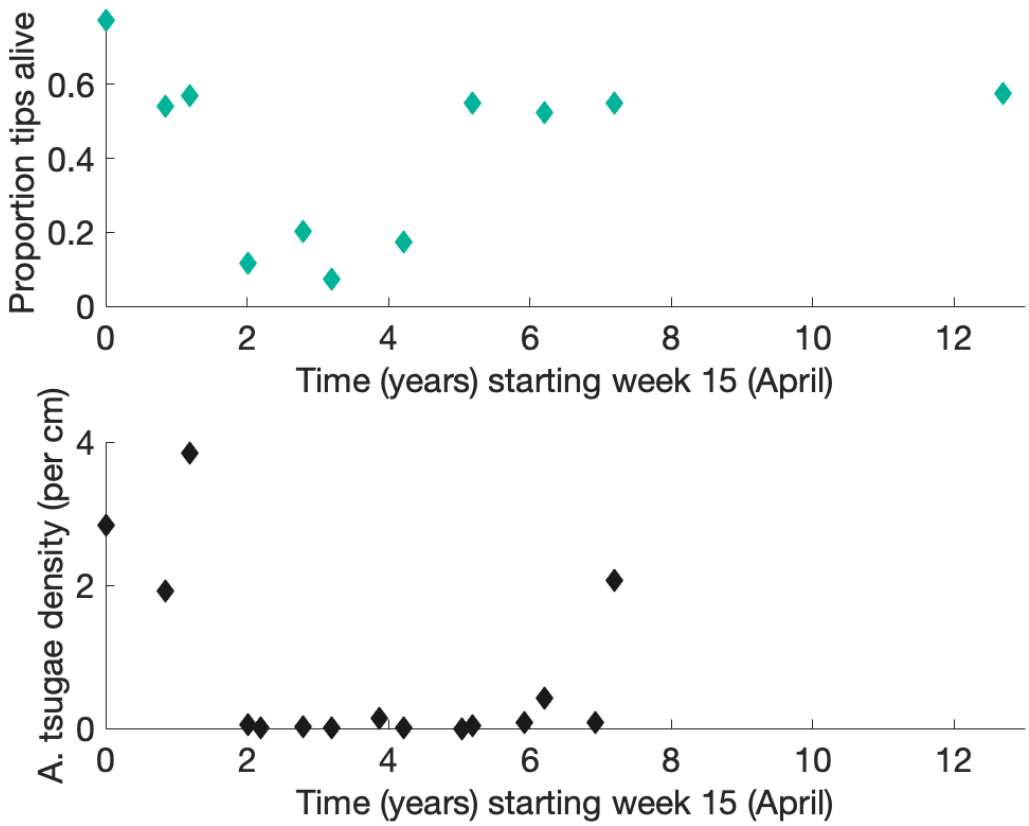


Figure 2.2: Group I data plotted over the 13 years of the study. The mean *T. canadensis* proportion tips alive are shown in the top plot and *A. tsugae* density is shown in the bottom plot. The first observation (time 0) was recorded April 11, 2001, week 15 of the calendar year.

Table 2.2: Mean *T. canadensis* proportion tips alive and *A. tsugae* density data for group II trees, including the number of living trees at each time point. The first observation (time 0) was recorded July 3, 2002.

Time (years)	Proportion tips alive	*A. tsugae* density (per cm)	Number of living trees
0	0.6611	2.4815	9
0.7115	0.2889	0.0491	9
0.9423		0	9
1.6346	0.2133	0.0287	9
1.9615	0.4056	0.0926	9
2.6346		0.1688	8
2.9808	0.6500	0.0219	8
3.8077		0	8
3.9808	0.6313	0.0271	8
4.7115		0.0938	8
4.9808	0.6125	0.0146	8
5.7115		0.0326	8
5.9808	0.5500	0.7354	8
12.4615	0.4375		8

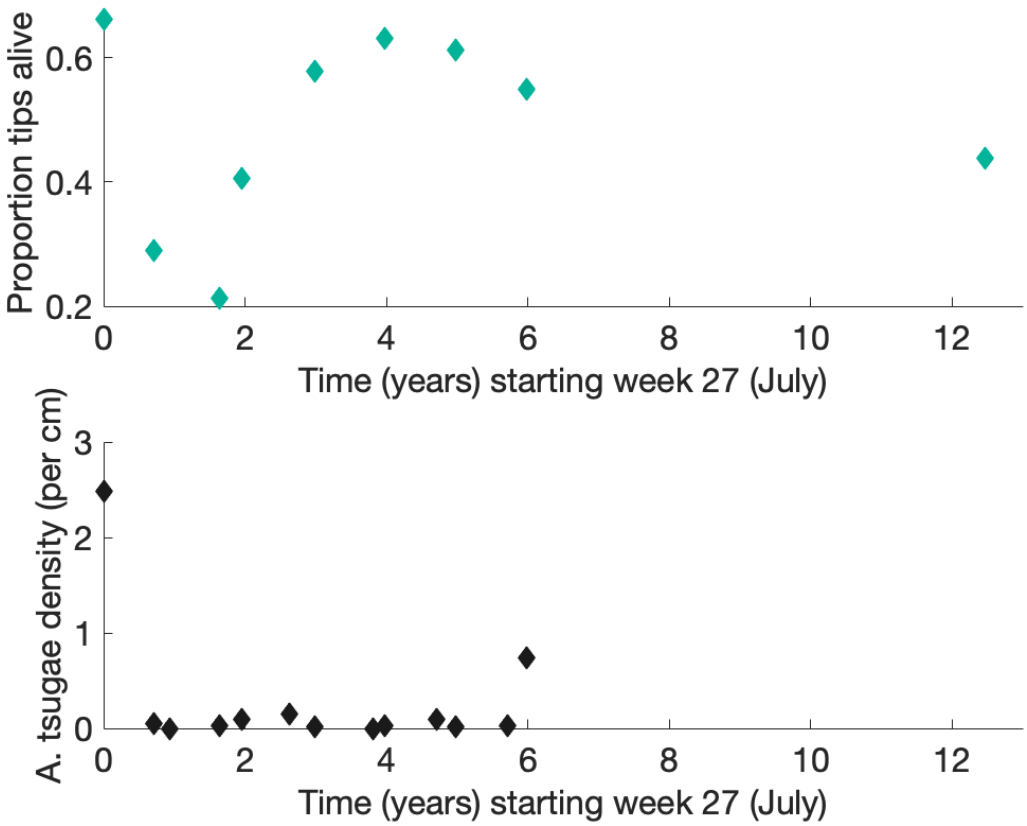


Figure 2.3: Group II data plotted over the 13 years of the study. The mean *T. canadensis* proportion tips alive are shown in the top plot and *A. tsugae* density is shown in the bottom plot. The first observation (time 0) was recorded July 3, 2002, week 27 of the calendar year.

Table 2.3: The number of trees with proportion tips alive recorded below the proportion tips alive value of interest at any time during the study, and the proportion of those trees that eventually died. The numbers of trees in the second column increases as the proportion tips alive of interest increases, as trees that were recorded below lower proportion tips alive were also recorded below a higher proportion tips alive.

Proportion tips alive	Trees recorded below this value	Proportion of trees that died
0	84	0.9881
0.05	92	0.9021
0.10	110	0.7545
0.15	147	0.5646
0.20	177	0.4689
0.25	198	0.4192
0.30	217	0.3825
0.35	235	0.3532
0.40	289	0.2872

and because of the management goals for *T. canadensis*. If a decision about whether to treat trees or not is being made, it may be better to treat trees that are relatively likely to die, even if some of the trees would survive without intervention.

2.3 Model Formulation

We develop a model of systems of ordinary differential equations to represent the interaction of *A. tsugae* and their host *T. canadensis*. We represent *A. tsugae* densities, A as a single class including all *A. tsugae* life stages except for eggs. We do not explicitly model *A. tsugae* eggs as the eggs do not impact *T. canadensis* either by consuming nutrients from the tree or by causing tree response as the other *A. tsugae* life stages do [26]. As in the data, *A. tsugae* densities in the model are in units of *A. tsugae* individuals per centimeter. We choose proportion tips alive, H, to represent hemlock health in the model as it is an early indicator of damage to a tree and reflects the severity of recent stress [60]. Proportion tips alive is related to crown dieback, one of the crown indicators used to assess forest health by the Forest Inventory and Analysis Program of the U.S. Forest Service. The sum of proportion tips alive and crown dieback is one. Proportion tips alive were recorded in the data, so that higher values of all indicators recorded corresponded to increased health [42]. Crown dieback, among other crown indicators, has been studied in *T. canadensis* in response to *A. tsugae* infestation. *Tsuga canadensis* health, including crown dieback, crown vigor, crown transparency, and crown density and *A. tsugae* infestation severity, measured as a proportion of tips with *A. tsugae*, were recorded annually at the Delaware Water Gap National Recreation Area for four years. The change in crown transparency and infestation severity were most strongly correlated in the study, but the change in crown dieback and infestation severity were also moderately correlated, with a weaker correlation of change in crown density and infestation severity [15]. Crown dieback, along with crown diameter, crown ratio, crown density, and crown transparency were also observed annually at 5 sites in Pennsylvania, Maryland and West Virginia, along with new growth on *T. canadensis* and *A. tsugae* density, measured as the proportion of infested tips. In this study, crown dieback and crown transparency showed the strong relationships with *A. tsugae* density [8].

Dieback was also studied at forest sites in northern Georgia [51]. *Adelges tsugae* density was recorded as the number of *A. tsugae* per utilized length of twig, where the length of twigs and the proportion of needles present are used to calculate the utilized length of twig. Site characteristics such as elevation and previous released of biological control organisms at the site as well as biotic characteristics such as percent new growth and presence of other insect species that use *T. canadensis* as a host were observed. Through linear mixed effect models, none of the studied factors had a significant impact on *T. canadensis* dieback, and only percent new growth had a significant effect on *A. tsugae* density. *Tsuga canadensis* in this study also survived at higher rates and for longer periods than expected for trees in the southern part of their range. Although crown dieback may not be the only canopy characteristic that could represent *T. canadensis* health, based on its use in studies, we believe it is a reasonable choice of how to represent *T. canadensis* health in our mathematical model.

We develop a model of *T. canadensis* proportion tips alive and and *A. tsugae* density seen in equations 2.1 and 2.2. We represent seasonality in the model with piecewise constant time dependent parameters that act as switches turning on seasonal processes. In implementing the model, throughout the year, we make switches between five different systems of equations with constant parameter values, using the state values at the final time of one time period as the initial conditions of the next. Thus both proportion tips alive and *A. tsugae* density are continuous functions of time. As the two groups in the data have the first data collected at different weeks in the calendar year, and we use the first data value as the initial conditions for each class, we implement two versions of the model with different initial times. The model that uses the group I data for parameter estimation has time 0 in week 1 at April 11, 2001, corresponding to week 15 in the calendar year, whereas the model that uses the group II data has time 0 at July 3, 2002, corresponding to week 27 in the calendar year.

$$\frac{dH}{dt} = g_H(t)\Big(\frac{-1}{1+e^{-b_1(A-b_2)}} + \ell\Big)H\big(1-\frac{H}{k}\big) \tag{2.1}$$

$$\frac{dA}{dt} = g_A(t)A - m_A(t)\frac{A}{H} - m_S(t)A^2 \tag{2.2}$$

We assume that in the absence of *A. tsugae*, proportion tips alive grows logistically, and thus over time would approach a carrying capacity, k. In the logistic term of the H differential equation, we interpret this carrying capacity as the proportion tips alive expected on a healthy, uninfested *T. canadensis*. The model is valid for $0 < H(0) < k$, which ensures $H(1 - \frac{H}{k}) > 0$ and thus that the sign of $\frac{dH}{dt}$ depends on *A. tsugae* density. We assume that the growth rate of proportion tips alive,

$$g_H(t)\Big(\frac{-1}{1 + e^{-b_1(A-b_2)}} + \ell\Big),$$

depends on *A. tsugae* density and represents the growth rate as a bounded, decreasing function of *A. tsugae* density. The parameter b_1 impacts the rate of change between a *T. canadensis* proportion tips alive growth rate, a positive rate, at low *A. tsugae* densities and a *T. canadensis* proportion tips alive decline rate, a negative rate, at high *A. tsugae* density, with higher b_1 values leading to a more rapid change from a positive to negative rate as *A. tsugae* density increases. The *A. tsugae* density, A, relative to the parameter b_2 determines the effect of the exponential term on the *T. canadensis* recovery or decay rate. When A is less than b_2, the exponent is positive, and the denominator of the term will be larger, which increases the growth rate of the proportion tips alive. As the logistic factors $H(1-\frac{H}{k})$ of the proportion tips alive, H, differential equation are positive, as $0 < H(0) < k$, and as $g_H(t)$ is nonnegative, we can find a *A. tsugae* threshold value by determining the sign of

$$\frac{-1}{1 + e^{-b_1(A-b_2)}} + \ell.$$

The threshold value is where the change in *T. canadensis* health (the right hand side of the H differential equation) is 0 and switches from positive rates at lower *A. tsugae* densities to negative rates at higher *A. tsugae* densities. The threshold *A. tsugae* density, A, is then

$$A = -\frac{1}{b_1} \ln\Big(\frac{1-\ell}{\ell}\Big) + b_2.$$

If ℓ is not less than 1, the *T. canadensis* is positive for all *A. tsugae* densities. We assume $\ell < 1$.

Adelges tsugae reproduction has rate $g_a A$ during the periods of the year when reproduction occurs. As *A. tsugae* eggs are not represented in the model, this reproduction occurs when *A. tsugae* eggs hatch into crawlers, rather than when *A. tsugae* eggs are laid. Reproduction occurs twice in the calendar year, as *A. tsugae* are bivoltine [26]. Reproduction occurs from during weeks 15 to 19 and weeks 26 to 29 in the calendar year, from late March to late May and from mid June to early July [38, 22]. We assume there are multiple mechanisms that produce *A. tsugae* density dependence as reported in the literature [62, 63, 47, 5, 7, 64, 66]. We assume that some of the density dependence observed is the result of *A. tsugae* interactions with the trees, and that other mechanisms may also contribute to observed density dependence. We represent both through *A. tsugae* mortality, with a seasonally dependent mortality rate,

$$m_A(t)\frac{A}{H},$$

which is a decreasing function of proportion tips alive and a density dependent mortality,

$$m_S(t)A^2,$$

which occurs during the summer when sexuparae mature and leave *T. canadensis*. We assume that the number of sistens offspring that become sexuparae instead of progrediens is not mediated by the tree health, but is *A. tsugae* density dependent as reported by McClure [47]. McClure found a strong positive correlation between *A. tsugae* density and the natural log transformed percent of the progrediens/sexuparae generation that was sexuparae. Sussky and Elkinton found that the proportion of sexuparae depended on the density of the progrediens/sexuparae generation, rather than the density of the previous sistens generation [62]. We choose a simple form for the density dependence with a quadratic function of *A. tsugae* density. The full model, composed of the five systems with constant parameters are shown in Systems A to E. Weeks for each system are given as calendar weeks, and the model weeks are shown in Table 2.4.

Table 2.4: The weeks each system of differential equations with constant parameter values determines *T. canadensis* proportion tips alive and *A. tsugae* density dynamics in the calendar year, in the group I model, and in the group II model. The differences in week numbering is due to the initial weeks of the two models, which are determined by the first observation in the data of these groups.

System	Calendar Weeks	Group I Model Weeks	Group II Model Weeks
E	1-13 and 52	38-51	26-39
B	14	52	40
A	15-19	1-5	41-45
B	20	6	46
C	21-25	7-11	47-51
A	26-29	12-15	1-3 and 52
B	30	26	4
D	31-46	17-32	5-20
B	47-51	33-37	21-25

System A

System A is used twice during a calendar year, during weeks 15-19, in late March and April, and weeks 26 to 29, mid June through early July. *Adelges tsugae* reproduction is occurring, so $g_A(t)$ takes a positive rate, g_a. During these times, *A. tsugae* experience the background mortality rate $m_a \frac{A}{H}$ and the *A. tsugae* density dependent mortality rate is not present. *Tsuga canadensis* proportions tips alive experience logistic growth at the *A. tsugae* dependent rate, $g_h\Big(\frac{-1}{1+e^{-b_1(A-b_2)}} + \ell\Big)$.

$$\frac{dH}{dt} = g_h\Big(\frac{-1}{1+e^{-b_1(A-b_2)}} + \ell\Big)H\big(1-\frac{H}{k}\big) \tag{2.3}$$

$$\frac{dA}{dt} = g_a A - m_a \frac{A}{H} \tag{2.4}$$

System B

System B applies for four time periods in a calendar year, as shown in Table 2.4. Three of these time periods are a week long, in week 14, in mid March, week 20, in late April and early May, and week 30, in mid July. System B also applies during weeks 47-51 from early November to mid December. During these weeks, *A. tsugae* reproduction is not occurring, so there is no positive term in the *A. tsugae* equation. *Adelges tsugae* mortality is at the background rate $m_a \frac{A}{H}$, as in System A. Also as in System A, the density dependent *A. tsugae* mortality rate is not present, and *T. canadensis* proportion tips alive changes based on *A. tsugae* density.

$$\frac{dH}{dt} = g_h\Big(\frac{-1}{1+e^{-b_1(A-b_2)}} + 1\ell\Big)H\big(1-\frac{H}{k}\big) \tag{2.5}$$

$$\frac{dA}{dt} = -m_a \frac{A}{H} \tag{2.6}$$

System C

System C is used during weeks 21-25 from early May to mid June. *Adelges tsugae* mortality is at the background rate $m_a \frac{A}{H}$, as in Systems A and B. There is an additional mortality rate as *A. tsugae* sexuparae are maturing and leaving *T. canadensis*, at a density

dependent rate $m_s A^2$. *Adelges tsugae* reproduction is not occurring during these weeks, as in System B and *T. canadensis* proportions tips alive change, at a *A. tsugae* density dependent rate, as in Systems A and B.

$$\frac{dH}{dt} = g_h\Big(\frac{-1}{1+e^{-b_1(A-b_2)}} + \ell\Big)H\big(1-\frac{H}{k}\big) \tag{2.7}$$

$$\frac{dA}{dt} = -m_a\frac{A}{H} - m_s A^2 \tag{2.8}$$

System D

During weeks 31-46, from mid July to early November, the proportion tips alive do not change. We assume that the proportion tips alive does not change over the summer, which gives 0 for its derivative, as sap flow slows at this time of the year [10]. As *A. tsugae* are aestivating during this period, they experience a different mortality rate, $m_{as}\frac{A}{H}$, as compared to in the winter or spring and fall. *Adelges tsugae* are not reproducing during these weeks, like in Systems B and C, and *A. tsugae* density dependent mortality is not present, like in Systems A and B.

$$\frac{dH}{dt} = 0 \tag{2.9}$$

$$\frac{dA}{dt} = -m_{as}\frac{A}{H} \tag{2.10}$$

System E

During weeks 52 and weeks 1-13, from mid December to mid March, *A. tsugae* experience a third seasonal mortality rate, $m_{aw}\frac{A}{H}$, rather than the background or summer seasonal mortality rate. *Adelges tsugae* density dependent mortality is not present, as in Systems A, B and D, and *A. tsugae* are not reproducing during these weeks, as in Systems B, C, and D. *Tsuga canadensis* proportion tips alive again change, with a nonzero derivative as in Systems A, B, and C, as sap flow occurs throughout the winter.

$$\frac{dH}{dt} = g_H\Big(\frac{-1}{\ell + e^{-b_1(A-b_2)}} + 1\Big)H\big(1 - \frac{H}{k}\big) \tag{2.11}$$

$$\frac{dA}{dt} = -m_{aw}\frac{A}{H} \tag{2.12}$$

Existence, Uniqueness and Nonnegativity

Each of Systems A to E are systems of ordinary differential equations with constant parameter values. We are only interested in solutions of these systems over finite times (less than one year), since each system dictates the dynamics for a time period in the year before the the final state values from one system are used as the initial conditions for the next system. As it can be shown that the right hand sides of the differential equations in each system are real-valued, continuous and Lipschitz, a unique solution of each system exists up to some finite time [27]. We have nonnegativity of the solutions following Smith [61], since for nonnegative initial conditions if $H(t_0) = 0$, then

$$\frac{dH}{dt} \geq 0$$

and if $A(t_0) = 0$, then

$$\frac{dA}{dt} \geq 0.$$

As solutions are nonnegative, we can find a uniform bound on the solutions and extend existence and uniqueness of the solutions to the time each system applies in a year [27]. As the initial conditions of the first system are positive, as they are taken from the data, solutions exist and are nonnegative for the first system, and the state variables at the final time will have nonnegative values. We can then use the values of the state variables at the final time for the first system as the nonnegative initial conditions for the second system. We continue in the same way for all systems, including the switch from the last system in a year to the first system of the next year. Each system will have a unique nonnegative solution from which we can take nonnegative initial conditions for the next system.

2.4 Parameter Estimation

We determine the value of the ten parameters in the model with parameter estimation implemented in MATLAB. The units and biological meaning of the parameters are shown in Table 2.5. The parameter estimation compares model simulation results to the data and minimizes the objective function value over a set of parameters. The objective function value is the sum of squares of the relative errors of the model results, which depend on the set of parameter values, compared to the data, that is

$$\sqrt{\frac{\sum_{i=1}^{n}(H_{\text{data}}(t_i) - H_{\text{model}}(t_i))^2}{\sum_{i=1}^{n}(H_{\text{data}}(t_i))^2}} + \sqrt{\frac{\sum_{i=1}^{m}(A_{\text{data}}(s_i) - A_{\text{model}}(s_i))^2}{\sum_{i=1}^{m}(A_{\text{data}}(s_i))^2}},$$

where n is the number of *T. canadensis* proportion tips alive data, with t_i the time of proportion tips alive data i and m is the number of *A. tsugae* density data, with s_i the time of density data i. For group I, $n = 10$ and $m = 14$ and for group II, $n = 8$ and $m = 12$.

We determine the range of each parameter based on the biological meaning of each parameter and the model behavior. The ranges of the parameters are shown in Table 2.6. The same parameter value ranges were used for both the group I and group II parameter estimation, except for g_a. When we performed parameter estimation with the group I data and the range for g_a listed in Table 2.6, the model achieved a good fit, but the *A. tsugae* density was unrealistically high, with densities over 25 *A. tsugae* per centimeter. *A. tsugae* density may vary significantly, but Paradis recorded adult sistens density between 0.80 and 17.23 *A. tsugae* per centimeter and Mech found densities between 0 and 13.7 *A. tsugae* per centimeter [56, 51]. Through parameter estimation, our goals are to find parameters that both produce a low objective function value, and produce a model with biological reasonable behavior, including the dynamics of the system and the sizes of the two classes. Thus, when *A. tsugae* densities were not biological reasonable, we made changes to the bounds of the parameters in the parameter estimation. We decreased the upper bound for g_a, to reduce the reproductive rate of *A. tsugae*, and thus the total density. For each upper bound we tested, the optimal value of g_a found through parameter estimation was at or near the upper boundary, so we fixed the value of g_a and tested different values without estimating

Table 2.5: The Hemlock-Adelgid model parameters' biological meaning and units. Initial conditions are taken from the data, the seasonality of time dependent parameters are taken from the literature and values of parameters are estimated.

Name	Description	Units
$H(0)$	initial condition of *T. canadensis* proportion tips alive	-
$A(0)$	initial condition of *A. tsugae* density	*A. tsugae* per centimeter
g_h	impacts *T. canadensis* proportion tips alive recovery and decay rate	per week
b_1	impacts rate of change of *T. canadensis* proportion tips alive growth rate from positive to negative as *A. tsugae* density increases	centimeters per *A. tsugae*
b_2	impacts threshold between positive and negative *T. canadensis* proportion tips alive growth rate	*A. tsugae* per centimeter
ℓ	impacts relative absolute value of upper and lower bounds of *T. canadensis* proportion tips alive recovery and decay rate	-
k	proportion tips alive of healthy, uninfested *T. canadensis*	-
g_a	*A. tsugae* reproductive rate	per week
m_a	*A. tsugae* mortality rate in the spring and fall	per week
m_{as}	*A. tsugae* mortality rate in the summer	per week
m_{aw}	*A. tsugae* mortality rate in the winter	per week
m_s	*A. tsugae* mortality rate due to sexuparae dispersal	centimeters per (*A. tsugae* $\cdot$ week)

Table 2.6: Bounds on parameter values used for parameter estimation.

Parameter	Lower Bound	Upper Bound
b_1	0.01	10
b_2	0.01	8
ℓ	0.01	1
g_h	0.0001	15
g_a	0.001	0.6
m_s	0.005	4
m_a	0.0005	0.2
m_{aw}	0.001	0.3
m_{ap}	0.001	0.3
k	$H(0)$	0.95

its value. Through these tests of values of g_a, we set $g_a = 0.27$. At this value for g_a, the set of parameters with the lowest objective function value found by the parameter estimation produces model result with cycles in *T. canadensis* proportion tips alive and *A. tsugae* densities, and with realistic *A. tsugae* densities.

The parameter estimation results are shown in Table 2.7 and the model output and data value for the optimal parameter values found through parameter estimation are shown in Figure 2.4 for group I and in Figure 2.5 for group II. The parameter values for the group I data were found through 42 runs of the parameter estimation with a total of approximately 197 starting points. Each staring point is a vector of parameter values with each entry within the bounds of that parameter. The parameter values for the group II data were found through 5 runs of the parameter estimation with a total of approximately 358 starting points.

For both groups of trees, cycles in *T. canadensis* proportion tips alive and *A. tsugae* density are seen in the model output using the parameter values found by parameter estimation. The cycles are more frequent in the group II results, with two peaks in proportion tips alive in the 13 year model results, and three peaks in *A. tsugae* density. In the group I results, there is one peak in proportion tips alive during the same length of time, with a recovery in proportion tips alive at the end of the this period, and two peaks in *A. tsugae* density. In the group II results, the second cycle in proportion tips alive occurs over a shorter time and the maximum proportion tips alive value is lower on the second recovery compared to the first recovery. In both groups, proportion tips alive decreases more rapidly than it recovers. This dynamic is more pronounced in the group I results.

We calculate the *A. tsugae* density threshold where the proportion tips alive change is 0 and switches from a positive rate at low *A. tsugae* densities to a negative rate. This threshold is where the *A. tsugae* density begins to have a negative impact on *T. canadensis* health, according to the model results. We calculate this threshold with

$$A = -\frac{1}{b_1} \ln\left(\frac{1-\ell}{\ell}\right) + b_2 = 2.20$$

Table 2.7: Parameter value results for the group I and group II data from the parameter estimation, including the objective function value.

Parameter	Group I	Group II
objective function value	0.4822	0.4460
b_1	9.9974	9.9999
b_2	2.4262	0.3617
ℓ	0.0915	0.1346
g_h	0.1500	0.1500
g_a	0.27	0.6000
m_s	0.0399	0.0803
m_a	0.0005	0.0613
m_{aw}	0.0010	0.0739
m_{as}	0.0412	0.0010
k	0.8789	0.9398

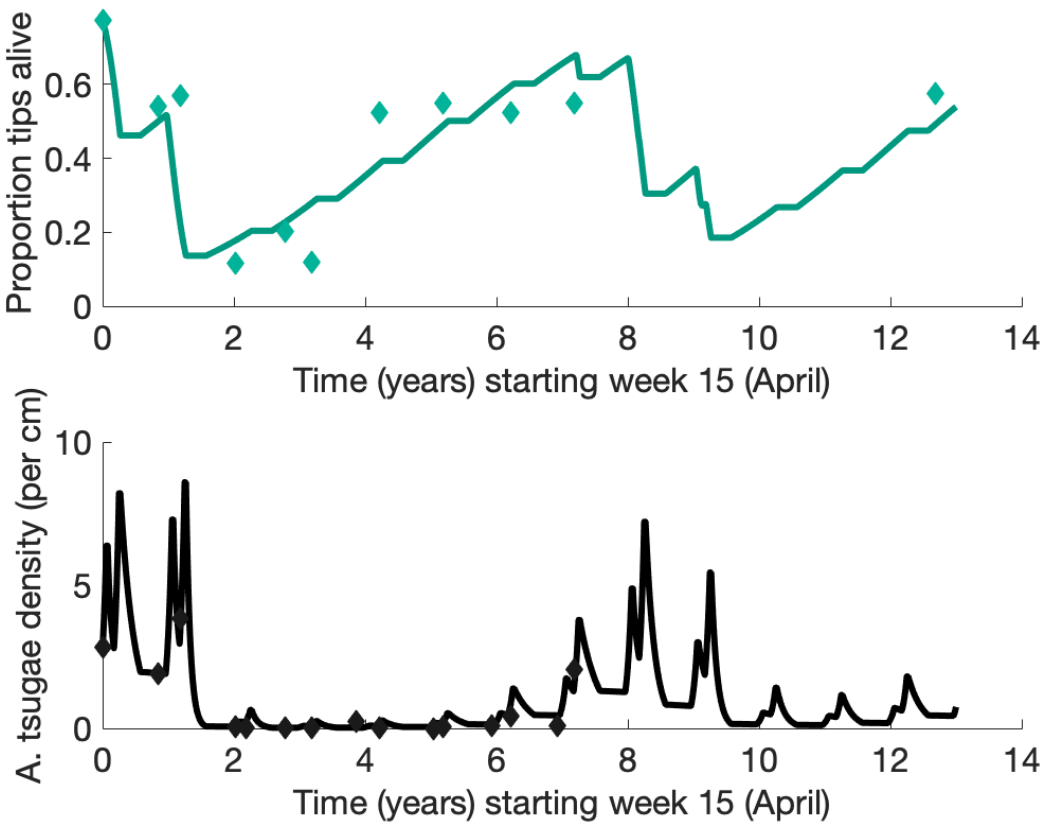


Figure 2.4: The group I data are shown with diamonds, and the model output is plotted as curves. The upper plot shows the proportion tips alive and the lower plot shows the adelgid density.

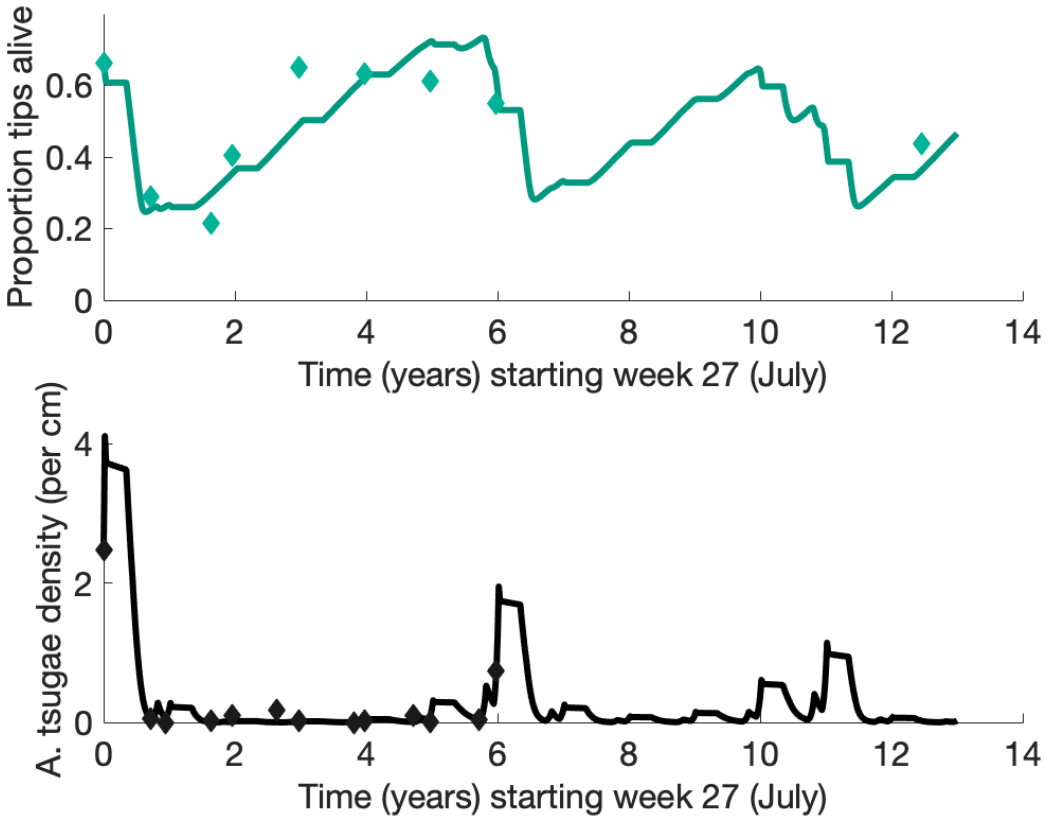


Figure 2.5: The group II data are shown with diamonds, and the model output is plotted as curves. The upper plot shows the proportion tips alive and the lower plot shows the adelgid density.

A. tsugae per centimeter for group I and $A = .18$ *A. tsugae* per centimeter for group II. Thus according to the model results, the group II *T. canadensis* are negatively impacted by *A. tsugae* at much lower densities than the group I trees. The value of this threshold for group I is closer to the value we expect from the literature. McClure found that *A. tsugae* densities above 4 *A. tsugae* per centimeter prevent *T. canadensis* new growth in the next year, while Paradis found that *T. canadensis* new growth could occur at higher *A. tsugae* densities [47, 56].

In both groups, two peaks in *A. tsugae* density can be seen each year as a results of the two generations, and thus two reproductive periods of *A. tsugae* per year. The sistens generation has higher densities in both models. In the group I model, the sistens generation has a peak and a rapid decline, where as in the group II model, there is a more gradual decline in the density. This difference is due to the m_{as} value, which is 0.0412 for group I and 0.0010 for group II. The other *A. tsugae* mortality rates, m_s, m_a and m_{aw} are higher for group II than for group I. Maximum *A. tsugae* densities are higher in the group I results, compared to the group II results.

2.5 Model Results

We use the *T. canadensis* proportion tips alive value found using the time series of all trees in the study to further study the model results. We use 0.1 as a proportion tips alive value from which *T. canadensis* are unlikely to recover, and likely to die as discussed in Section 2.2. For both group I and group II, we use the parameter values found through parameter estimation, but vary the initial conditions for *T. canadensis* proportion tips alive and *A. tsugae* density. We run simulations of the model for 15 years and determine whether the *T. canadensis* proportion tips alive reaches 0.1 during this time. We vary *T. canadensis* proportion tips alive initial conditions in increments of 0.5 from 0.15 to 0.85 for group I and from 0.15 to 0.90 for group II. We use 0.90 for group II and not for group I, as $k = 0.93$ for group II and $k = 0.8789$ for group I and we assume that the proportion tips alive initial condition is less than the *T. canadensis* carrying capacity, k, which we interpret as the proportion tips alive we would expect on a healthy, uninfested tree. We vary *A. tsugae* initial conditions from

0.1 to 8 *A. tsugae* per centimeter, in increments of 0.1. The results of all combinations of *T. canadensis* proportion tips alive and *A. tsugae* density initial conditions are shown in Table 2.8. Since we use only these combinations of initial conditions, we have not shown that all initial conditions near or between the chosen value have the same behavior or result.

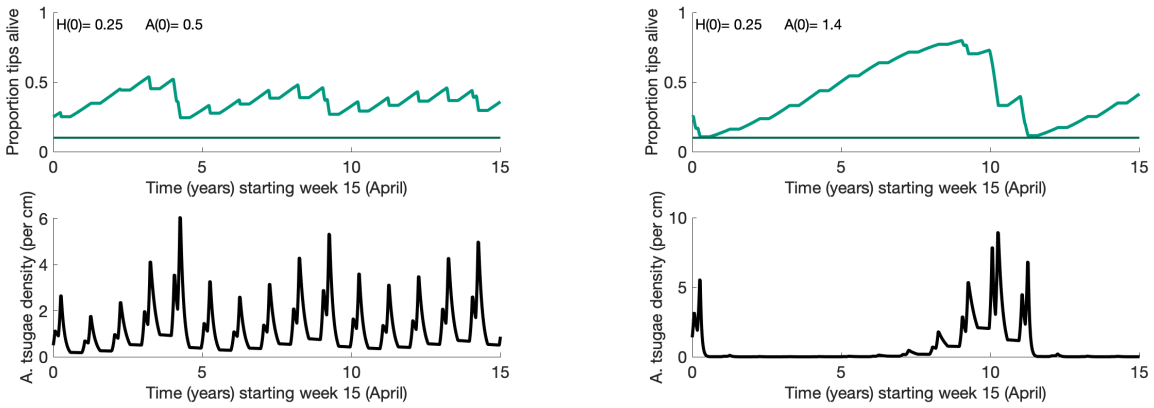
For the group I parameter values, at low *T. canadensis* proportion tips alive initial conditions, between 0.15 and 0.4 and at sufficiently high *A. tsugae* densities initial conditions, proportion tips alive falls below 0.1 within 15 years and the trees are likely to die. As the proportion tips alive initial condition increases, the minimum *A. tsugae* density initial conditions likely to lead to *T. canadensis* death increases. At larger proportion tips alive initial conditions, between 0.45 and 0.65, no *A. tsugae* initial conditions tested lead to likely death within 15 years. At 0.7 and 0.75 proportion tips alive initial conditions, high *A. tsugae* initial conditions, above 5.5 and 6.1 respectively, lead to likely *T. canadensis* death. At the highest proportion tips alive initial conditions, there are several ranges of *A. tsugae* density initial conditions that lead to *T. canadensis* mortality.

Model simulations for some combinations of initial conditions are shown in Figures 2.6-2.9. Each figure has one *T. canadensis* proportion tips alive initial condition, and shows simulations for varying *A. tsugae* density initial conditions. The threshold of likely *T. canadensis* mortality, at a proportion tips alive of 0.1 is shown in the plots of proportion tips alive. Model results show recovery from proportion tips alive below 0.1. Our analysis of the data to find this value does not suggest that *T. canadensis* that reach 0.1 proportion tips alive immediately die, but that they are likely to die in the future. Thus, we interpret model simulations where *T. canadensis* proportion tips alive falls below 0.1 as showing conditions where *T. canadensis* mortality is likely, even if the *T. canadensis* proportion tips alive later recover above the threshold in the simulation. Our model does not include the mechanisms that may prevent *T. canadensis* from recovering from extreme *A. tsugae* damage represented by very low proportions tips alive and therefore should not be used to predict *T. canadensis* proportion tips alive dynamics after reaching these low proportion tips alive values.

Figure 2.6 shows results for $H(0) = 0.25$, when sufficiently high *A. tsugae* density initial conditions lead to likely *T. canadensis* mortality. As *T. canadensis* proportion tips alive falls below 0.1 when $A(0) = 1.5$ and $A(0) = 5.0$, the model results suggest, as we would expect,

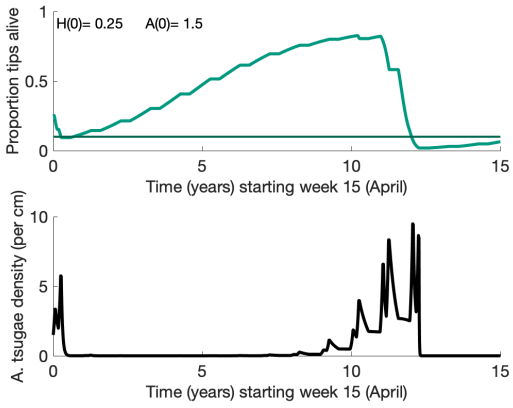
Table 2.8: The combinations of *T. canadensis* proportion tips alive initial conditions, $H(0)$, and *A. tsugae* density initial conditions, $A(0)$, that lead to *T. canadensis* proportion tips alive less than 0.1, and thus likely mortality, within 15 years for the group I and group II models. Ranges of initial conditions are listed for *A. tsugae* densities, but the initial conditions were only tested at increments of 0.1. We have not shown that every initial condition, $A(0)$, in each of the ranges will lead to *T. canadensis* proportion tips alive less than 0.1 within 15 years. If none of the *A. tsugae* density initial conditions we test lead to likely *T. canadensis* mortality, we mark that entry with a dash.

$H(0)$	$A(0)$ for group I	$A(0)$ for group II
0.15	1.1-8.0	1.5-8.0
0.2	1.3-8.0	2.2, 3.8-8.0
0.25	1.5-8.0	3.1, 4.5-4.6
0.3	1.7-8.0	5.7-5.8
0.35	2.0-8.0	-
0.4	2.4-8.0	-
0.45	-	-
0.5	-	-
0.55	-	-
0.6	-	-
0.65	-	-
0.7	5.5-8.0	-
0.75	6.1-8.0	7.9
0.8	0.1-0.2, 0.5-0.8, 2.8-8.0	5.3
0.85	0.1-0.2, 0.4-1.2, 1.6-8.0	1.6, 2.4-3.1, 7.5-8.0
0.9	not tested	3.9-8.0

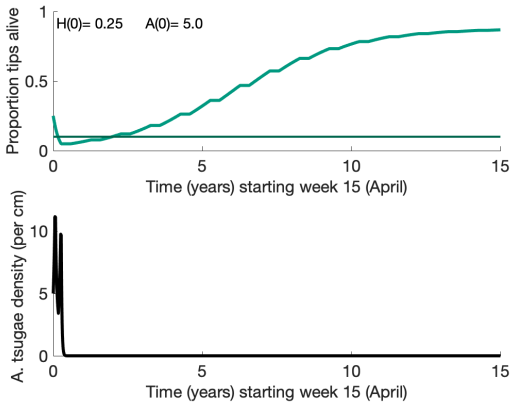


(a) $A(0) = 0.5$

(b) $A(0) = 1.4$

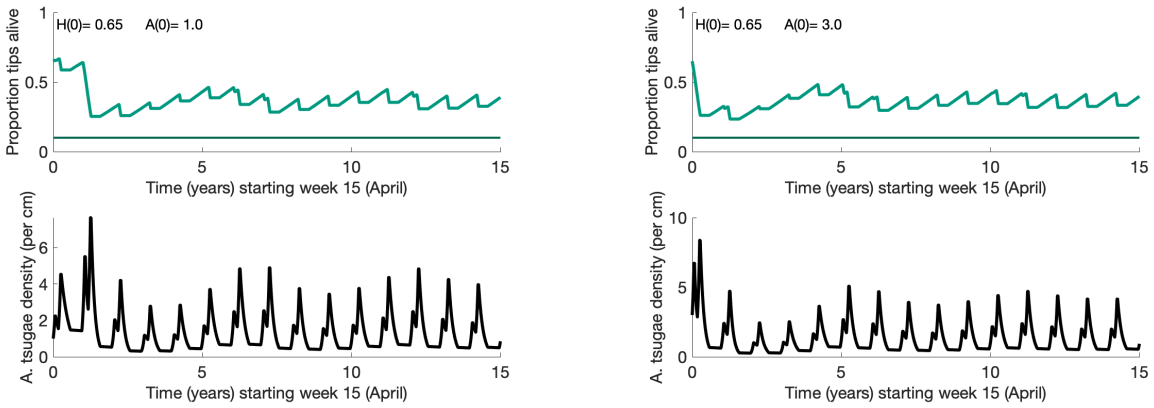


(c) $A(0) = 1.5$



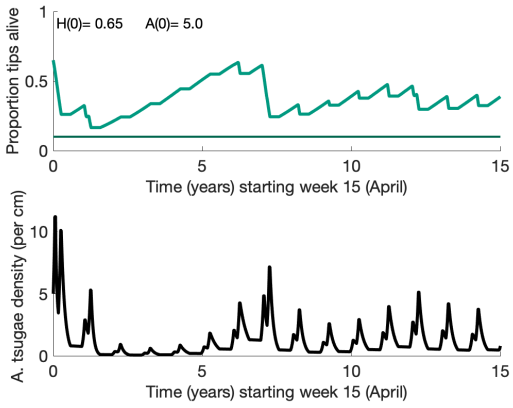
(d) $A(0) = 5.0$

Figure 2.6: Model simulation results for group I, with *T. canadensis* proportion tips alive initial condition at $H(0) = 0.25$, and varying *A. tsugae* density initial conditions $A(0)$. The threshold of likely *T. canadensis* mortality of 0.1 proportion tips alive is plotted with the proportion tips alive results. As *A. tsugae* density initial conditions increase, the length of the multiyear cycle in *T. canadensis* health increases, and the declines in *T. canadensis* proportion tips alive become more severe until proportion tips alive falls below 0.1, as when $A(0) = 1.5$ and $A(0) = 5.0$.

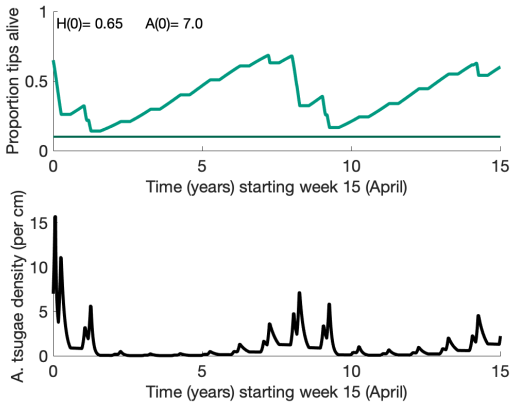


(a) $A(0) = 1.0$

(b) $A(0) = 3.0$

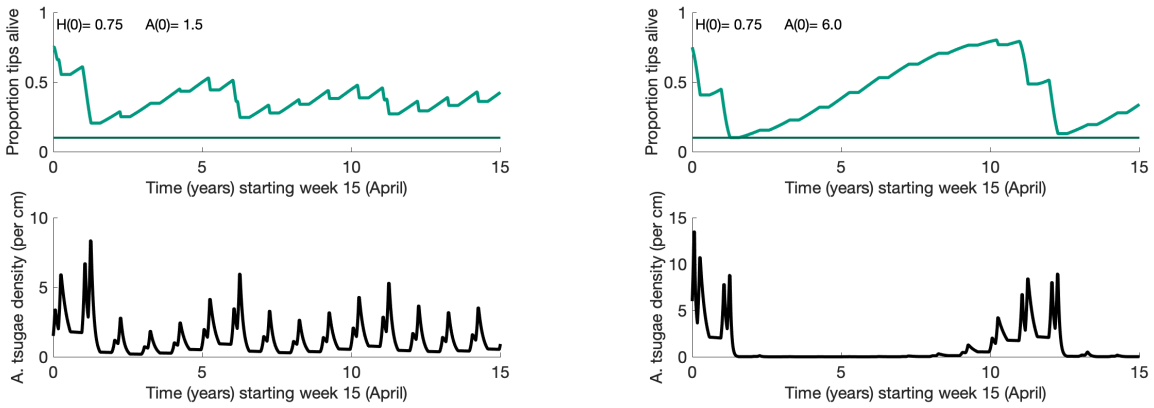


(c) $A(0) = 5.0$



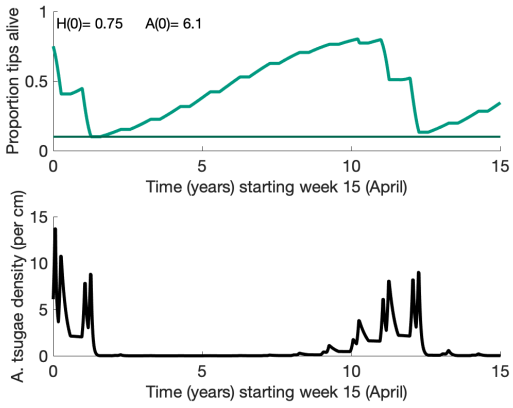
(d) $A(0) = 7.0$

Figure 2.7: Model simulation results for group I, with *T. canadensis* proportion tips alive initial condition at $H(0) = 0.65$, and varying *A. tsugae* density initial conditions $A(0)$. The threshold of likely *T. canadensis* mortality of 0.1 proportion tips alive is plotted with the proportion tips alive results. As *A. tsugae* density initial conditions increase, multiyear cycles, rather than yearly cycles in *T. canadensis* proportion tips alive and *A. tsugae* density, become more pronounced. None of *A. tsugae* density initial conditions tested lead to likely *T. canadensis* mortality within 15 years.

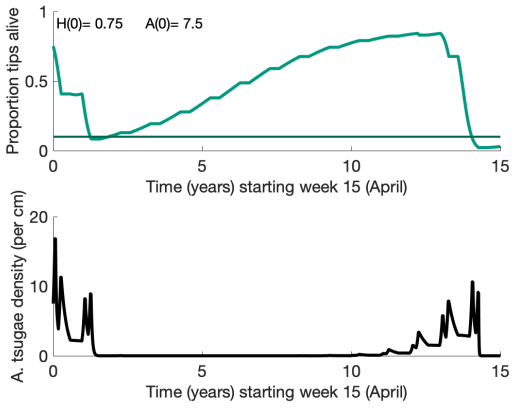


(a) $A(0) = 1.5$

(b) $A(0) = 6.0$

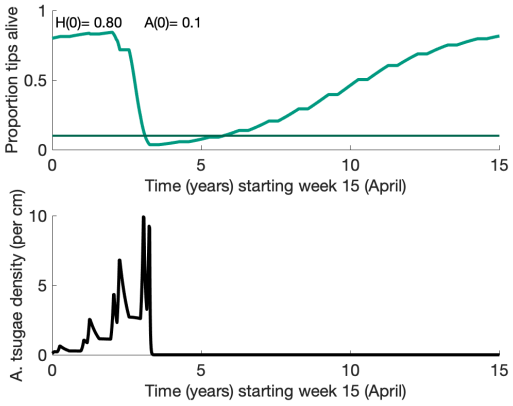


(c) $A(0) = 6.1$

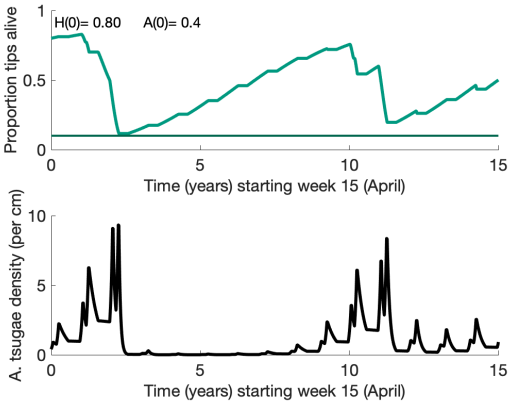


(d) $A(0) = 7.5$

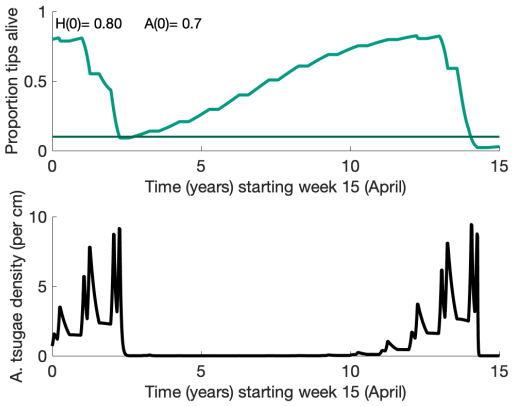
Figure 2.8: Model simulation results for group I, with *T. canadensis* proportion tips alive initial condition at $H(0) = 0.75$, and varying *A. tsugae* density initial conditions $A(0)$. The threshold of likely *T. canadensis* mortality of 0.1 proportion tips alive is plotted with the proportion tips alive results. As *A. tsugae* density initial conditions increase to $A(0) = 6.1$ and $A(0) = 7.5$, the multiyear cycles increase in length and peaks in *A. tsugae* density increase sufficiently to cause declines in *T. canadensis* proportion tips alive below 0.1.



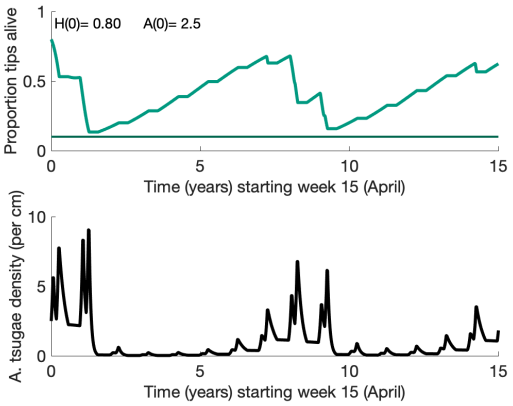
(a) $A(0) = 0.1$



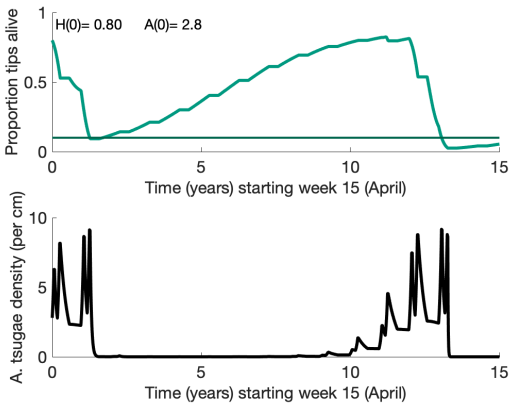
(b) $A(0) = 0.4$



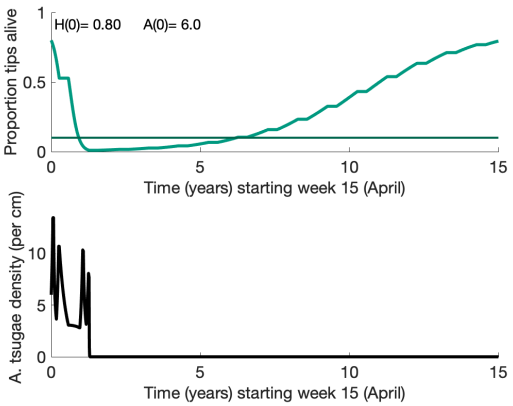
(c) $A(0) = 0.7$



(d) $A(0) = 2.5$



(e) $A(0) = 2.8$

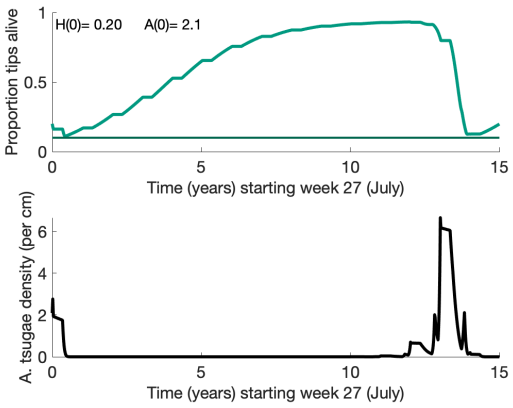


(f) $A(0) = 6.0$

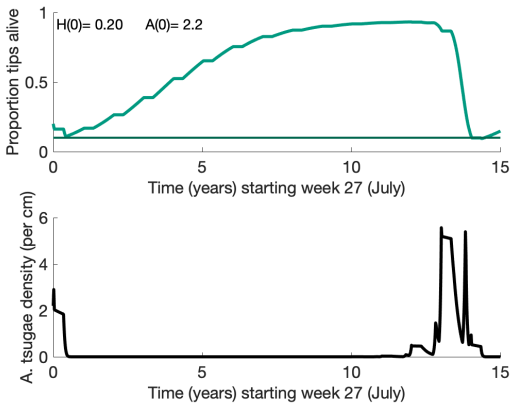
Figure 2.9: Model simulation results for group I, with *T. canadensis* proportion tips alive initial condition at $H(0) = 0.80$, and varying *A. tsugae* density initial conditions $A(0)$. The threshold of likely *T. canadensis* mortality of 0.1 proportion tips alive is plotted with the proportion tips alive results. As *A. tsugae* density initial conditions increase, the length of cycles in proportion tips alive does not change monotonically, but the time to the first decline in proportion tip alive decreases.

that *T. canadensis* with low proportion tips alive and higher *A. tsugae* densities are likely to die. At a higher *T. canadensis* proportion tips alive initial conditions, such as $H(0) = 0.65$ as shown in Figure 2.7, no *A. tsugae* density initial conditions tested lead to likely *T. canadensis* mortality. The *T. canadensis* dependent mortality rate of *A. tsugae* prevent *A. tsugae* densities from reaching high densities quickly enough to pull *T. canadensis* proportion tips alive below 0.1. At higher *T. canadensis* proportion tips alive initial conditions, such as $H(0) = 0.75$ as shown in Figure 2.8, at high *A. tsugae* density initial conditions, *A. tsugae* densities can grow enough to pull *T. canadensis* below 0.1 proportion tips alive. When proportion tips alive is initially larger, like when $H(0) = 0.75$, higher peaks in *A. tsugae* density are required to cause *T. canadensis* proportions to fall below 0.1 proportion tips alive. At high *T. canadensis* initial conditions, such as $H(0) = 0.80$, as shown in Figure 2.9, even at some low *A. tsugae* density initial conditions, trees are likely to die. At low *A. tsugae* density initial conditions, the *A. tsugae* density may increase more gradually, but eventually cause a decline in proportion tips alive, as when $A(0) = 0.1$ in Figure 2.9. At higher *A. tsugae* density initial conditions, the high proportion tips alive may support a high *A. tsugae* density for long enough to cause a severe decline in proportion tips alive, as when $A(0) = 2.8$ or 6.0 in Figure 2.9.

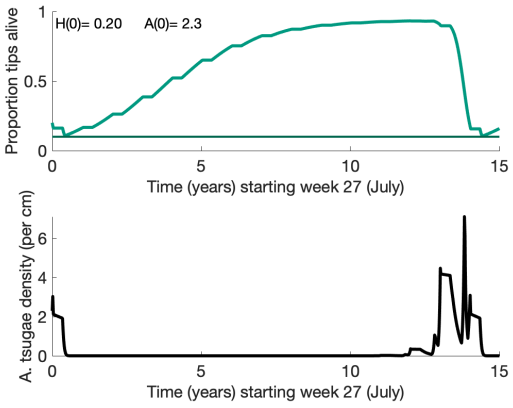
For the group II parameter values, model simulations for some combinations of initial conditions are shown in Figures 2.10-2.13. For low *T. canadensis* proportion tips alive initial conditions, 0.15 and 0.2, we see a similar pattern as in group I, with sufficiently high *A. tsugae* density initial conditions leading to likely *T. canadensis* death. However, an isolated (among the values we test) *A. tsugae* density initial condition also leads to likely *T. canadensis* mortality, at $H(0) = 0.2, A(0) = 2.2$, when *A. tsugae* density initial conditions between 2.3 and 3.7 do not reach 0.1 proportion tips alive within 15 years, as shown in Figure 2.10. When $A(0) = 2.2$, *T. canadensis* proportion tips alive do not decline past 0.1 until the second, more dramatic decline in proportion tips alive, while at higher *A. tsugae* density initial conditions, the minimum of the first decline in proportion tips alive falls below 0.1. When $H(0) = 0.3$ as shown in Figure 2.11, the initial decline in proportion tips alive does not fall below 0.1, but the second cycle may lead to proportion tips alive passing this value, as when $A(0) = 5.8$. At higher *T. canadensis* proportion tips alive initial conditions, between



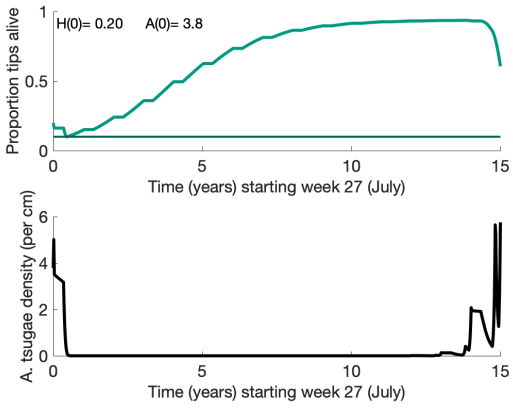
(a) $A(0) = 2.1$



(b) $A(0) = 2.2$

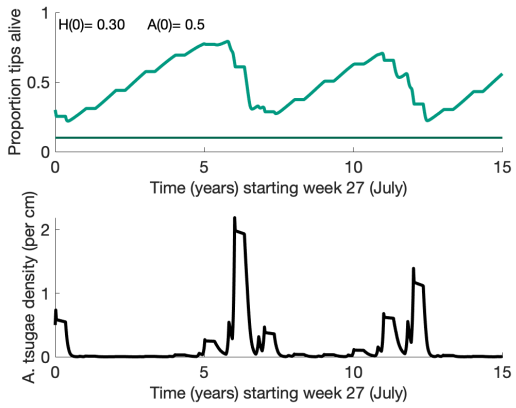


(c) $A(0) = 2.3$

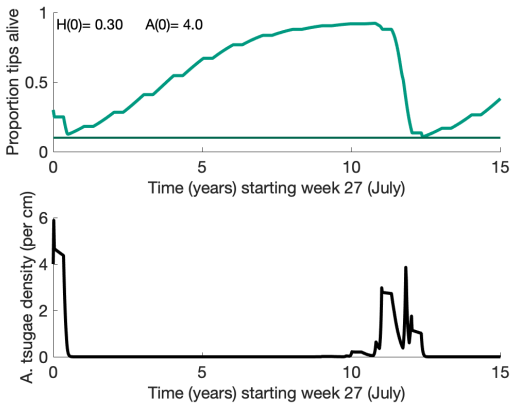


(d) $A(0) = 3.8$

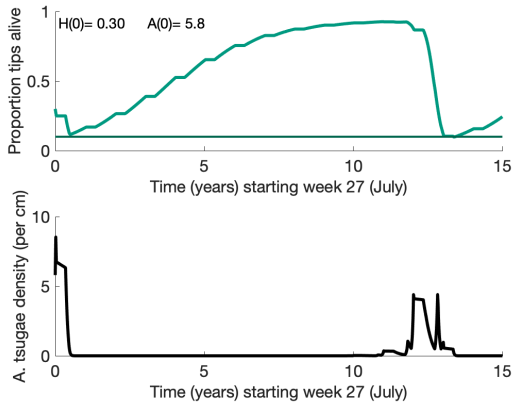
Figure 2.10: Model simulation results for group II, with *T. canadensis* proportion tips alive initial condition at $H(0) = 0.20$, and varying *A. tsugae* density initial conditions $A(0)$. The threshold of likely *T. canadensis* mortality of 0.1 proportion tips alive is plotted with the proportion tips alive results. As the *A. tsugae* density initial conditions increase, the length of time until the second decline in *T. canadensis* proportion tips alive increases.



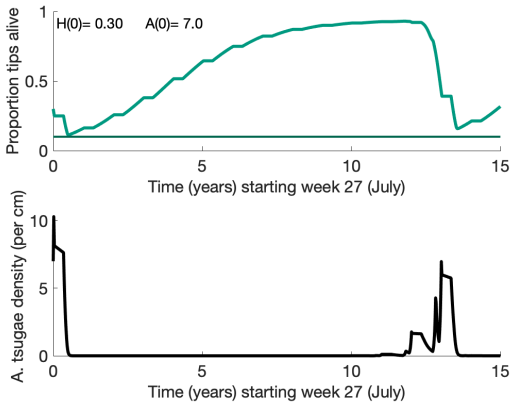
(a) $A(0) = 0.5$



(b) $A(0) = 4.0$

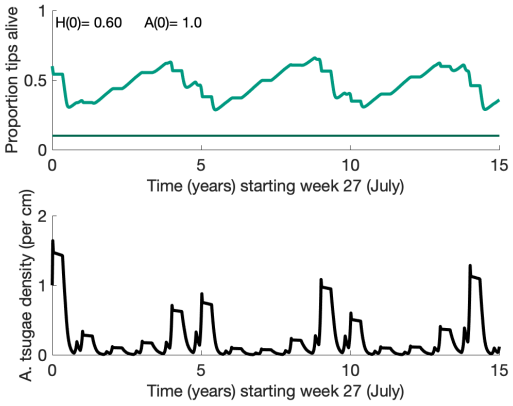


(c) $A(0) = 5.8$

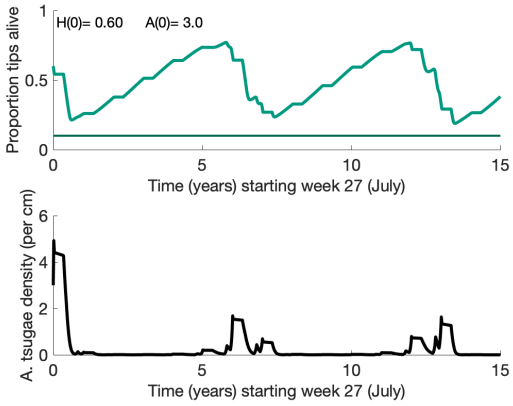


(d) $A(0) = 7.0$

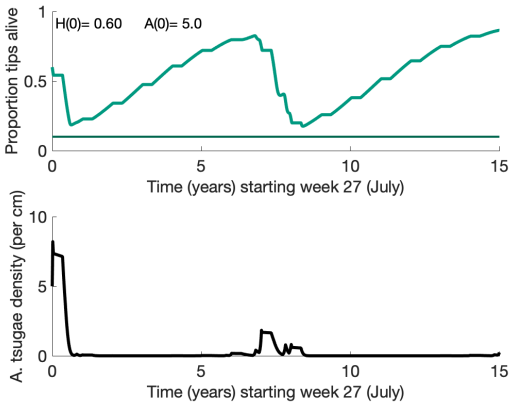
Figure 2.11: Model simulation results for group II, with *T. canadensis* proportion tips alive initial condition at $H(0) = 0.30$, and varying *A. tsugae* density initial conditions $A(0)$. The threshold of likely *T. canadensis* mortality of 0.1 proportion tips alive is plotted with the proportion tips alive results. Increasing *A. tsugae* density initial conditions, increases the length of cycles, but can lead to likely *T. canadensis* mortality, as when $A(0) = 5.8$.



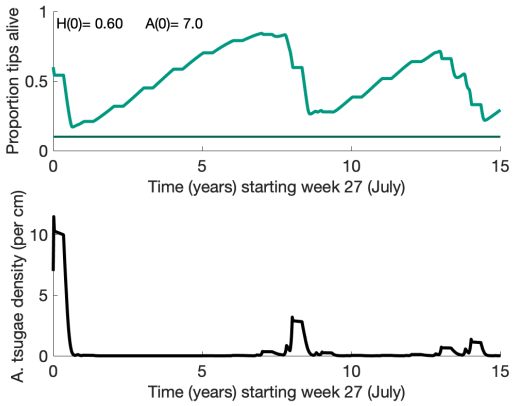
(a) $A(0) = 1.0$



(b) $A(0) = 3.0$

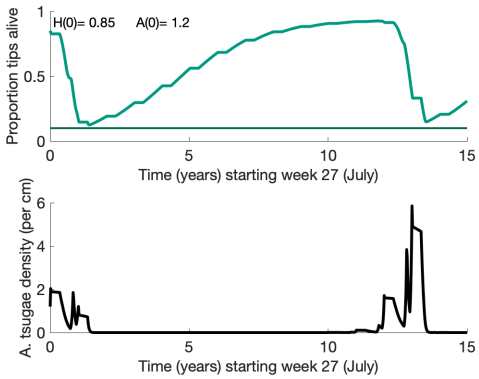


(c) $A(0) = 5.0$

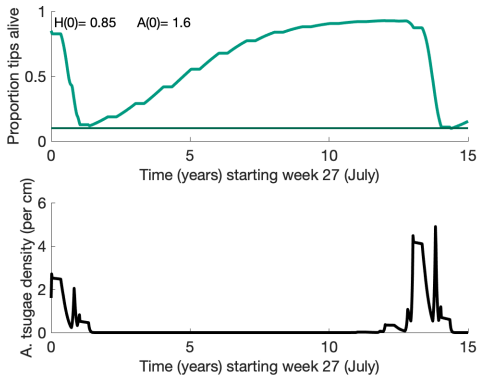


(d) $A(0) = 7.0$

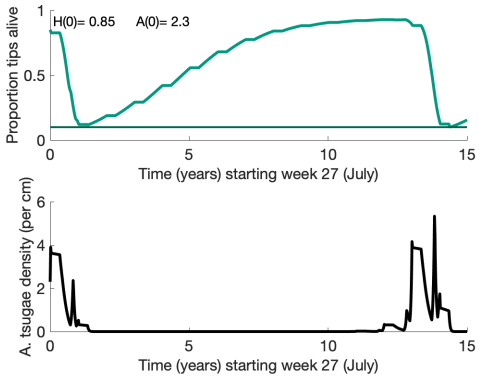
Figure 2.12: Model simulation results for group II, with *T. canadensis* proportion tips alive initial condition at $H(0) = 0.60$, and varying *A. tsugae* density initial conditions $A(0)$. The threshold of likely *T. canadensis* mortality of 0.1 proportion tips alive is plotted with the proportion tips alive results. Increasing *A. tsugae* initial densities lead to more pronounced cycles in proportion tips alive and *A. tsugae* density. At $A(0) = 7.0$, the second recovery of *T. canadensis* proportion tips alive occurs over a shorter time and the maximum proportion tips alive value reached is lower in the first recovery.



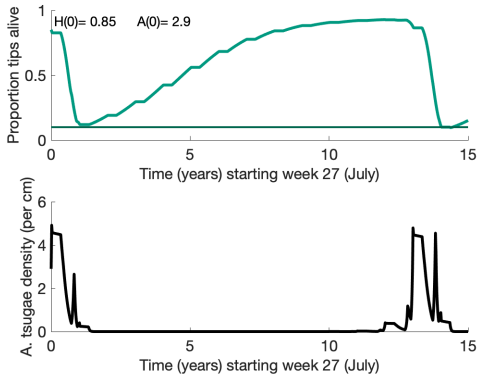
(a) $A(0) = 1.2$



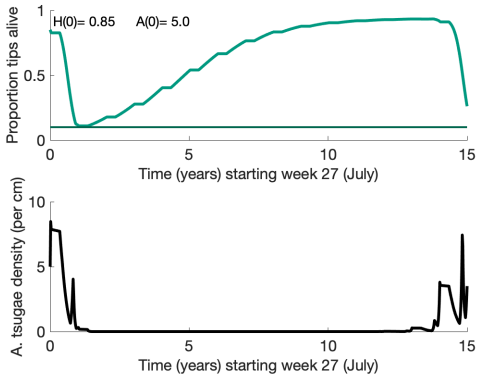
(b) $A(0) = 1.6$



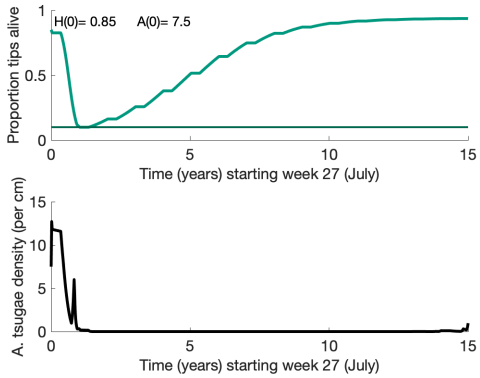
(c) $A(0) = 2.3$



(d) $A(0) = 2.9$



(e) $A(0) = 5.0$



(f) $A(0) = 7.5$

Figure 2.13: Model simulation results for group II, with *T. canadensis* proportion tips alive initial condition at $H(0) = 0.85$, and varying *A. tsugae* density initial conditions $A(0)$. The threshold of likely *T. canadensis* mortality of 0.1 proportion tips alive is plotted with the proportion tips alive results. At lower *A. tsugae* initial conditions, $A(0) = 1.6$ or 2.9, proportion tips alive does not fall below 0.1 until the second decline in *T. canadensis* health, whereas with $A(0) = 7.5$, the first decline in *T. canadensis* health leads to proportion tips alive below 0.1.

0.35 and 0.7, no *A. tsugae* initial conditions tested lead to likely *T. canadensis* mortality. An example of this is shown in Figure 2.12, where $H(0) = 0.6$. Cycles in proportion tips alive and *A. tsugae* density become more extreme as *A. tsugae* initial conditions increase, but within the initial conditions tested, do not produce likely *T. canadensis* mortality. At *T. canadensis* proportion tips alive of 0.75 to 0.9, some *A. tsugae* density initial conditions lead to likely *T. canadensis* mortality. *Tsuga canadensis* proportion tips alive initial condition $H(0) = 0.85$ is shown in Figure 2.13. Increasing *A. tsugae* initial densities delay the second decline in *T. canadensis* proportion tips alive. For lower *A. tsugae* density initial conditions, such as $A(0) = 1.6$ or 2.9, the proportion tips alive do not fall below the 0.1 until the second decline, while at higher *A. tsugae* initial densities, like $A(0) = 7.5$, the initial decline in proportion tips alive leads to likely *T. canadensis* mortality.

We also study longer term dynamics of the model. We plot model simulation results using the parameters found through parameter estimation for the group I and for the group II data. A model simulation for the group I model for fifty years is shown in Figure 2.14. The multiyear cycles in *T. canadensis* proportion tips alive and *A. tsugae* densities decrease in length of time and magnitude, until only yearly cycles, as dictated by the seasonality included in the model, are present. After sufficiently long, the highest *A. tsugae* densities occur at the beginning of the sistens generation. Similarly, in the group II model simulation, after sufficient time, multiyear cycles in *T. canadensis* proportion tips alive and *A. tsugae* density decrease in magnitude, and only yearly cycles remain. However, for the group II model, multiyear cycles remain present much longer. Figure 2.15 shows the model results for 250 years, but multiyear cycles are still observable. The magnitude and length of time of cycles do not decrease monotonically in this model simulation, although eventually multiyear cycles do disappear. Both the group I and group II results have the same scale from 0 to 1 for the vertical axis in the *T. canadensis* proportion tips alive plots.

2.6 Conclusions

We present a novel model of *T. canadensis* proportion tips alive and *A. tsugae* densities that achieves a good fit to the data and is able to capture the coupled cycles seen in these

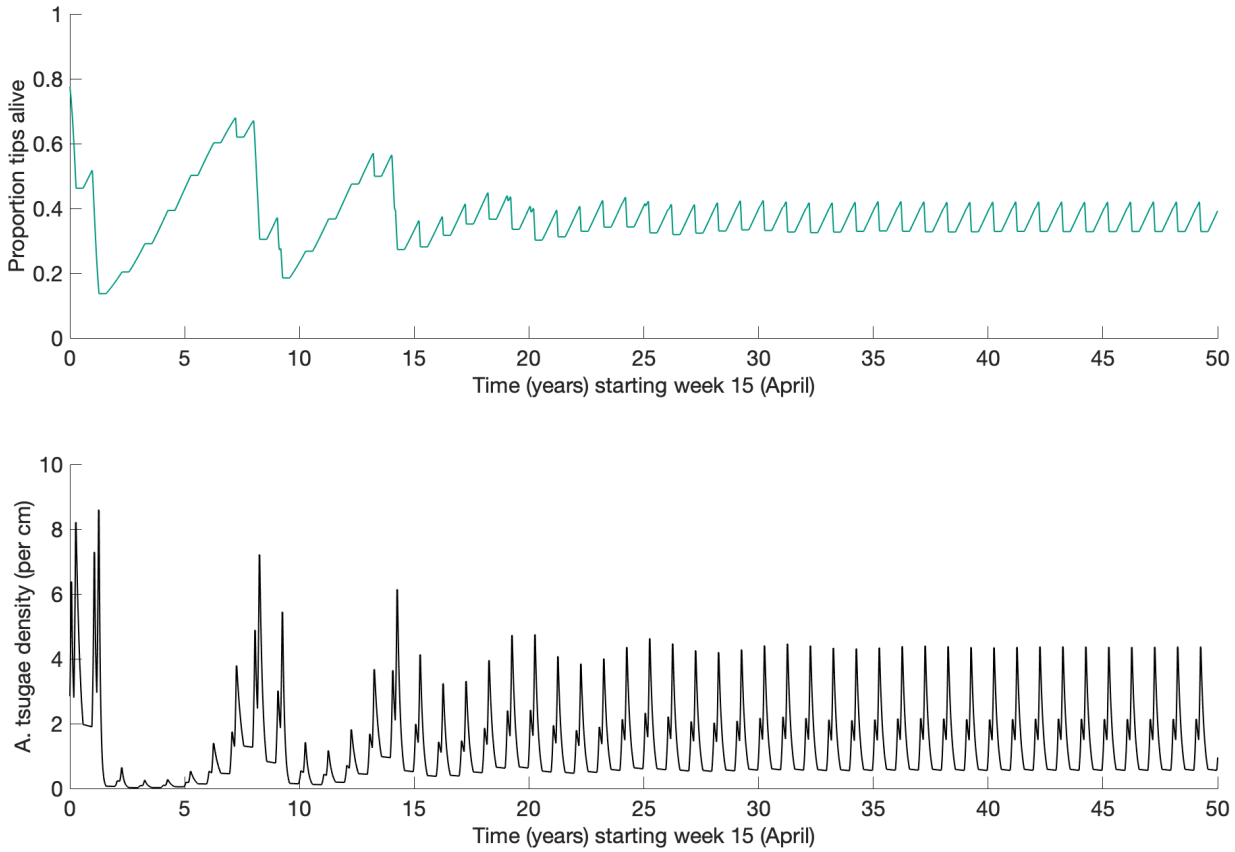


Figure 2.14: Group I model simulation results over 50 years. Multiyear cycles disappear and only yearly cycles in *T. canadensis* proportion tips alive and *A. tsugae* density, as determined by the seasonality in the model, remain.

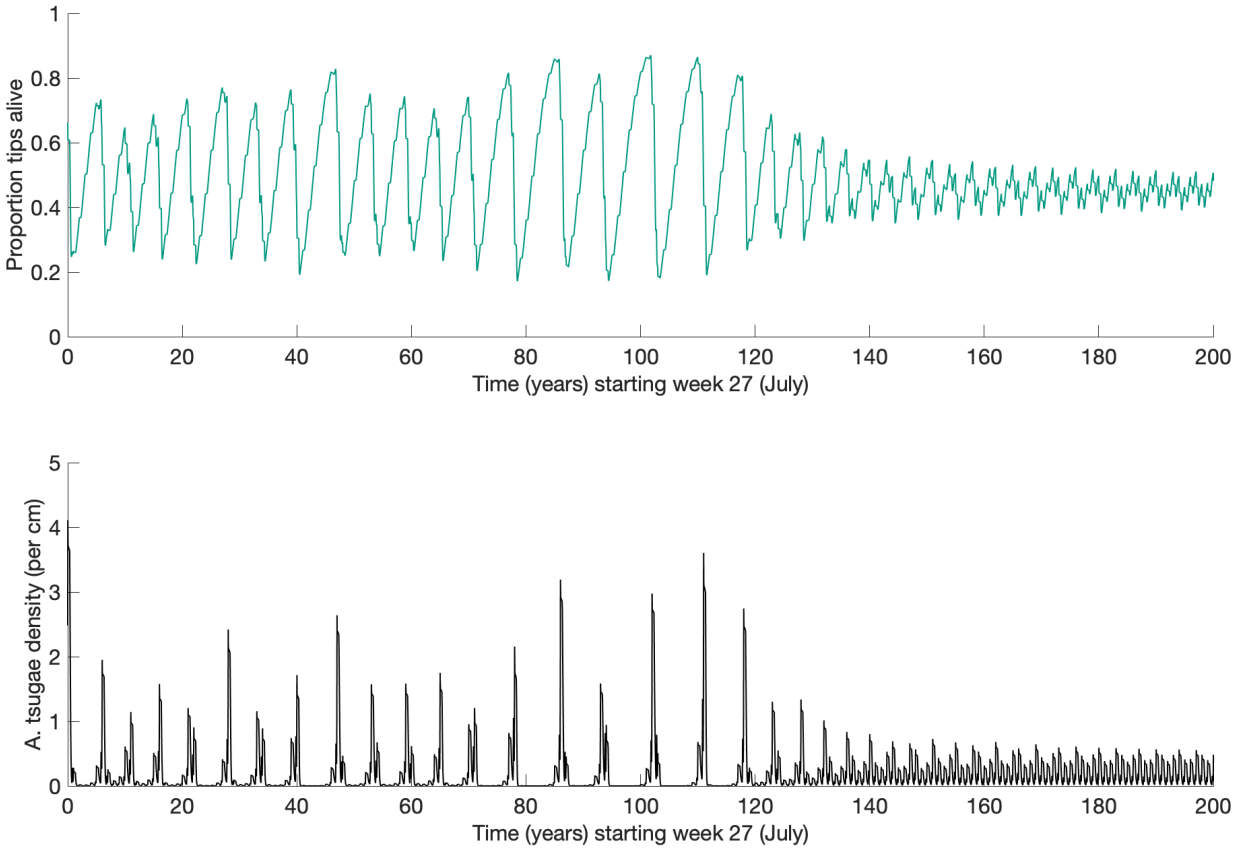


Figure 2.15: Group II model simulation results over 200 years. Multiyear cycles persist throughout this time, but decrease in magnitude after approximately year 110.

two species in the field. The mechanisms in the model, including the seasonality of the two species, *A. tsugae* density dependent *T. canadensis* proportion tips alive growth rate, *T. canadensis* proportion tips dependent *A. tsugae* mortality, and density dependent *A. tsugae* mortality are enough to produce these cycles, at least over the short term. When we consider longer term dynamics of the model, eventually, multiyear cycles in *T. canadensis* proportion tips alive and *A. tsugae* densities are damped, and only yearly cycles, as produced by the seasonality in the model, remain. However, the length that multiyear cycles persist varied between the simulations based on the parameter values estimated for the two groups of data, so large magnitude multiyear cycles may continue for the length of time our model represents the system well before other factors such as natural mortality of *T. canadensis* or climate change may cause new dynamics. To our knowledge, this model is the first mechanistic, tree-scale model of interacting *T. canadensis* health and *A. tsugae* densities with seasonality and other system specific biological features. Other mathematical and simulation modeling studies on the *T. canadensis*-*A. tsugae* system represent other scales and processes. Several models have been used to describe and predict *A. tsugae* spread or the consequences of *A. tsugae* infestation and *T. canadensis* mortality on the ecosystem [30, 14]. Kantola et al. examine how climate change any impact the range of *A. tsugae* in the future [30]. Domec et al. developed a mechanistic model of the impact of *A. tsugae* infestation on *T. canadensis* physiological processes to determine the impact on whole plant water use and carbon uptake, but did not represent the impact of *T. canadensis* health on an *A. tsugae* population [11]. Moore et al. included a modified three species logistic predator prey system of differential equations model representing *T. canadensis* health, *A. tsugae* infestation, and biological and chemical controls as part of their hierarchical bioeconomic model, but did not include seasonality, stage structure or other mechanisms [53]. Elkinton et al. use a difference equation model that represents the two generations of *A. tsugae* per year and their generation specific survival and fecundity, including density dependence through using linear statistical models of survival and fecundity as the rates in the difference equations [13, 12]. Their model does not represent the impact of *T. canadensis* health on *A. tsugae* population dynamics [9].

Our model results from testing various combinations of initial conditions suggest that at low *T. canadensis* proportion tips alive, sufficiently high *A. tsugae* densities will lead to likely *A. tsugae* mortality. At moderate *T. canadensis* proportion tips alive, increased *A. tsugae* mortality due to decreased *T. canadensis* health will prevent *A. tsugae* densities from reaching sustained high densities that drive more extreme cycles in proportion tips alive and eventually likely *T. canadensis* mortality. This scenario, where despite some impacts on *T. canadensis* health due to *A. tsugae* infestation, *T. canadensis* damage and mortality is reduced, is the goal of management efforts in this system [39]. The use of chemical control methods, biological control or both through integrated pest management attempts to reduce *A. tsugae* densities sufficiently to prevent major health impacts and mortality of *T. canadensis*. However, our model results also suggest that at high *T. canadensis* proportion tips alive, even some low *A. tsugae* densities can lead to likely *T. canadensis* mortality. This is because healthy *T. canadensis* can support the rapid growth of high *A. tsugae* densities, leading to declines in *T. canadensis* proportion tips alive, ultimately resulting in tree mortality.

These model results suggest that *T. canadensis* with low proportion tips alive would require intervention from managers to survive an *A. tsugae* infestation. As model results suggest that healthy *T. canadensis*, with the highest proportion tips alive, may be at risk of mortality, these trees should be prioritized for chemical treatment over trees with midrange proportion tips alive, which, according to the model results, may be able to survive without intervention. The conclusions we reach from these model results depend on the timing of changes in *A. tsugae* densities and *T. canadensis* health relative to each other. As our model does not represent the mechanisms of *A. tsugae* impact on *T. canadensis*, but rather the effect, and as we have biannual or annual *T. canadensis* and *A. tsugae* data, further study of the timing of these processes would be useful to determine the validity of these results. Another limitation to our modeling approach is in representing the history of *T. canadensis* health and *A. tsugae* infestation. Our model does not include mechanisms that prevent *T. canadensis* recovery from repeated or severe decline. In addition, other factors that may be important to the *T. canadensis* and *A. tsugae* system such as temperature and seasonality

variability, and site characteristics such as elevation or water stress are not represented in our model.

Chapter 3

Adelgid-Predator Model

3.1 Introduction

Adelges tsugae, the hemlock woolly adelgid, is an invasive insect pest in the eastern United States that has greatly impacted the growth and survival of hemlock trees, *Tsuga canadensis* [47, 26]. Two insect predator species, *Sasajiscymnus tsugae* and *Laricobius nigrinus* have been introduced into the eastern United States in an attempt to limit health impacts and mortality of *T. canadensis* by reducing *A. tsugae* density. *Sasajiscymnus tsugae* (formerly *Pseudoscymnus tsugae*) is a lady beetle which was identified by Sasaji and McClure through studying the native natural enemies of *A. tsugae* in Japan to find potential biological control organisms to be used in the eastern United States [59]. *Sasajiscymnus tsugae* can complete development on other adelgid species such as the balsam woolly adelgid, pine bark adelgid and Cooley spruce gall adelgid [49]. However, *S. tsugae* show preference for *A. tsugae* adults [2]. Given the eggs of multiple adelgid species, *S. tsugae* either prefer *A. tsugae* eggs or show no preference. Both larvae and adults are mobile and consume all life stages of *A. tsugae* [3]. The first releases of *S. tsugae* occurred in 1995 [3]. Millions of *S. tsugae* have been reared and released in the eastern US, but in recent years biological control efforts have focused on other predator species [39].

Laricobius nigrinus are beetles native to the Pacific Northwest and predators of *A. tsugae* found on the western hemlock. They exhibit synchrony with the *A. tsugae* prey life stages. *L. nigrinus* and *A. tsugae* aestivate and break aestivation synchronously, and oviposition

by *L. nigrinus* coincides with oviposition by the sistens generation of *A. tsugae* [70]. In host specificity tests with other adelgid and Homoptera prey species, *L. nigrinus* larvae only completed development on *A. tsugae* [71]. Over 400,000 *L. nigrinus* have been released in the eastern United States since 2003 [39].

A native species of *Laricobius* is present in the eastern United States. *Laricobius rubidus* is a predator of pine bark adelgids which live on Eastern white pine, but has also been found on *T. canadensis* with *A. tsugae* [26]. *Laricobius rubidus* can develop with exclusively *A. tsugae* prey, but prefer pine bark adelgids [69]. A field study of ten sites in Tennessee, North Carolina, Virginia, Maryland and Pennsylvania suggested *L. nigrinus* may displace *L. rubidus* on *T. canadensis*, but does not displace *L. rubidus* on Eastern white pine [17]. Hybridization of *L. nigrinus* and *L. rubidus* has occurred in the eastern United States. The hybrids are fertile and have been collected on both tree species, but the fitness and predation rates of hybrids relative to *L. nigrinus* or *L. rubidus* are not known [25, 17].

In lab and caged branch field studies of the interaction of *S. tsugae* and *L. nigrinus*, Flowers et al. found that survival, reproduction, and predation rates of each species are not significantly impacted by the presence of the other species [18, 19]. Therefore, interspecific interference competition does not seem to be an important aspect of this system. The joint impact of the coexistence of these two predators on an *A. tsugae* population in the field is not well known, although the two species have established and been recovered on the same tree at a site near Walland, Blount County, Tennessee [23]. Our goal is to use a mathematical model to investigate the population dynamics of *L. nigrinus*, *S. tsugae*, and *A. tsugae* and estimate the joint impact of the predators on an *A. tsugae* population. We use data from our collaborator, Gregory Wiggins, collected in the Great Smoky Mountains National Park to perform parameter estimation of the model. The model formulation, parameter estimation and analysis presented here is joint work with Suzanne Lenhart and Gregory Wiggins.

3.2 Data

We use data collected by Wiggins et al. in the Great Smoky Mountains National Park from 2010-2013 to develop the model and for parameter estimation [68, 67]. Data were collected

at a site near Elkmont Campground, as part of a study on *L. nigrinus* assessing the use of emergence traps, which collect adult *L.nigrinus* as they emerge from the soil where pupation and aestivation takes place [68]. From October 3, 2010 to August 3, 2013 beat-sheet sampling was conducted on limbs accessible from the ground on ten trees every five to fourteen days. Five beat-sheet samples were collected from each tree. For each sample, a 71 by 71 centimeter canvas beat sheet was held under a limb which was hit five to ten times with a one meter long wooden rod to collect predators dislodged from the tree. The number of larval and adult *L. nigrinus* and *S. tsugae* were recorded [68].

Due to the generation lengths of the insects, with one or two generations of each species each year, we use the week the data were collected, instead of the day the data were collected as the time associated with each observation. For each sampling date in the data, we determine the week number in the calendar year that data was collected. If two collections fall within the same calendar week, we assign the integer week value at the time associated with the first observation and the integer week value plus 0.5 as the time associated with the second collection.

The number of predators collected by beat sheet is not the number of predators present on the tree, but rather an indication that predators are at sufficiently high densities to be detected. For each date where beat-sheet sampling occurred, we sum the number of individuals of each life stage collected from each tree and calculate the mean of the number of beetles collected for only the trees with a positive count. Due to the seasonality of the predators, we expect that for each species, there are times of the year when the predator would not be present. At times of the year when we expect predators to be present, such as between sampling dates where positive densities of that stage were recorded, we do not believe that failure to collect individuals in a sample indicates no individuals are present.

We demonstrate our method of calculating the density of a predator class with the data from October 22, 2010 shown in Table 3.1. This date is the first sampling date from which we use data. There were two previous beat-sheet sampling dates, but no individuals of any class were collected. We use the *L. nigrinus* adult density calculated here as the initial condition for the *L. nigrinus* adult class in the model, and set time 0 in the model to be week 43 of the calendar year corresponding to October 22 to October 28, 2010. As *L. nigrinus* larvae,

Table 3.1: Data from October 22, 2010 showing the number of predators collected in each beat-sheet sample and the calculation of the value used in parameter estimation to compare to the model output. We include only the trees on which predators of any stage were collected. The *L. nigrinus* data shown here and used for parameter estimation were among the data reported in Wiggins et al. [68].

Tree	Beat	*L. nigrinus* larvae	*L. nigrinus* adults	*S. tsugae* larvae	*S. tsugae* adults
1	1	0	1	0	0
1	2	0	1	0	0
1	3	0	0	0	0
1	4	0	1	0	0
1	5	0	0	0	0
1	Sum	0	3	0	0
2	1	0	0	0	0
2	2	0	1	0	0
2	3	0	0	0	0
2	4	0	1	0	0
2	5	0	0	0	0
2	Sum	0	2	0	0
4	1	0	1	0	0
4	2	0	1	0	0
4	3	0	2	0	0
4	4	0	0	0	0
4	5	0	0	0	0
4	Sum	0	4	0	0

S. tsugae larvae, and *S. tsugae* adults were not collected in the beat-sheet sampling on this date, we do not include this time point in the data for these classes for parameter estimation. Because adult *L. nigrinus* were collected from three of the ten trees, we calculate the mean of 3, 2, and 4, the total individuals collected from each of these three trees, and use the mean 3 as the *L. nigrinus* adult density initial condition.

Hybridization of the two *Laricobius* species was also assessed at this site in 2010 and 2011, with 16.67 and 12.12 percent of the total *Laricobius* population collected being hybrids [68]. Hybridization was assessed with molecular genetic testing. *Laricobius nigrinus* and *L. rubidus* adults can be identified morphologically by the shape of male genitalia and by the color of the elytra, the forewings that act as wing covers [25]. *Laricobius nigrinus* have black elytra and *L. rubidus* have red and black elytra. Hybrid individuals show intermediate morphology, but within the range of each pure species. The larvae of these two species cannot be morphological distinguished. Thus, in these data, the larval counts may include *L. rubidus* and hybrid individuals, and the adult counts may include hybrid individuals. Since behavioral differences between hybrids and *L. nigrinus* are not known and as relatively few *L. rubidus* adults were observed, we interpret the data as a representation of *L. nigrinus* density.

Adelges tsugae densities were recorded twice as part of this study. On February 3, 2011, five observations of *A. tsugae* density per tree were recorded. Each density is a count of the number of *A. tsugae* individuals or woolly masses (each containing a single adult) on the terminal 30 centimeters of a branch. On October 14, 2011, five samples were taken on 8 out of the 10 trees. We calculate the *A. tsugae* density per centimeter on each tree, by taking the mean of the *A. tsugae* densities for the samples with positive *A. tsugae* counts. We determined the mean density for the stand by calculating the mean *A. tsugae* density for trees with positive *A. tsugae* densities. We have no reason to believe that the conditions are different for the sampled versus the excluded trees for the data taken on October 14, 2011, so we use the mean *A. tsugae* density as a representation of the mean density in the stand.

3.3 Model Formulation

We develop a stage structured model of systems of ordinary differential equations to represent interactions among *A. tsugae*, *L. nigrinus* and *S. tsugae* densities. Each of the three species is represented as two classes. *Adelges tsugae* are divided into an egg class, A_e, and a class representing all other life stages, A. We divide the population into these classes because the density of eggs and other life stages are of different magnitudes. A single adult *A. tsugae* may lay 74.5 eggs on average [43]. In addition, *L. nigrinus* larvae consume only *A. tsugae* eggs, while other predator life stages consume both eggs and other life stages of *A. tsugae* [72, 70, 37]. Both predators are divided into larval and adult classes with L_l larval *L. nigrinus*, L_a adult *L. nigrinus*, S_l larval *S. tsugae* and S_a adult *S. tsugae*. We do not explicitly represent predator eggs in the model, as we do not have data on predator egg densities and because predator eggs do not consume *A. tsugae*.

We represent seasonality in the model by using time dependent parameters and different systems of equations to represent the active life stages and processes in the biological system for each time of year. For many of the transitions between systems of equations, populations are taken to be continuous across the switch from one system to the next. We use the density of a class at the final time in one system as the initial condition of that class in the next system. Other initial conditions are used to represent biological processes connecting appropriate classes. For example, predator reproduction is represented as initial conditions for larval *L. nigrinus*, L_l, and larval *S. tsugae*, S_l, which depend on previous adult densities at the appropriate times of year.

We determine the seasonality of *L. nigrinus* and *S. tsugae* in the model using the literature and the presence of predator larvae and adults as shown in the data. We compare the range of weeks in the calendar year when predators were collected between the years in the data as shown in Figure 3.1. We model the density of each class in at least the weeks when that class was present in any of the years and extend the time where classes are present in the model as indicated by the literature. Table 3.2 shows the weeks, in the calendar year and the weeks in the model (beginning in week 43 of the calendar year), where each life stage is present based on the data.

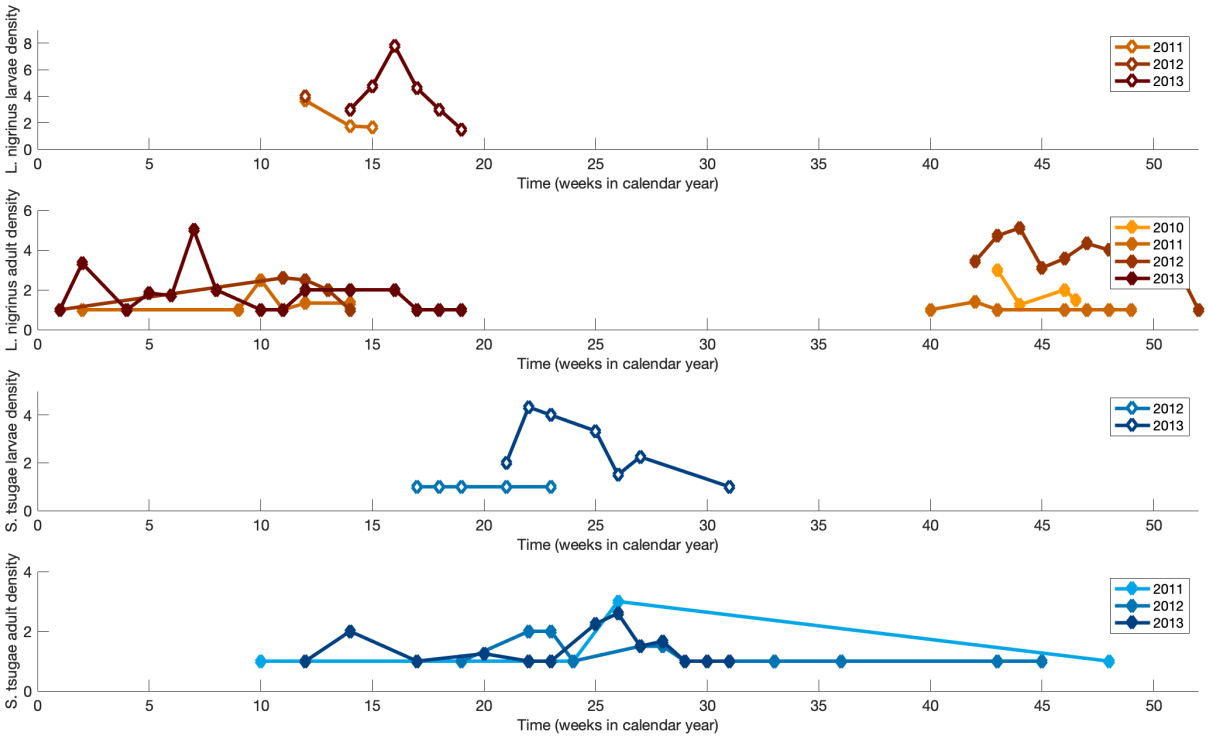


Figure 3.1: Seasonality of predator data. Mean densities of *L. nigrinus* are shown in orange, with different years depicted in the different shades. *Sasajiscymnus tsugae* densities are show in blue. Open diamonds show larval densities and closed diamonds represent adult densities. Time is in weeks of the calendar year.

Table 3.2: Weeks each class of predators is present in at least one year of the data.

Predator class	Weeks in calendar year	Weeks in model
L. nigrinus larvae	12-19	21-28
L. nigrinus adults	40-19	49-28
S. tsugae larvae	17-31	26-40
S. tsugae adults	10-48	19-5

As some classes are not explicitly modeled at some times of the year and as there are discontinuities in the state variables, this model cannot be fully represented as a single system of differential equations with time dependent parameters, as the Hemlock-Adelgid model was in Chapter 2. However, as with the Hemlock-Adelgid Model, we implement this model as multiple systems of ordinary differential equations with constant parameter values. We first present a single system of differential equations with all terms ever present in each differential equation to discuss the biological mechanism represented in the model, but the full model is presented in Systems 1-15. The mechanism represented in the model are also displayed in the schematic diagram Figure 3.2.

$$\frac{dA_e}{dt} = r_A(t)A - c_A(t)A_e - f_{ll}A_eL_l - f_{la}A_eL_a - f_{sl}A_eL_l - f_{sa}A_eS_a \tag{3.1}$$

$$\frac{dA}{dt} = c_A(t)A_e - \frac{m_A(t)}{z}A - m_S(t)A^2 - g_{la}AL_a - g_{sl}AS_l - g_{sa}AS_a \tag{3.2}$$

$$\frac{dL_l}{dt} = -m_{ll}(1 + \frac{d_l}{A_e + 0.1})L_l \tag{3.3}$$

$$\frac{dL_a}{dt} = -m_{la}\big(1 + \frac{d_a}{(A_e + A) + 0.1}\big)L_a \tag{3.4}$$

$$\frac{dS_l}{dt} = -m_{sl}S_l - c_S(t)S_l \tag{3.5}$$

$$\frac{dS_a}{dt} = c_S(t)S_l - m_{sa}S_a \tag{3.6}$$

Parameters are denoted as functions of t here if the parameter has multiple values at different times when the state variables in the term are explicitly modeled. The time dependent parameters are piecewise constant. The parameters $r_A(t)$, $c_A(t)$, $m_S(t)$, and $c_S(t)$ each take two values, zero and a single positive value. The parameters $r_A(t) = r_a$, $c_A(t) = c_a$, $m_S(t) = m_s$, and $c_S(t) = c_s$ when they are positive. The parameter $m_A(t)$ takes three positive values representing seasonal *A. tsugae* mortality rates.

As there is geographic variation in seasonality of *A. tsugae* [10, 32, 26], we use the seasonality reported in a field study including the mean monthly densities of all *A. tsugae* life stages, performed at Baxter Orchard in Great Smoky Mountains National Park [10]. The two generations of *A. tsugae* begin oviposition in early February and in late April, with the

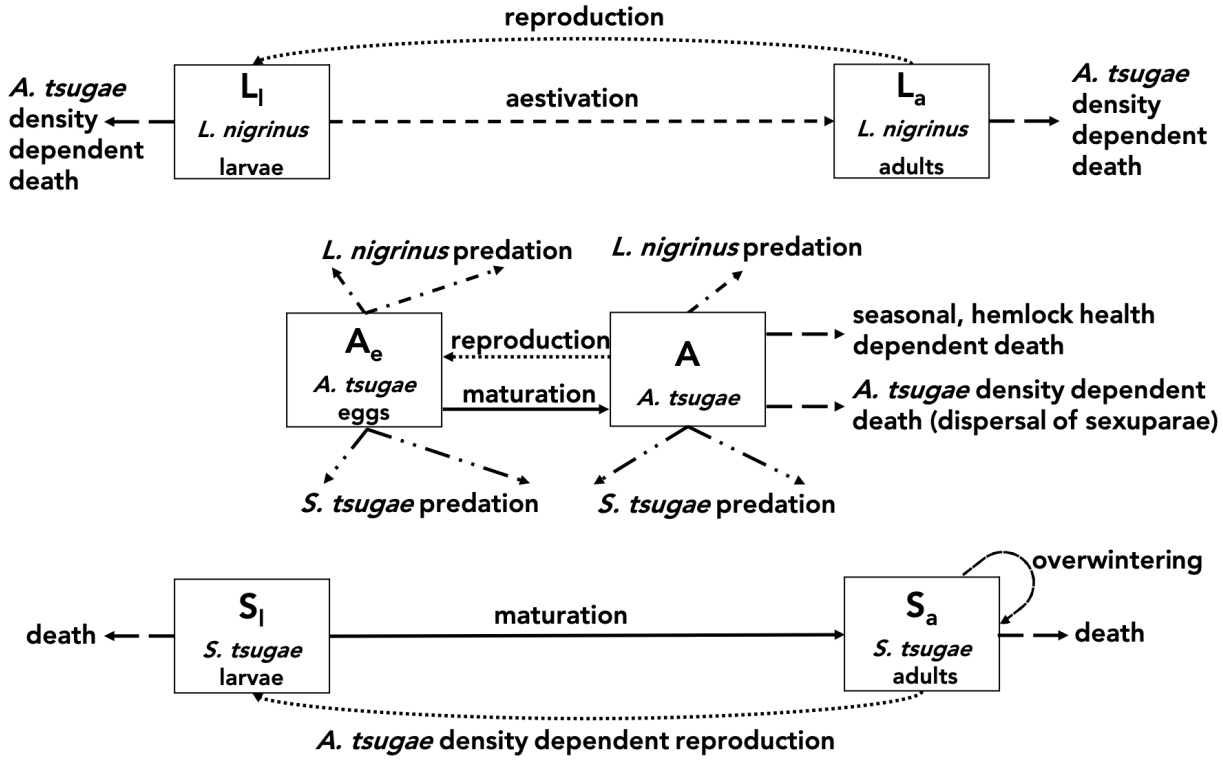


Figure 3.2: Schematic diagram of the Adelgid-Predator model. The six classes in the model are represented as boxes. Only the solid arrows represent direct transitions from one class to another. The other styles of arrows indicate mortality or the processes that depend on the density of another class.

highest egg densities in March and April [10]. Thus in the model, we assume the sistens generation lays eggs from weeks 17 to 23, from mid February to the end of March, and the progrediens generation lays eggs from weeks 27 to 30, from mid April to mid May. At these times, there is a positive term, $r_a A$ in the *A. tsugae* eggs class, A_e, which depends on the density of the other *A. tsugae* class, A. We use $r_a A$ as the reproductive rate for the progrediens adults as well, even though the oviposition period is shorter, as sistens adults have been observed to have higher fecundity than progrediens adults [44, 24].

Adelges tsugae eggs are present in the model from weeks 17 to 24, from mid February to early April, and from weeks 27 to 31, from mid April to late May. The eggs hatch, making the transition from the *A. tsugae* egg class to the other *A. tsugae* class quickly [45, 22, 28]. In the model, *A. tsugae* eggs, A_e, transition to the other *A. tsugae* class, A, starting a week after the oviposition period for the sistens generation begins and the same week oviposition by the progrediens generation starts, as warmer temperatures may allow a faster development [28]. In both generations, eggs continue to hatch and individuals transition to the other *A. tsugae* class for a week after oviposition ends. The first initial condition of the oviposition period for each generation, at weeks 17, in mid February, and 27, in mid April, is 0 as eggs will not survive from one generation to the next. The transition rate $c_a A_e$, depends not only on the rate that eggs hatch, and individual *A. tsugae* survive from eggs to crawlers, the next *A. tsugae* life stage, but also on the dispersal of crawlers, since crawlers are the only mobile stage of *A. tsugae*. Thus we estimate c_a, rather than using the length of time *A. tsugae* individuals spend in the egg class to find c_a.

We include two types of *A. tsugae* mortality in the non-egg class, A, that take the same forms as in the Hemlock-Adelgid model in Chapter 2. The first rate is seasonal and is *T. canadensis* health dependent of the form

$$\frac{m_A(t)}{z} A.$$

The first mortality rate is a decreasing function of *T. canadensis* health. However, instead of a state variable representing *T. canadensis* health as in the Hemlock-Adelgid model, we have a fixed parameter, z representing *T. canadensis* proportion tips alive. As in

the Hemlock-Adelgid model, $m_A(t)$ takes three positive values, where $m_A(t)$ is m_a, the background mortality rate, in the spring and fall, with different rates during the summer and winter. The summer mortality rate, m_{as}, is used from weeks 37 to 52, from July to mid October coinciding with *A. tsugae* sistens aestivation [10]. We use the winter mortality rate, m_{aw} for December through February, in weeks 14 to 38, following Cheah's use of the meterological definition of winter in her 15 year study of winter mortality of *A. tsugae* [4].

The second type of *A. tsugae*, A, mortality in both models is the dispersion of sexuparae from the trees with a density dependent mortality rate,

$$m_s A^2.$$

This mortality occurs when the second type of offspring of the sistens generation, the sexuparae, are adults and leave *T. canadensis* and die without reproducing as no spruce species support their reproduction in the eastern United States [45]. This term is nonzero from weeks 27 to 32, from mid April to early June, to reflect the seasonality reported by Deal, who observed the highest density of sexuparae in the third week in May in 2005 and 2006 [10]. These mortality rates, m_a, m_{as}, m_{aw}, and m_s were taken from the parameter estimation done in Chapter 2. As no *T. canadensis* health data was recorded as part of this study, we estimate z, the proportion tips alive.

Adelges tsugae eggs, A_e, experience predation by all four predator classes, while the other *A. tsugae* life stages class, A, experience predation by *L. nigrinus* adults and *S. tsugae* larvae and adults. All predation in the model is represented as a type I functional response. *Adelges tsugae* eggs are predated by *L. nigrinus* larvae at rate $f_{ll}A_eL_l$, by *L. nigrinus* adults at rate $f_{la}A_eL_a$, by *S. tsugae* larvae at rate $f_{sl}A_eS_l$, and by *S. tsugae* adults at rate $f_{sa}A_eS_a$. Similarly, the other *A. tsugae* class are predated by *L. nigrinus* adults at rate $g_{la}A_eL_a$, by *S. tsugae* larvae at rate $g_{sl}A_eS_l$, and by *S. tsugae* adults at rate $g_{sa}A_eS_a$. Predation occurs during all times when both the predator and prey classes are present and active in the system, that is, when both state variables are represented in the model. The rate of predation of biocontrol species has been studied in lab and field settings, for example see [18, 19, 48, 71, 29]. These study examine consumption rates of individuals or groups of

predators or the impact of the presence or absence of predators on an *A. tsugae* population. The field data we use records *A. tsugae* densities per centimeter and predator counts collected by beat sheet. Since these measures do not measure *A. tsugae* and predators on comparable areas of a tree, these data are representations of densities of the species on the tree, but not comparable numbers of individuals interacting in the same space. Thus the predation rates found in literature cannot be used in our model and we estimate these parameter values.

As *L. nigrinus* are specialist predators, and do not have an alternate food source available in the absence of *A. tsugae*, we assume that the mortality rates of *L. nigrinus* larvae and adults are decreasing functions of *A. tsugae* densities. We choose

$$m_{ll}\big(1+\frac{d_l}{A_e+0.1}\big)L_l$$

as the rate of *L. nigrinus* larvae mortality and

$$m_{la}\big(1+\frac{d_a}{A_e+A+0.1}\big)L_a$$

as the rate of adult mortality. At high *A. tsugae* densities, the mortality rates approach m_{ll} and m_{la}. The denominator in each function includes 0.1 to prevent division by zero, and the maximum mortality rates, $m_{ll}(1+10d_l)$ and $m_{la}(1+10d_a)$ occur when *A. tsugae* densities are 0. The adult mortality rate includes both classes of *A. tsugae* as the adults are predators of both classes, whereas *L. nigrinus* larvae consume only *A. tsugae* eggs. We calculate the value of m_{la} with the survival rate found by Flowers et al. in a field cage study [19]. Conspecific groupings of *L. nigrinus* adults on heavily *A. tsugae* infested *T. canadensis* had a survival rate of 72.2% over 6 weeks. We use this as the survival rate at high *A. tsugae* densities and calculate m_{la} from the solution to the the differential equation

$$\frac{dL_a}{dt}=-m_{la}L_a.$$

We solve

$$0.722L_a(0)=L_a(0)e^{-m_{la}\cdot 6}$$

for m_{la} and find that $m_{la} = 0.054$. We use the survival rates from lab experiments by Zilahi-Balogh et al. in a similar way to calculate m_{ll}. *Laricobius nigrinus* survival from Instar 1, the youngest larvae to pre-pupa was 42% [71]. As the larval stage lasts for 10 weeks in the model, we find $m_{ll} = 0.087$.

Laricobius nigrinus larvae pupate in the soil one to two weeks after dropping from *T. canadensis* [72]. Adult *L. nigrinus* mature from the pupal stage soon after and usually remain the soil and do not engage in predation over the summer. Thus, in the model, the *L. nigrinus* adult initial condition at week 50, in late September, depends on the *L. nigrinus* larvae density at the end of the spring. In the field, *L. nigrinus* emerge as adults over a period of 7 to 15 weeks [68], but we represent this the emergence of *L. nigrinus* adults as an instantaneous event, with a proportion, p_l of the *L. nigrinus* larvae density as the initial condition for the *L. nigrinus* adult class. The survival rate of *L. nigrinus* pupation and aestivation in the field is not well known, so we estimate this proportion [57].

As we do not explicitly model *L. nigrinus* eggs, the initial condition of *L. nigrinus* larvae each year in week 19, in late February, is a function of the number of *L. nigrinus* adults present two weeks previously. In a lab study performed at 12°C, *L. nigrinus* eggs hatched after a mean of 11.8 days [72]. In a field insectary study in Montgomery county Virginia, tracking the proportion of the population in various life stages, the first *L. nigrinus* eggs were observed on February 24, and the first *L. nigrinus* larvae were observed on March 11, with one observation date, March 3 in between [38]. Based on temperatures in the Great Smoky Mountains National Park during March, and the field study conducted in Virginia, we estimate the *L. nigrinus* eggs are laid two weeks before they begin to hatch, and thus that the initial condition of the *L. nigrinus* larvae should depend on the *L. nigrinus* adult density two weeks previously, as those adults lay the eggs that hatch into the larvae. Although *L. nigrinus* lay eggs for at least several weeks during the year [38, 72], and thus we expect eggs to hatch for a corresponding time period, we model the input into *L. nigrinus* larvae class at a single time point as an initial condition to reduce complexity in the model, since we do not see a clear increasing trend in the *L. nigrinus* larvae density in Figure 3.1. Although the earliest *L. nigrinus* larvae were collected in week 21, in mid March, as listed in Table 3.2, we begin modeling *L. nigrinus* larvae in week 19 as the first two instars of *L. nigrinus* may be

too small to detect through beat-sheet sampling. The mean body length of a second instar *L. nigrinus* larvae is 2.2 millimeters, whereas the mean body length of a third instar is 3.5 millimeters [72]. When raised at 12°C in the lab, the mean duration of the first two instars was 10.4 days [72].

As *S. tsugae* are generalist predators, in that they can successfully develop on other species of adelgids present in the eastern United States, we assume that the *S. tsugae* could persist in the absence of *A. tsugae*, but that that their birth rate is an increasing function of *A. tsugae* density. Therefore, the initial condition of *S. tsugae* larvae is a function of both *A. tsugae* and *S. tsugae* adult densities from a previous time point. The form of this function is discussed in System 7. *Sasajiscymnus tsugae* adults are present in the data from weeks 19 to 5, from early March to late November, as shown in Table 3.2. However, two different generations of adults are present over the course of the year as *S. tsugae* survive over winter as adults [6]. Three generations in a single year were identified in a caged field study in Connecticut, with adults of the second and third generation of the year surviving overwinter to reproduce in the next year. Based on the collection dates of *S. tsugae* larvae as shown in Figure 3.1, we do not believe three generations of *S. tsugae* were present in a calendar year. As *S. tsugae* are not active or engaging in predation during the winter and *S. tsugae* adults were not collected in any of the years from weeks 5 to 19, from late November to early March, we do not explicitly model the *S. tsugae* adult density during this time. Instead, we assume a proportion, p_s of the *S. tsugae* present at the end of the fall overwinter to become active again in early spring, lay eggs, which then hatch into larvae, which are present in weeks 26 to 40, from mid April to late July in the data, as shown in Table 3.2. Cheah and McClure tracked overwintering mortality of *S. tsugae* adults in field cages, and found 15.6% mortality [6]. We use this mortality rate to calculate the proportion of *S. tsugae* to survive overwinter $p_s = 0.844$. We assume that *S. tsugae* adults do not survive longer than a year, and thus assume that overwinter adults die prior to the transition of the current years' *S. tsugae* larvae to adults. Thus the initial condition of *S. tsugae* adults is 0 in week 29, the first week of May.

Similarly to *L. nigrinus*, *S. tsugae* first and second instar larvae may not be detected. A second instar *S. tsugae* larvae has mean length 1.51 millimeters, while third and fourth

instar *S. tsugae* larvae have mean lengths 1.94 and 2.67 millimeters, respectively [5]. Thus, as development through the first and second instars takes 4 to 12.5 days at a constant temperature of 20°C [5], we have *S. tsugae* larvae present in the model a week before they are seen in the data, starting at week 25 in mid April. The initial condition for the larvae, depends on both the previous *S. tsugae* adult density and the sum of the two *A. tsugae* classes, as *S. tsugae* adults consume both eggs and other life stages of *A. tsugae*. As egg hatch occurs 8-12 days after oviposition at 20°C, the initial condition, representing *S. tsugae* eggs hatching depends on *S. tsugae* and *A. tsugae* densities from two weeks previously, in week 23. As development from egg hatch to adult takes 27- 34.5 days at 20°C [5], transition from the *S. tsugae* larvae to adult class begins in week 29, 4 weeks after we assume the larvae hatch from eggs. *S. tsugae* mature from larvae to adults in the spring, and we represent this process at a constant per capita transition rate, c_s from the larvae class to the adult class during weeks 29 to 41, from early May to early August. We assume the transition rate $c_s = 0.25$, or the reciprocal of the time spent in the larval class. We determine the constant per capita mortality rates for *S. tsugae* adults and larvae from the literature. In a caged field study Flowers et al. found that 73.7% of adults in conspecific grouping survived 6 weeks [19]. Using this survival information and the solution to the differential equation

$$\frac{dS_a}{dt} = -m_{sa}S_a,$$

as we did in finding the mortality rates of *L. nigrinus*, we found mortality rates of $m_{sa} = 0.051$. Based on lab studies by Flowers et al. we use the maximum survival rate of *S. tsugae* larvae over a week when observed in different grouping of conspecific life stages and other species, which was found to be 86.6%. Using the same method, we calculate $m_{sl} = 0.14$.

The model is composed of 15 systems of equations, each representing a time period during the year. System i controls the system from time t_{i-1}^+ to time t_i^- each year, where these t values are times during the year, which restart at $0 = t_0 = t_{15}$ each year. Model time is tracked in years so that in the nth year, system i controls the dynamics from model time $n-1+t_{i-1}^+$ to model time $n-1+t_i^-$. Figure 3.3 shows the presence of the classes throughout the year.

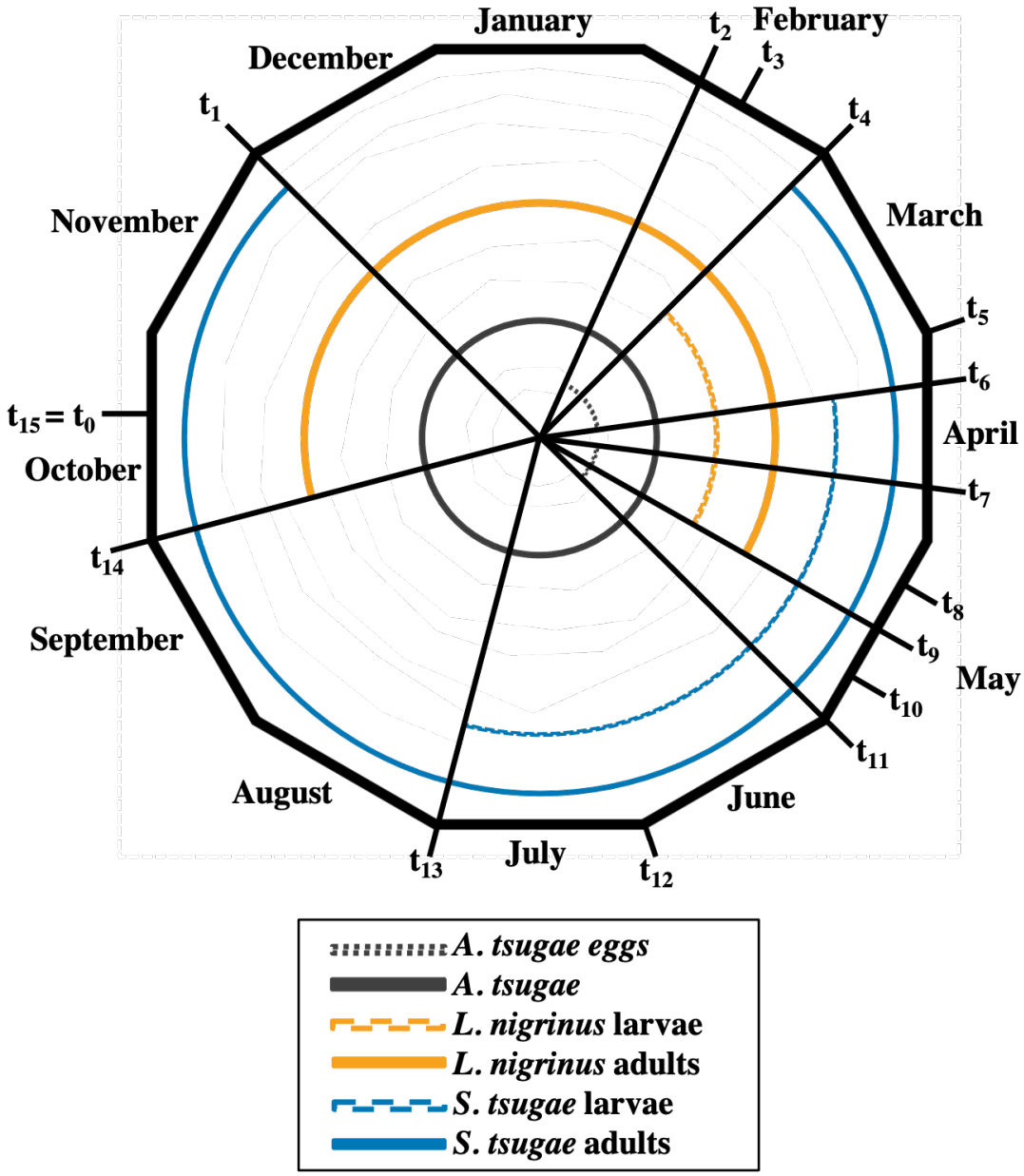


Figure 3.3: Illustration of Adelgid-Predator model seasonality. Arcs represent the presence of a class during each time period throughout the year. Lines from the center of the figure show a change in the presence or absence of or more classes. The time period between those changes may be controlled by more than one system of equations, as shown by the time points along the outside of the figure. For example, between times t_2 and t_3, *A. tsugae* reproduction is occurring, but the *A. tsugae* eggs are not hatching and transitioning to the other *A. tsugae* class. This changes at time t_3. Between times t_3 and t_4, reproduction of *A. tsugae* continues, but *A. tsugae* eggs are also hatching and transitioning to the other *A. tsugae* class. Therefore there is an additional nonzero term in the *A. tsugae* egg class and other *A. tsugae* class representing that transition, as controlled by a change in the value of the time dependent parameter, $c_A(t)$, from 0 to the positive rate c_a.

System 1

System 1 represents weeks 1 (time 0 = t_0) to 6 (time t_1) , from mid October to mid November with classes of non-egg *A. tsugae*, A, *L. nigrinus* adults, L_a and *S. tsugae* adults, S_a. In the first year, the *L. nigrinus* adult initial condition is taken from the data. The initial conditions for *A. tsugae* and *S. tsugae* adults are estimated, as there are no data for these classes at this time point. After the first year, initial conditions for the three classes in this system are taken to be the densities of the these class at the final time of System 15. During this time period, *A. tsugae* are experiencing background seasonal mortality which depends on *T. canadensis* proportion tips alive, z, at rate $\frac{m_a}{z}A$, and predation by the present predator classes with type I functional responses, at rate $g_{la}AL_a$ by *L. nigrinus* adults and rate $g_{sa}AS_a$ by *S. tsugae* adults. The mortality rate of *L. nigrinus* is a decreasing function of *A. tsugae* density of the form $m_{la}\big(1+\frac{d_a}{A+0.1}\big)L_a$. The mortality rate of *S. tsugae* is $m_{sa}S_a$.

$$\frac{dA}{dt} = -\frac{m_a}{z}A - g_{la}AL_a - g_{sa}AS_a \tag{3.7}$$

$$\frac{dL_a}{dt} = -m_{la}\big(1+\frac{d_a}{A+0.1}\big)L_a \tag{3.8}$$

$$\frac{dS_a}{dt} = -m_{sa}S_a \tag{3.9}$$

In the first year, the model has initial conditions

$$A(0), \text{ estimated}$$

$$L_a(0), \text{ directly from data}$$

$$S_a(0), \text{ estimated.}$$

After the first year, at the transition from one year to the next, the values of the state variables at the final time of the previous year are used as the initial conditions for this System 1, so

$$A(t_0^+) = A(t_0^-)$$
$$L_a(t_0^+) = L_a(t_0^-)$$
$$S_a(t_0^+) = S_a(t_0^-).$$

System 2

System 2 represents weeks 7 (time t_1) to 16 (time t_2), from early December to early February with classes of *A. tsugae*, A, and *L. nigrinus* adults, L_a. *S. tsugae* are now assumed to be overwintering, and are no longer active predators, so we do not model the density of *S. tsugae* adults during this time. Thus, as only one predator class is present, the only predation *A. tsugae* experience is from *L. nigrinus* adults at rate $g_{la}AL_a$. The *A. tsugae* and *L. nigrinus* classes have continuous boundary conditions from the previous system, where the initial conditions of these classes are equal to the final conditions from the previous system. The seasonal mortality rate of *A. tsugae* has changed from the previous system, from the background rate, m_a, to the winter mortality rate, m_{aw}. Thus the *A. tsugae* mortality rate is $\frac{m_{aw}}{z}A$ where z is the proportion tips alive. *Laricobius nigrinus* adults continue to experience *A. tsugae* density dependent mortality.

$$\frac{dA}{dt} = -\frac{m_{aw}}{z}A - g_{la}AL_a \tag{3.10}$$
$$\frac{dL_a}{dt} = -m_{la}\big(1 + \frac{d_a}{A + 0.1}\big)L_a \tag{3.11}$$

$$A(t_1^+) = A(t_1^-)$$
$$L_a(t_1^+) = L_a(t_1^-)$$

System 3

System 3 represents week 17 (from time t_2 to t_3), in mid February, with classes of *A. tsugae* eggs, A_e, *A. tsugae*, A, and *L. nigrinus* adults, L_a. *Adelges tsugae* sistens adults begin oviposition during this week, with rate $r_a A$, thus we have a new class, the *A. tsugae* eggs present in this system. *Adelges tsugae* eggs experience predation by *L. nigrinus* adults at rate $f_{la} A_e L_a$. As with *A. tsugae*, predation of *A. tsugae* eggs is represented as a type I functional response. The initial condition of *A. tsugae* eggs is 0, as we assume that the eggs from the previous generation do not survive the winter. As *A. tsugae* eggs are present in the system, and *L. nigrinus* adults will consume them, the *L. nigrinus* adult mortality rate now depends on the sum of the densities of both classes of *A. tsugae*, at rate $m_{la}\big(1+\frac{d_a}{(A_e+A)+0.1}\big)L_a$. *Adelges tsugae* continue to experience predation by *L. nigrinus* adults at rate $g_{la} A L_a$ and mortality, at the winter specific rate, and depending on proportion tips alive z, $\frac{m_{aw}}{z}A$. Initial conditions for the *A. tsugae* and *L. nigrinus* classes are the final conditions for those classes from the previous system.

$$\frac{dA_e}{dt} = r_a A - f_{la} A_e L_a \tag{3.12}$$

$$\frac{dA}{dt} = -\frac{m_{aw}}{z} A - g_{la} A L_a \tag{3.13}$$

$$\frac{dL_a}{dt} = -m_{la}\big(1 + \frac{d_a}{(A_e + A) + 0.1}\big) L_a \tag{3.14}$$

$$A_e(t_2^+) = 0$$

$$A(t_2^+) = A(t_2^-)$$

$$L_a(t_2^+) = L_a(t_2^-)$$

System 4

System 4 represents weeks 18 and 19, in late February and early March, with classes of *A. tsugae* eggs, A_e, *A. tsugae*, A and *L. nigrinus* adults, L_a. *Adelges tsugae* eggs begin hatching and transitioning from the *A. tsugae* egg to the other *A. tsugae* class at rate $c_a A_e$ during this week. *A. tsugae* oviposition continues at rate $r_a A$. Both *A. tsugae* eggs

and *A. tsugae* continue to experience predation by *L. nigrinus* adults at rates $f_{la}A_eL_a$ and $g_{la}AL_a$ respectively. *Adelges tsugae* mortality continues at the winter, proportion tips alive dependent rate $\frac{m_{aw}}{z}A$. *Laricobius nigrinus* mortality continues at a rate dependent on the sum of the density of both *A. tsugae* classes. The initial conditions of all three classes are the final condition of each of the classes from the previous system.

$$\frac{dA_e}{dt} = r_aA - c_aA_e - f_{La}A_eL_a \tag{3.15}$$

$$\frac{dA}{dt} = c_aA_e - \frac{m_{aw}}{z}A - g_{la}AL_a \tag{3.16}$$

$$\frac{dL_a}{dt} = -m_{la}\big(1 + \frac{d_a}{(A_e + A) + 0.1}\big)L_a \tag{3.17}$$

$$A_e(t_3^+) = A_e(t_3^-)$$

$$A(t_3^+) = A(t_3^-)$$

$$L_a(t_3^+) = L_a(t_3^-)$$

System 5

System 5 represents weeks 20 to 23, in March, with classes of *A. tsugae* eggs, A_e, *A. tsugae*, A, *L. nigrinus* larvae, L_l, *L. nigrinus* adults, L_a and *S. tsugae* adults, S_a. At the beginning of week 20, the overwintering *S. tsugae* adults become active again, and thus this class is present in the model in this system. We assume a proportion, p_s, of the adults present in early December, at time t_1, survive the winter, and use this density as the initial condition for the *S. tsugae* adult class. During this same week, we assume *L. nigrinus* are hatching from eggs and entering the larvae class, and thus we have the *L. nigrinus* larvae class present in this system as well. We represent this reproduction with a *L. nigrinus* larvae initial condition that depends on density of adults present when eggs were laid, at time t_3, and reproductive rate r_l. *A. tsugae* reproduction, at rate r_aA and transfer from the *A. tsugae* egg class to the *A. tsugae* class, at rate c_aA_e, continue during this time period. As three predator classes are present during this time, *A. tsugae* eggs experience predation by *L. nigrinus* larvae, *L. nigrinus* adults, *S. tsugae* adults at rates $f_{ll}A_eL_l$, $f_{la}A_eL_a$ and

$f_{sa}A_eS_a$ respectively. *Adelges tsugae* mortality occurs at rate $\frac{m_a}{z}A$, depending on proportion tips alive z and the background seasonal mortality rate m_a, instead of the winter mortality rate, m_{aw} as in the previous system. As *L. nigrinus* larvae exclusively consume *A. tsugae* eggs, the *A. tsugae* experience predation by two classes, the *L. nigrinus* adult class, at rate $g_{la}AL_a$ and the *S. tsugae* adult class, at rate $g_{sa}AS_a$. The *L. nigrinus* larval class has a mortality rate depending on *A. tsugae* egg density of the same form as the *L. nigrinus* adult class, $m_{ll}(1+\frac{d_l}{A_e+0.1})L_l$. As *L. nigrinus* consume only *A. tsugae* eggs, only the *A. tsugae* egg density is included in the mortality rate. As in the previous system, the *L. nigrinus* adult mortality rate depends on the sum of densities of the *A. tsugae* classes. As in System 1, the *S. tsugae* adult mortality rate is $m_{sa}S_a$. The initial conditions for the *A. tsugae* eggs, *A. tsugae* and *L. nigrinus* adults, which were present in the previous system, are the final condition of each of these classes from the previous system.

$$\frac{dA_e}{dt} = r_aA - c_AA_e - f_{ll}A_eL_l - f_{la}A_eL_a - f_{sa}A_eS_a \tag{3.18}$$

$$\frac{dA}{dt} = c_aA_e - \frac{m_a}{z}A - g_{la}AL_a - g_{sa}AS_a \tag{3.19}$$

$$\frac{dL_l}{dt} = -m_{ll}(1+\frac{d_l}{A_e+0.1})L_l \tag{3.20}$$

$$\frac{dL_a}{dt} = -m_{la}\big(1+\frac{d_a}{(A_e+A)+0.1}\big)L_a \tag{3.21}$$

$$\frac{dS_a}{dt} = -m_{sa}S_a \tag{3.22}$$

$$A_e(t_4^+) = A_e(t_4^-)$$

$$A(t_4^+) = A(t_4^-)$$

$$L_l(t_4^+) = r_lL_a(t_3^-)$$

$$L_a(t_4^+) = L_a(t_4^-)$$

$$S_a(t_4^+) = p_sS_a(t_1^-)$$

System 6

System 6 represents week 24, in early April, with classes of *A. tsugae* eggs, A_e, *A. tsugae*, A, *L. nigrinus* larvae, L_l, *L. nigrinus* adults, L_a, and *S. tsugae* adults, S_a. We assume that *A. tsugae* oviposition has stopped, and thus there is no positive term in the *A. tsugae* egg class. Transition from the *A. tsugae* egg class to the *A. tsugae* class continues at rate $c_a A_e$. *Adelges tsugae* mortality occurs at rate $\frac{m_a}{z}A$, as in the previous system. *A. tsugae* eggs experience predation by *L. nigrinus* larvae, *L. nigrinus* adults, *S. tsugae* adults at rates $f_{ll}A_eL_l$, $f_{la}A_eL_a$, and $f_{sa}A_eS_a$. *A. tsugae* experience predation from *L. nigrinus* adults and *S. tsugae* adults at rate $g_{la}AL_a$ and $g_{sa}AS_a$. As in the previous system, the *L. nigrinus* classes have *A. tsugae* density dependent morality rates. The mortality rate for *L. nigrinus* larvae depends on *A. tsugae* egg density, with the form $m_{ll}(1+\frac{d_l}{A_e+0.1})L_l$, while the mortality rate of *L. nigrinus* adults depend on the sum of the densities of the *A. tsugae* classes. The mortality rate of *S. tsugae* adults is $m_{sa}S_a$. The initial conditions for all classes are the densities at the final time for the corresponding classes from the previous system.

$$\frac{dA_e}{dt} = -c_aA_e - f_{ll}A_eL_l - f_{la}A_eL_a - f_{sa}A_eS_a \tag{3.23}$$

$$\frac{dA}{dt} = c_aA_e - \frac{m_a}{z}A - g_{la}AL_a - g_{sa}AS_a \tag{3.24}$$

$$\frac{dL_l}{dt} = -m_{ll}(1+\frac{d_l}{A_e+0.1})L_l \tag{3.25}$$

$$\frac{dL_a}{dt} = -m_{la}\big(1+\frac{d_a}{(A_e+A)+0.1}\big)L_a \tag{3.26}$$

$$\frac{dS_a}{dt} = -m_{sa}S_a \tag{3.27}$$

$$A_e(t_5^+) = A_e(t_5^-)$$

$$A(t_5^+) = A(t_5^-)$$

$$L_l(t_5^+) = L_l(t_5^-)$$

$$L_a(t_5^+) = L_a(t_5^-)$$

$$S_a(t_5^+) = S_a(t_5^-)$$

System 7

System 7 represents weeks 25 and 26, in mid April, with classes of *A. tsugae*, A, *L. nigrinus* larvae, L_l, *L. nigrinus* adults, L_a, *S. tsugae* larvae, S_l, and *S. tsugae* adults, S_a. The *A. tsugae* progrediens/sexuparae generation is maturing during this period, and is not yet reproducing, so there is not an *A. tsugae* eggs class during this time. As there are no *A. tsugae* eggs present, and the *L. nigrinus* mortality rate is a function of *A. tsugae* density, we use $m_{ll}L_l$ as the mortality rate of *L. nigrinus* larvae for this two week period. *S. tsugae* larvae are assumed to hatch this week, with the initial condition for the *S. tsugae* larvae class depending on *S. tsugae* adults density at time t_s, week 22, in mid March, a week before the end of system 5. We denote t_s without a positive or negative superscript as the same system of differential equations controls the model to the left and right of t_s. The initial condition is an increasing function of the sum of two *A. tsugae* densities at time t_s, with rate

$$r_s\Big(1+\frac{b(A(t_s)+A_e(t_s))}{1+h(A(t_s)+A_e(t_s))}\Big)S_a(t_s).$$

At low total *A. tsugae* density, the per capita reproductive rate approaches r_s. At high total *A. tsugae* density, the per capita reproductive rate approaches $r_s(1+\frac{b}{h})$. We choose the form of this function as it is increasing and bounded above, since *S. tsugae* reproduction would be limited even at high *A. tsugae* densities. The other initial conditions for this system are the densities of the corresponding classes at the final time of the previous system. *S. tsugae* adults have mortality rate $m_{sa}S_a$. Like *S. tsugae* adults, the larvae class experiences mortality at a constant per capita rate m_{sl}. The *A. tsugae* population has mortality rate $\frac{m_a}{z}A$, as in the previous system, and is experiencing predation by *L. nigrinus* adults at rate $g_{la}AL_a$, *S. tsugae* larvae at a rate of $g_{sl}AS_l$ and *S. tsugae* adults at rate $g_{sa}AS_a$.

$$\frac{dA}{dt} = -\frac{m_a}{z}A - g_{la}AL_a - g_{sl}AS_l - g_{sa}AS_a \tag{3.28}$$
$$\frac{dL_l}{dt} = -m_{ll}L_l \tag{3.29}$$
$$\frac{dL_a}{dt} = -m_{la}\big(1 + \frac{d_a}{A+0.1}\big)L_a \tag{3.30}$$
$$\frac{dS_l}{dt} = -m_{sl}S_l \tag{3.31}$$
$$\frac{dS_a}{dt} = -m_{sa}S_a \tag{3.32}$$

$$A(t_6^+) = A(t_6^-)$$
$$L_l(t_6^+) = L_l(t_6^-)$$
$$L_a(t_6^+) = L_a(t_6^-)$$
$$S_l(t_6^+) = r_s\Big(1 + \frac{b(A(t_s) + A_e(t_s))}{1 + h(A(t_s) + A_e(t_s))}\Big)S_a(t_s)$$
$$S_a(t_6^+) = S_a(t_6^-)$$

System 8

System 8 represents weeks 27 and 28, in late April and early May with classes of *A. tsugae*, A, *L. nigrinus* larvae, L_l, *L. nigrinus* adults, L_a, *S. tsugae* larvae, S_l, and *S. tsugae* adults, S_a. The progrediens generation begins reproduction at this time, so *A. tsugae* reproduction occurs at rate r_a, and transition to *A. tsugae* class occurs at rate c_aA_e. The mortality rate for *A. tsugae* is $\frac{m_a}{z}A$, depending on the proportion tips alive, z, and the background seasonal death rate m_a. Both *A. tsugae* classes experience predation by the present predation classes. *A. tsugae* eggs experience predation by *L. nigrinus* larvae, *L. nigrinus* adults, *S. tsugae* larvae and *S. tsugae* adults at rates $f_{ll}A_eL_l$, $f_{la}A_eL_a$, $f_{sl}A_eS_l$ and $f_{sa}A_eS_a$ respectively. *Adelges tsugae* experience predation by *L. nigrinus* adults, *S. tsugae* larvae and *S. tsugae* adults at rates $g_{la}AL_a$, $g_{sl}AS_l$ and $g_{sa}AS_a$. In addition, *A. tsugae* experience an addition form of mortality due to the maturation and departure from the *T. canadensis* of sexuparae, at rate m_sA^2. *Laricobius nigrinus* have mortality rates depending on the densities of their prey, as in System 6. The mortality rate of *S. tsugae* larvae and adults are $m_{sl}S_l$ and $m_{sa}S_a$

respectively. As *A. tsugae* eggs will not survive from one generation to the next, the initial condition for the *A. tsugae* egg class is zero. The other initial conditions are the densities of the corresponding classes at the final time of the previous system.

$$\frac{dA_e}{dt} = r_a A - c_a A_e - f_{ll} A_e L_l - f_a A_e L_a - f_{sl} A_e L_l - f_{sa} A_e S_a \tag{3.33}$$

$$\frac{dA}{dt} = c_a A_e - \frac{m_a}{z} A - m_s A^2 - g_{la} A L_a - g_{sl} A S_l - g_{sa} A S_a \tag{3.34}$$

$$\frac{dL_l}{dt} = -m_{ll}(1 + \frac{d_l}{A_e + 0.1}) L_l \tag{3.35}$$

$$\frac{dL_a}{dt} = -m_{la}\big(1 + \frac{d_a}{(A_e + A) + 0.1}\big) L_a \tag{3.36}$$

$$\frac{dS_l}{dt} = -m_{sl} S_l \tag{3.37}$$

$$\frac{dS_a}{dt} = -m_{sa} S_a \tag{3.38}$$

$$\begin{aligned} A_e(t_7^+) &= 0 \\ A(t_7^+) &= A(t_7^-) \\ L_l(t_7^+) &= L_l(t_7^-) \\ L_a(t_7^+) &= L_a(t_7^-) \\ S_l(t_7^+) &= S_l(t_7^-) \\ S_a(t_7^+) &= S_a(t_7^-) \end{aligned}$$

System 9

System 9 represents week 29, in early May, with classes of *A. tsugae* eggs, A_e, *A. tsugae*, A, *L. nigrinus* larvae, L_l, *L. nigrinus* adults, L_a, *S. tsugae* larvae, S_l, and *S. tsugae* adults, S_a. *S. tsugae* larvae begin to mature into adults during this week, and transition from the *S. tsugae* larvae class to the *S. tsugae* adult class at rate $c_s S_l$. We assume all overwintering *S. tsugae* adults have died, and produce this in the model with a zero initial condition for the *S. tsugae* adult class. The initial conditions of the other classes are the densities of the corresponding classes at the final time in the previous system. As in the previous system, *A.*

tsugae reproduction occurs at rate $r_a A$, and transition to *A. tsugae* class occurs at rate $c_a A_e$. The mortality rate for *A. tsugae* is $\frac{m_a}{z} A$. *A. tsugae* eggs experience predation by *L. nigrinus* larvae, *L. nigrinus* adults, *S. tsugae* larvae and *S. tsugae* adults at rates $f_{ll} A_e L_l$, $f_{la} A_e L_a$, $f_{sl} A_e S_l$ and $f_{sa} A_e S_a$. *A. tsugae* experience predation by *L. nigrinus* adults, *S. tsugae* larvae and *S. tsugae* adults at rates $g_{la} A L_a$, $g_{sl} A S_l$ and $g_{sa} A S_a$. The maturation and departure of sexuparae occurs at rate $m_s A^2$. *L. nigrinus* have mortality rates depending on the densities of the *A. tsugae* classes, like in the previous system. The mortality rate of *S. tsugae* larvae and adults are $m_{sl} S_l$ and $m_{sa} S_a$ respectively.

$$\frac{dA_e}{dt} = r_a A - c_a A_e - f_{ll} A_e L_l - f_{la} A_e L_a - f_{sl} A_e S_l - f_{sa} A_e S_a \tag{3.39}$$

$$\frac{dA}{dt} = c_a A_e - \frac{m_a}{z} A - m_s A^2 - g_{la} A L_a - g_{sl} A S_l - g_{sa} A S_a \tag{3.40}$$

$$\frac{dL_l}{dt} = -m_{ll}(1 + \frac{d_l}{A_e + 0.1}) L_l \tag{3.41}$$

$$\frac{dL_a}{dt} = -m_{la}\big(1 + \frac{d_a}{(A_e + A) + 0.1}\big) L_a \tag{3.42}$$

$$\frac{dS_l}{dt} = -c_s S_l - m_{sl} S_l \tag{3.43}$$

$$\frac{dS_a}{dt} = c_s S_l - m_{sa} S_a \tag{3.44}$$

$$A_e(t_8^+) = A_e(t_8^-)$$

$$A(t_8^+) = A(t_8^-)$$

$$L_l(t_8^+) = L_l(t_8^-)$$

$$L_a(t_8^+) = L_a(t_8^-)$$

$$S_l(t_8^+) = S_l(t_8^-)$$

$$S_a(t_8^+) = 0$$

System 10

System 10 represents week 30, in mid May, with classes of *A. tsugae* eggs A_e, *A. tsugae*, A, *S. tsugae* larvae, S_l, and *S. tsugae* adults, S_a. We assume that *L. nigrinus* adults have

died at this time, and the *L. nigrinus* larvae leave the tree to pupae in the soil over the summer, thus we do not have equations for *L. nigrinus* larvae or adults in this system. *A. tsugae* are continuing to reproduce at rate $r_a A$ and mature from *A. tsugae* eggs to the *A. tsugae* at rate $c_a A_e$. *A. tsugae* have mortality rate $\frac{m_a}{z} A$. In addition, sexuparae are assumed to be continuing to mature and leave *T. canadensis* at rate $m_s A^2$. *A. tsugae* eggs and *A. tsugae* are each experiencing predation by *S. tsugae* larvae, at rates $f_{sl} A_e S_l$ and $g_{sl} A S_l$ and *S. tsugae* adults, at rates $f_{sa} A_e S_a$ and $g_{sa} A S_a$. As in the previous system, *S. tsugae* larvae mature into adults at rate $c_s S_l$, and have mortality rate $m_{sl} S_l$, and *S. tsugae* adults have mortality rate $m_{sa} S_a$. The initial conditions for this system are the final condition of the corresponding classes from the previous system.

$$\frac{dA_e}{dt} = r_A A - c_A A_e - f_{Sl} A_e S_l - f_{Sa} A_e S_a \tag{3.45}$$

$$\frac{dA}{dt} = c_A A_e - \frac{m_A}{z} A - m_S A^2 - g_{Sl} A S_l - g_{Sa} A S_a \tag{3.46}$$

$$\frac{dS_l}{dt} = -c_S S_l - m_{Sl} S_l \tag{3.47}$$

$$\frac{dS_a}{dt} = c_S S_l - m_{Sa} S_a \tag{3.48}$$

$$A_e(t_9^+) = A_e(t_9^-)$$

$$A(t_9^+) = A(t_9^-)$$

$$S_l(t_9^+) = S_l(t_9^-)$$

$$S_a(t_9^+) = S_a(t_9^-)$$

System 11

System 11 represents week 31, in late May, with classes of *A. tsugae* eggs, A_e, *A. tsugae*, A, *S. tsugae* larvae, S_l, and *S. tsugae* adults, S_a. During this week, we assume the progrediens generation has stopped laying eggs, and so there are no positive terms in the *A. tsugae* egg equation, but that previous laid sistens eggs are continuing to hatch and transition to the other *A. tsugae* class at rate $c_a A_e$. As previously, *A. tsugae* experience predation by

S. tsugae larvae and adults at rate $f_{sl}A_eS_l$ and $f_{sa}A_eS_a$. *A. tsugae* have the background seasonal mortality rate, depending on proportions tip alive $\frac{m_a}{z}A$, and sexuparae are adults and leaving *T. canadensis* at rate m_sA^2. *A. tsugae* experience predation by *S. tsugae* larvae and adults at rates $g_{sl}AS_l$ and $g_{sa}AS_a$. As in the previous system, *S. tsugae* larvae are maturing and transitioning to *S. tsugae* adults at rate c_sS_l, and have mortality rate $m_{sl}S_l$. *S. tsugae* adults have mortality rate $m_{sa}S_a$. The initial conditions for all four classes are the final conditions of the previous system.

$$\frac{dA_e}{dt} = -c_aA_e - f_{sl}A_eS_l - f_{sa}A_eS_a \tag{3.49}$$
$$\frac{dA}{dt} = c_aA_e - \frac{m_a}{z}A - m_sA^2 - g_{sl}AS_l - g_{sa}AS_a \tag{3.50}$$
$$\frac{dS_l}{dt} = -c_sS_l - m_{sl}S_l \tag{3.51}$$
$$\frac{dS_a}{dt} = c_sS_l - m_{sa}S_a \tag{3.52}$$

$$A_e(t_{10}^+) = A_e(t_{10}^-)$$
$$A(t_{10}^+) = A(t_{10}^-)$$
$$S_l(t_{10}^+) = S_l(t_{10}^-)$$
$$S_a(t_{10}^+) = S_a(t_{10}^-)$$

System 12

System 12 represents weeks 32 to 36, in late May and June. It has equations representing *A. tsugae*, A, *S. tsugae* larvae, S_l, and *S. tsugae* adults, S_a. During this week, we assume all the eggs laid by progrediens, from time t_7 to t_{10} have hatched, and transitioned to the *A. tsugae* class or will not hatch. Thus, there is no *A. tsugae* egg class represented in this system. We assume that the sexuparae have left the trees by this time and thus *A. tsugae* experience morality at rate $\frac{m_a}{z}$ and predation by *S. tsugae* larvae at rate g_{sl} and *S. tsugae* adults at rate g_{sa}. As in the previous system, *S. tsugae* larvae are maturing to adults and transitioning to the *S. tsugae* adult class at rate c_s. Both classes of *S. tsugae* have constant

per capita mortality rates, m_{sl} for *S. tsugae* larvae, and m_{sa} for *S. tsugae* adults. All initial conditions for this system are the final conditions of the corresponding classes in the previous system.

$$\frac{dA}{dt} = -\frac{m_a}{z}A - g_{sl}AS_l - g_{sa}AS_a \tag{3.53}$$
$$\frac{dS_l}{dt} = -c_sS_l - m_{sl}S_l \tag{3.54}$$
$$\frac{dS_a}{dt} = c_sS_l - m_{sa}S_a \tag{3.55}$$

$$A(t_{11}^+) = A(t_{11}^-)$$
$$S_l(t_{11}^+) = S_l(t_{11}^-)$$
$$S_a(t_{11}^+) = S_a(t_{11}^-)$$

System 13

System 13 represents weeks 37 to 41, in July and early August, with classes of *A. tsugae*, A, *S. tsugae* larvae, S_l, and *S. tsugae* adults, S_a. As the *A. tsugae* will now be entering summer aestivation, the seasonal death rate is now changed to the summer rate m_{as}, and thus *A. tsugae* experience mortality at rate $\frac{m_{as}}{z}A$. As two predator classes are present, *A. tsugae* experience predation by *S. tsugae* larvae and adults at rate $g_{sl}AS_l$ and $g_{sa}AS_a$. As in the previous system, *S. tsugae* larvae are maturing and transitioning to *S. tsugae* adults at rate c_sS_l, and have mortality rate $m_{sl}S_l$. *S. tsugae* adults have mortality rate $m_{sa}S_a$. The initial conditions for all three classes are the final conditions of the previous system.

$$\frac{dA}{dt} = -\frac{m_{as}}{z}A - g_{sl}AS_l - g_{sa}AS_a \tag{3.56}$$
$$\frac{dS_l}{dt} = -c_sS_l - m_{sl}S_l \tag{3.57}$$
$$\frac{dS_a}{dt} = c_sS_l - m_{sa}S_a \tag{3.58}$$

$$A(t_{12}^+) = A(t_{12}^-)$$
$$S_l(t_{12}^+) = S_l(t_{12}^-)$$
$$S_a(t_{12}^+) = S_a(t_{12}^-)$$

System 14

System 14 represents weeks 42 to 49, in August and September, with classes of *A. tsugae*, A, and *S. tsugae* adults, S_a. *A. tsugae* mortality occurs at summer rate also depending on *T. canadensis* proportion tips alive, $\frac{m_{as}}{z}A$, as in the previous system, and as there is only one predator class, as *S. tsugae* larvae are assumed to have matured to *S. tsugae* adults or died by this time, *A. tsugae* experience predation by *S. tsugae* adults only at rate $g_{sa}AS_a$. *S. tsugae* adults die rate $m_{sa}S_a$. The initial condition for both classes is the final condition of those classes in the previous system.

$$\frac{dA}{dt} = -\frac{m_{as}}{z}A - g_{sa}AS_a \tag{3.59}$$
$$\frac{dS_a}{dt} = -m_{sa}S_a \tag{3.60}$$

$$A(t_{13}^+) = A(t_{13}^-)$$
$$S_a(t_{13}^+) = S_a(t_{13}^-)$$

System 15

System 15 represents weeks 50 to 52, from late September to mid October, with classes of *A. tsugae*, A, *L. nigrinus* adults, L_a, and *S. tsugae* adults, S_a. We assume that *L. nigrinus* emerge as adults from their pupation and aestivation, and thus the *L. nigrinus* adult class is present in this system. The *L. nigrinus* adult initial condition for this system is a proportion, p_l, of the *L. nigrinus* larvae present at the end of the spring, at time t_9. The initial conditions for *A. tsugae* and *S. tsugae* adult classes are the final conditions of these classes from the

end of the previous system. *A. tsugae* experience mortality at the summer rate $\frac{m_{as}}{z}A$ during this time, like in the previous system, as well as predation by *L. nigrinus* adults and *S. tsugae* adults at rates $g_{la}AL_a$ and $g_{sa}AS_a$. *L. nigrinus* adults die at *A. tsugae* dependent rate $m_{la}(1+\frac{d_a}{A+0.1})L_a$, whereas *S. tsugae* adult mortality is at rate $m_{sa}S_a$.

$$\frac{dA}{dt} = -\frac{m_{as}}{z}A - g_{la}AL_a - g_{sa}AS_a \tag{3.61}$$

$$\frac{dL_a}{dt} = -m_{la}(1+\frac{d_a}{A+0.1})L_a \tag{3.62}$$

$$\frac{dS_a}{dt} = -m_{sa}S_a \tag{3.63}$$

$$A(t_{15}^+) = A(t_{15}^-)$$
$$L_a(t_{15}^+) = p_l L_l(t_9^-)$$
$$S_a(t_{15}^+) = S_a(t_{15}^-)$$

Using the same argument as in Chapter 2, it can be shown that solutions to this model exist and are unique and nonnegative.

3.4 Parameter Estimation

Through parameter estimation we determine the value of 17 parameters and two initial conditions in the model, using the field data shown in Figure 3.4 [68, 67]. The units and biological meaning of the all parameters in the model, are shown in Table 3.3 for the fixed parameters and in Table 3.4 for the parameter values that are estimated. The initial condition of *L. nigrinus* adults $L_a(0)$ is taken directly from the data, while the initial conditions for *S. tsugae* adults $S_a(0)$ and the *A. tsugae*, *A* class, $A(0)$ are estimated. The mortality rates of *A. tsugae*, m_a, m_{as}, m_{aw} and m_s are taken from the Hemlock- Adelgid model in Chapter 2. We use the values found through the parameter estimation with the group II data. The remaining fixed parameters are taken from the literature as discussed in Section 3.3.

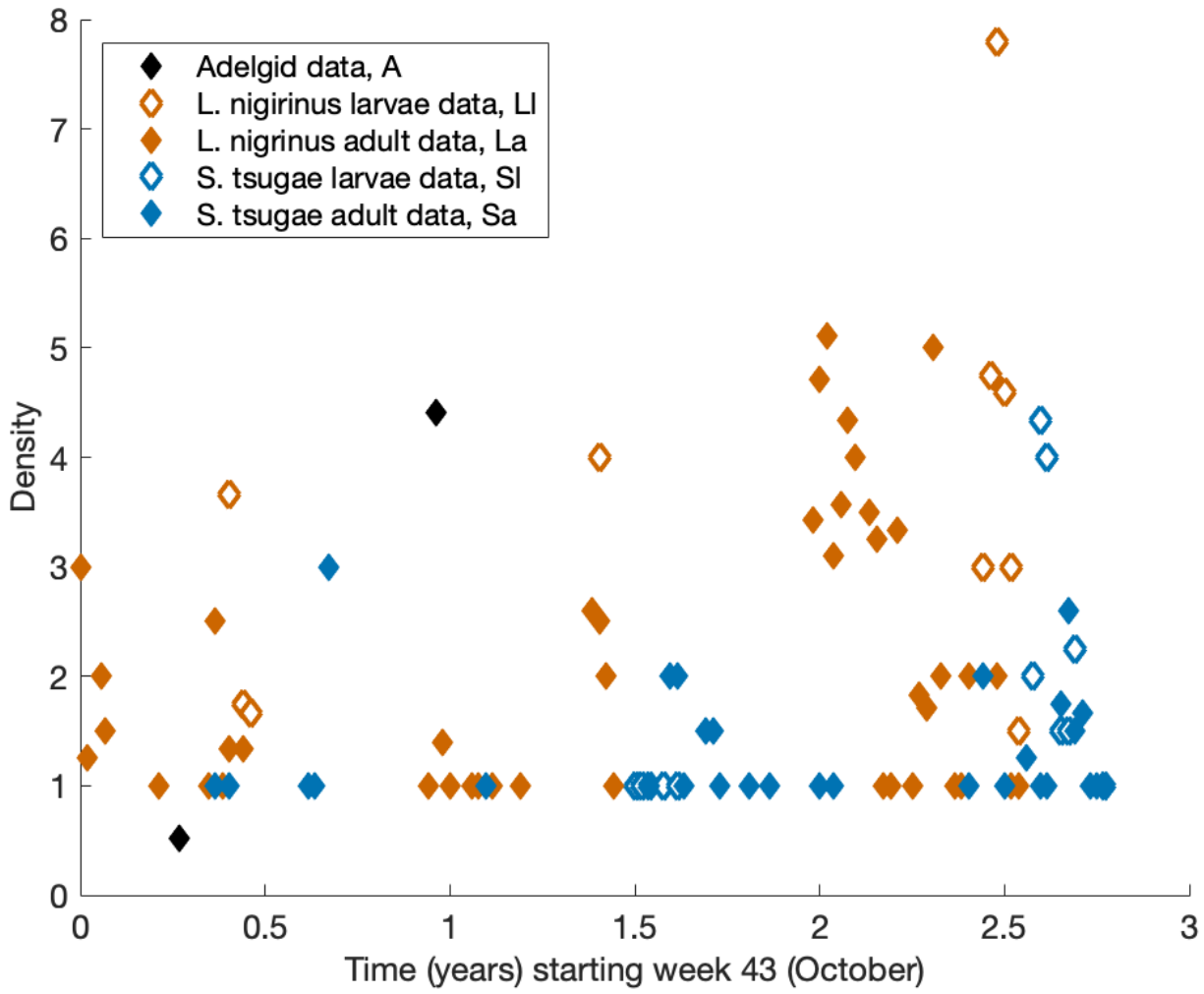


Figure 3.4: Field data of densities of *A. tsugae*, *L. nigrinus* larvae and adults, and *S. tsugae* larvae and adults used in parameter estimation for Adelgid-Predator model.

Table 3.3: Biological meaning and source, in parentheses, units and values for fixed parameter values in Adelgid-Predator model.

Name	Description	Units	Value
$L_a(0)$	the initial condition for *L. nigrinus* adults (directly from data)	*L. nigrinus*	3
c_s	transition rate from *S. tsugae* larvae, S_l, to *S. tsugae* adults, S_a (literature)	per week	0.25
m_a	*A. tsugae*, A, background seasonal mortality rate (Hemlock-Adelgid model parameter estimation)	per week	0.0613
m_{aw}	*A. tsugae*, A, winter seasonal mortality rate (Hemlock-Adelgid model parameter estimation)	per week	0.0739
m_{as}	*A. tsugae*, A, summer seasonal mortality rate (Hemlock-Adelgid model parameter estimation)	per week	0.0010
m_s	*A. tsugae*, A, mortality rate sexuparae mortality rate (Hemlock-Adelgid model parameter estimation)	per (*A. tsugae* $\cdot$ week)	0.0803
m_{ll}	minimum *L. nigrinus* larval mortality rate at high *A. tsugae* egg density (literature)	per week	0.087
m_{la}	minimum *L. nigrinus* adult mortality rate at high *A. tsugae* egg and *A. tsugae* density (literature)	per week	0.054
m_{sl}	*S. tsugae* larval mortality rate (literature)	per week	0.14
m_{sa}	*S. tsugae* adult mortality rate (literature)	per week	0.051
p_s	the proportion of *S. tsugae* adults from the previous year that survive overwinter (literature)	-	0.844

Table 3.4: Biological meaning, and units for estimated parameter values in Adelgid-Predator model.

Name	Description	Units
$A(0)$	initial condition of *A. tsugae*, A	*A. tsugae* per centimeter
$S_a(0)$	initial condition of *S. tsugae* adults, S_a	*S. tsugae*
f_{ll}, f_{la}, f_{sl}, f_{sa}	predation rate on *A. tsugae* eggs, A_e, by predator classes	per (predator · week)
g_{la}, g_{sl}, g_{sa}	predation rate on *A. tsugae*, A, by predator classes	per (predator · week)
r_a	the oviposition rate of *A. tsugae*	per week
r_l	the reproductive rate of *L. nigrinus*	-
r_s	the reproductive rate of *S. tsugae* in the absence of *A. tsugae*	-
c_a	transition rate from *A. tsugae* egg, A_e, to *A. tsugae*, A	per week
p_l	the proportion of the *L. nigrinus* larvae that survived aestivation to emerge as adults	-
d_l, d_a	these parameters control how much higher the *L. nigrinus* larvae (l), adult (a) death rate is when the *A. tsugae* population is small	*A. tsugae*
b	this parameter controls the maximum rate at which *S. tsugae* overwintering adults can lay eggs	centimeters per *A. tsugae*
h	this parameter controls how quickly the rate at which *S. tsugae* overwintering adults lay increases with increased *A. tsugae* population	centimeters per *A. tsugae*
z	*T. canadensis* proportion tips alive	-

We use the same parameter estimation method as in Chapter 2. We minimize, over a set of parameters, the objective function value that is the sum of squares of the relative error between the data and the model results. The objective function value is

$$\sqrt{\frac{\sum_{i=1}^{2}(A_{\text{data}}(s_i)-A_{\text{model}}(s_i))^2}{\sum_{i=1}^{2}(A_{\text{data}}(s_i))^2}}+\sqrt{\frac{\sum_{i=1}^{10}(Ll_{\text{data}}(t_i)-Ll_{\text{model}}(t_i))^2}{\sum_{i=1}^{10}(Ll_{\text{data}}(t_i))^2}}+$$

$$\sqrt{\frac{\sum_{i=1}^{46}La_{\text{data}}(u_i)-La_{\text{model}}(u_i))^2}{\sum_{i=1}^{46}(La_{\text{data}}(u_i))^2}}+\sqrt{\frac{\sum_{i=1}^{12}(Sl_{\text{data}}(v_i)-Sl_{\text{model}}(v_i))^2}{\sum_{i=1}^{12}(Sl_{\text{data}}(v_i))^2}}+$$

$$\sqrt{\frac{\sum_{i=1}^{30}(Sa_{\text{data}}(w_i)-Sa_{\text{model}}(w_i))^2}{\sum_{i=1}^{30}(Sa_{\text{data}}(w_i))^2}},$$

where s_i is the time of *A. tsugae* density data i, t_i is the time of *L. nigrinus* larvae density data i, u_i is the time of *L. nigrinus* adult density data i, v_i is the time of *S. tsugae* larvae density data i, and w_i is the time of *S. tsugae* adult density data i. We perform a run with approximately 300 starting points. The range from which parameter were estimated and the parameter estimation results are shown in Table 3.5. Model results and data are shown in Figure 3.5.

The model achieves a good fit to the data with objective function value 2.5136 and reasonable dynamics for the six classes. Over the three years of results, the *A. tsugae* densities increase, with high *A. tsugae* densities in the third year. There are two peaks in *A. tsugae* density each year, corresponding to reproduction of the two *A. tsugae* generations. In the first two years, the highest densities in *A. tsugae* eggs are associated with the sistens generation, whereas in the third year, the progrediens generation has a higher *A. tsugae* egg density. The density of the larval classes of both predators decrease rapidly. The reproductive rates of both *L. nigrinus* and *S. tsugae*, which impact the initial densities of the larval classes each year, are high as are the larval mortality rates which we determine through survival rates reported in the literature. Predator densities are relatively consistent between the years, but the densities of all predator classes are slowly increasing between the years. All predation rates, f_x and g_x are low. *Laricobius nigrinus* adults have the highest predation rate on *A. tsugae* eggs, with $f_{la} = 0.0224$.

Table 3.5: Parameters found through parameter estimation on the Adelgid-Predator model and the bounds on each parameter used in parameter estimation.

Parameter	Estimated value	Lower bound	Upper bound
objective function value	2.5136		
$A(0)$	1.4602	1	3
$S_a(0)$	0.5001	0.5	5
f_{ll}	0.0195	0.001	0.5
f_{la}	0.0224	0.001	0.5
f_{sl}	0.00121	0.001	0.5
f_{sa}	0.00222	0.001	0.5
g_{la}	0.0010	0.001	0.5
g_{sl}	0.00113	0.001	0.5
g_{sa}	0.00101	0.001	0.5
r_a	6.5676	0.5	7
r_l	14.9930	0.01	15
r_s	2.2295	0.01	15
c_a	0.0404	0.001	0.05
p_L	0.9000	0.1	0.9
d_l	0.7573	0.001	15
d_a	1.2593	0.001	15
b	64.5590	0.1	100
h	0.1001	0.1	20
z	0.9499	0.15	0.95

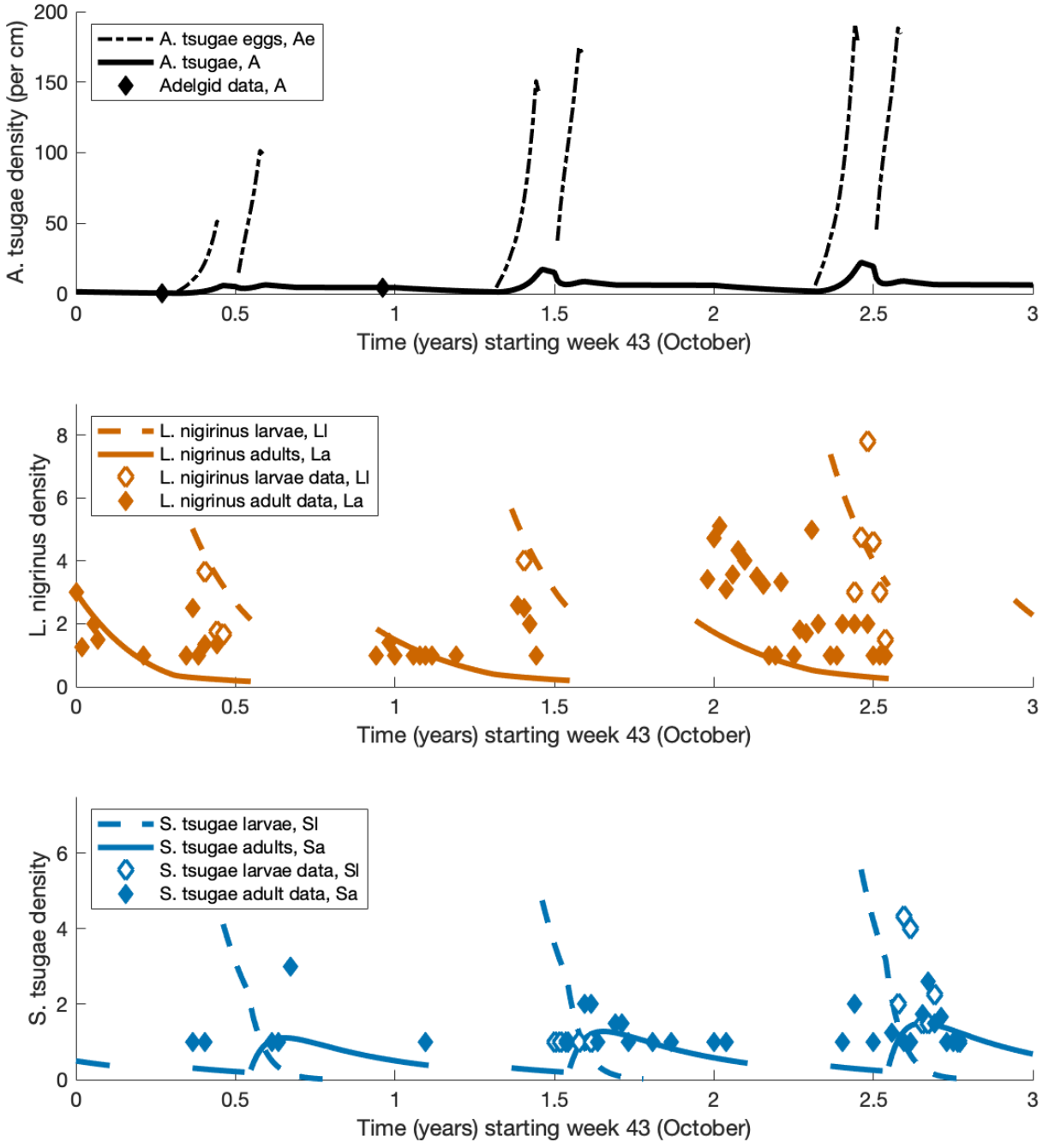
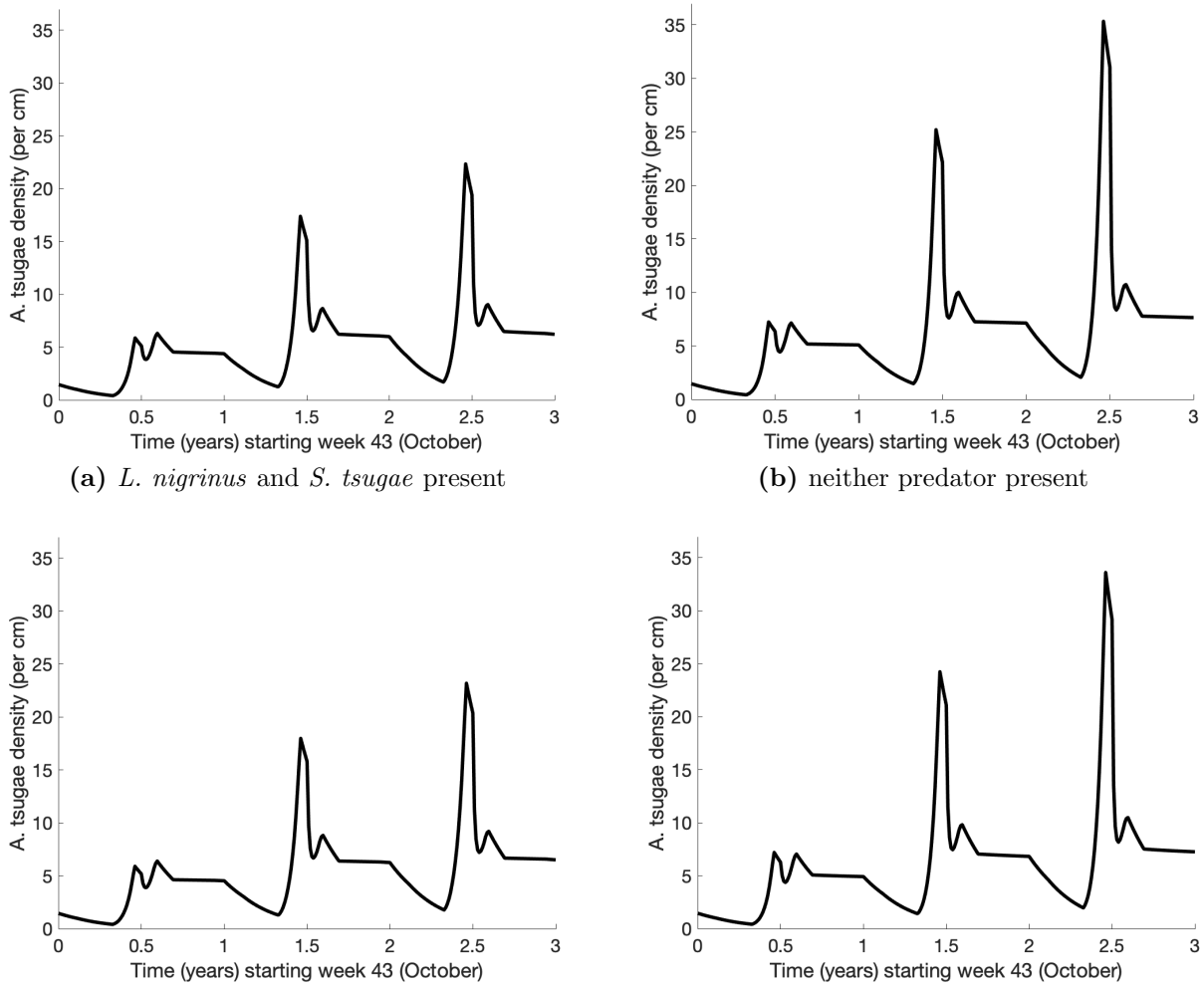


Figure 3.5: Parameter estimation results for Adelgid-Predator model. Density data are shown with diamonds and model output using parameter values from parameter estimation is plotted as curves. Immature life stages are plotted with dashed lines, and mature life stages are plotted with solid lines. Legends do not obscure data or model results on plots.

3.5 Model Results

Using the parameter values found through parameter estimation, we studied the dynamics of the system in the absence of one or both predator species. The dynamics of the non-egg *A. tsugae* class density under different predation scenarios are shown in Figure 3.6. We focus on the density of this class since it is the class that impacts *T. canadensis* health, and increased *A. tsugae* density in the absence of predators will cause more severe damage. The qualitative dynamics remain the same in the presence or absence of each species of predator. In all scenarios tested, the *A. tsugae* densities increase over the three years, and there are two peaks in the *A. tsugae* density each year corresponding to the beginning of each generation of *A. tsugae*. The density of the progrediens generation is higher in the second and third year for all predation scenarios. However, if one or both predators are removed from the system, the peak *A. tsugae* densities are higher. Even in the presence of predators, the peak *A. tsugae* density seen in these simulations are high compared to field observations. The variation and magnitude of *A. tsugae* densities is also discussed in Section 2.4. The highest *A. tsugae* densities are seen in the absence of both predators, and the lowest densities are seen in the presence of both predators. However, the second lowest maximum densities are seen in the presence of *L. nigrinus*. Thus, at the population levels produced by the estimated parameter values and initial conditions in the model, *L. nigrinus* appears to be a more effective predator. Despite the variation in seasonality between the two predator species, predation acting at different times of the year does not impact the yearly cycles in *A. tsugae* density much. Although not shown in this figure, the absence of the other predator species does not impact the dynamics or densities of a predator significantly, despite the differences in the *A. tsugae* densities.

We also varied the value of z, the parameter representing the fixed *T. canadensis* proportion tips alive for the Adelgid-Predator model. Using the rest of the estimated parameter values, we varied z and studied the dynamics of the three species. The results are show in Figures 3.7-3.10 with dashed lines for immature life stages (*A. tsugae* eggs, *L. nigrinus* larvae and *S. tsugae* larvae) and solid lines for mature life stages (non-egg *A. tsugae*, *L. nigrinus* adults and *S. tsugae* adults). At low *T. canadensis* proportion tips alive, for



(a) *L. nigrinus* and *S. tsugae* present

(b) neither predator present

(c) only *L. nigrinus* present

(d) only *S. tsugae* present

Figure 3.6: Simulation results of the Adelgid-Predator model using parameter values from parameter estimation, but different scenarios of the presence or absence of the two predator species. The density of the non-egg *A. tsugae* class is show over three years.

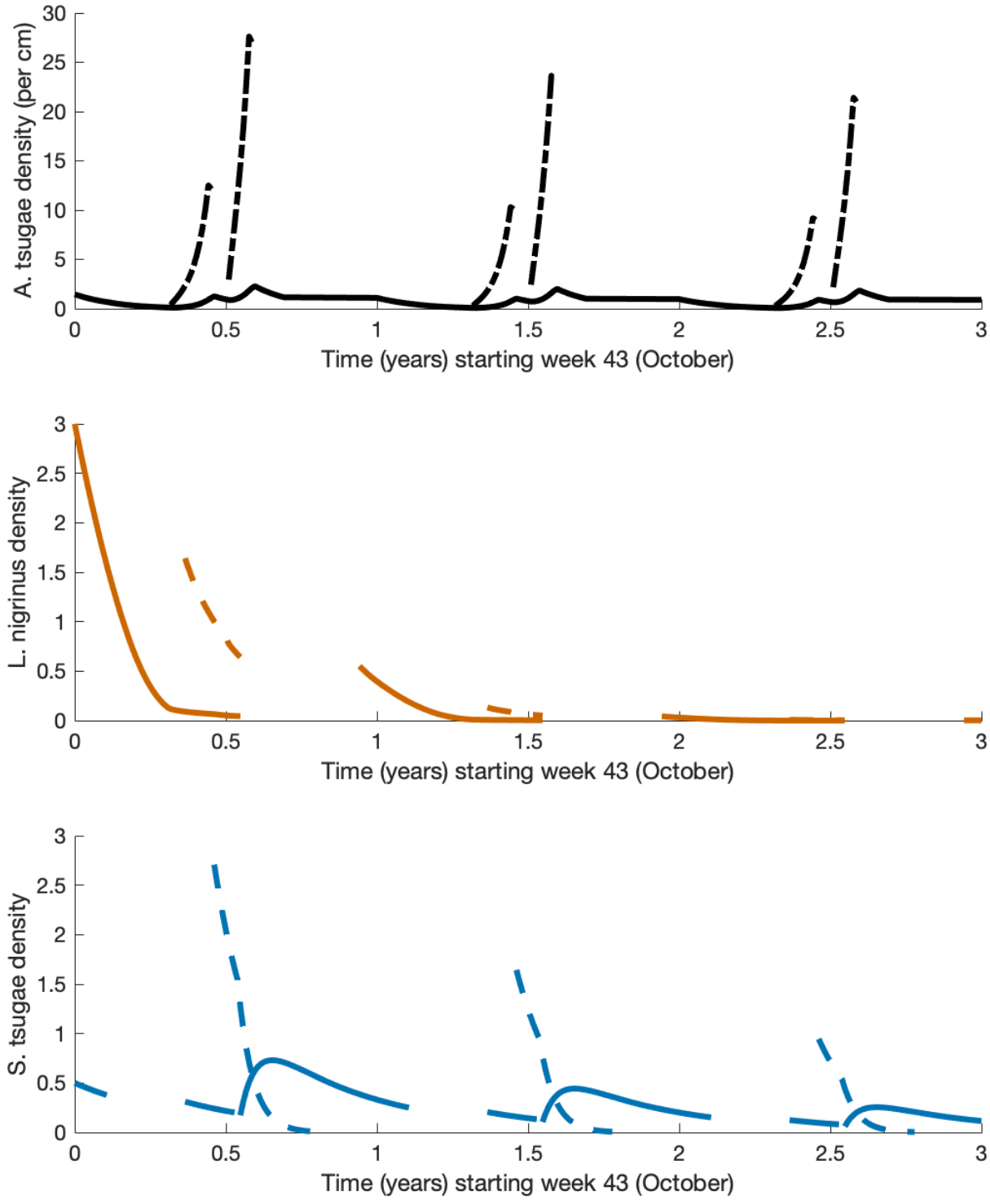


Figure 3.7: Simulation results with proportion tips alive set at $z = 0.45$. Dashed curves represent the immature life stage (*A. tsugae* eggs, predator larvae) and solid curves represent the mature class (non-egg *A. tsugae*, predator adults) for each species.

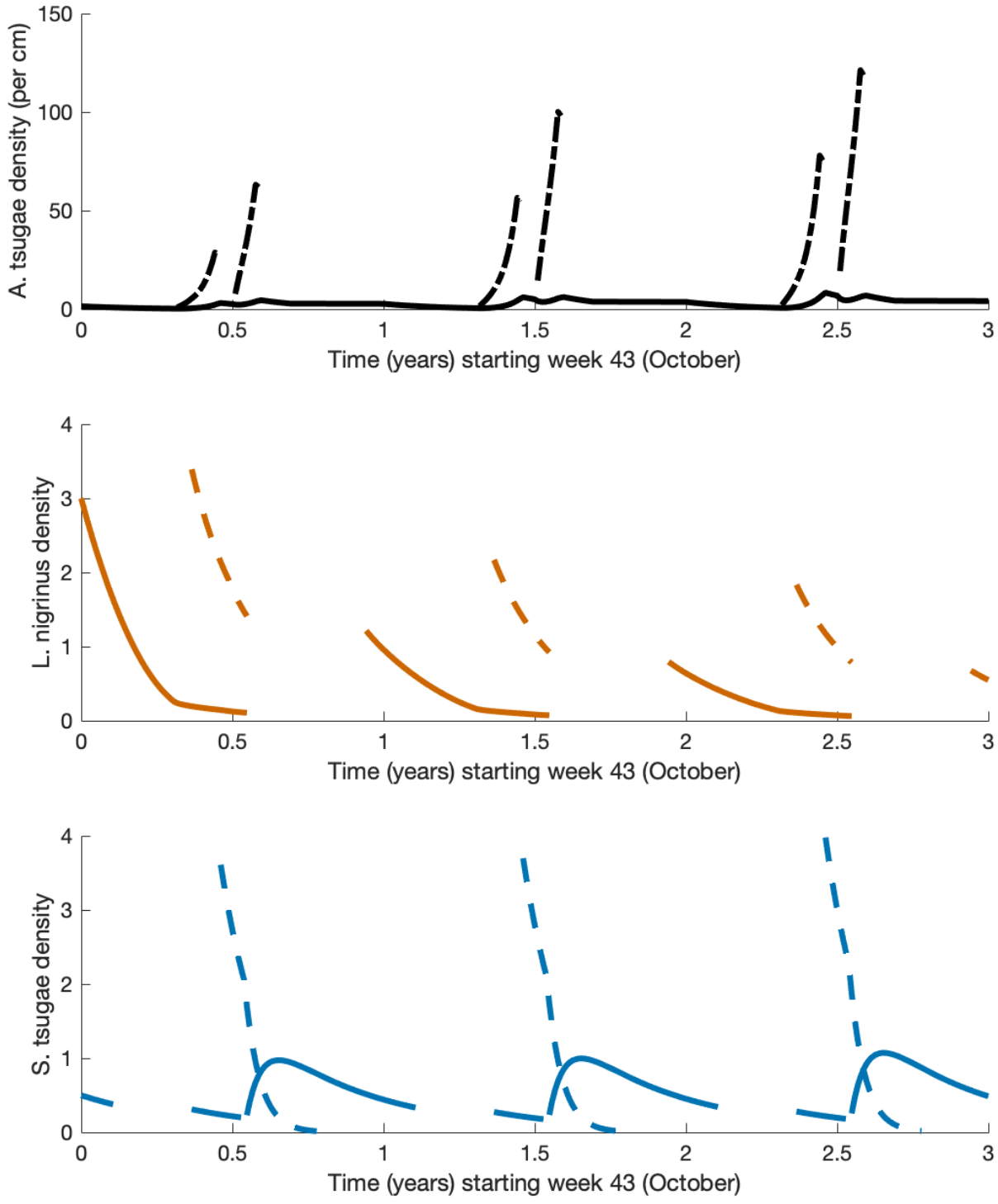


Figure 3.8: Simulation results with proportion tips alive set at $z = 0.65$. Dashed curves represent the immature life stage (*A. tsugae* eggs, predator larvae) and solid curves represent the mature class (non-egg *A. tsugae*, predator adults) for each species.

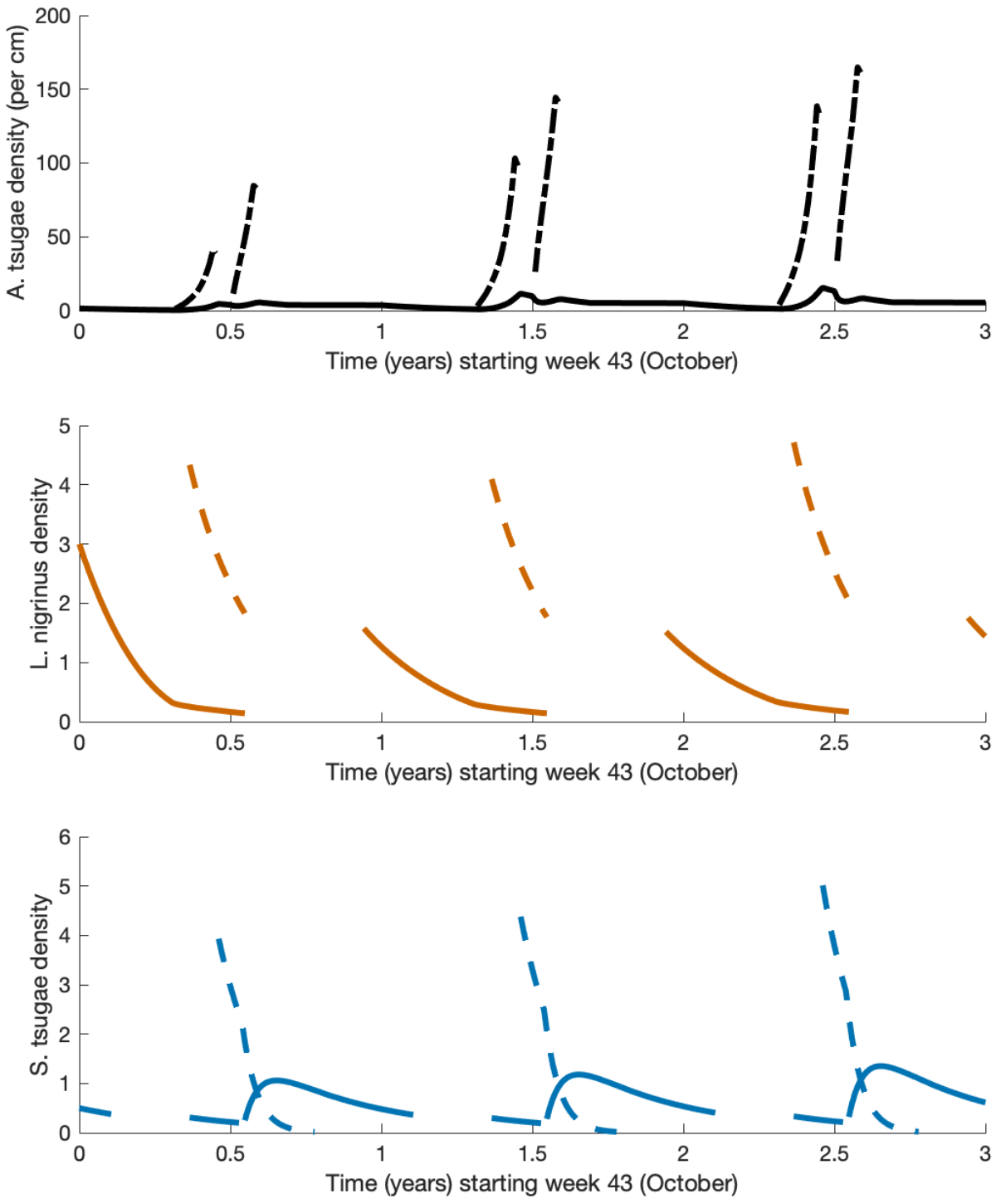


Figure 3.9: Simulation results with proportion tips alive set at $z = 0.80$. Dashed curves represent the immature life stage (*A. tsugae* eggs, predator larvae) and solid curves represent the mature class (non-egg *A. tsugae*, predator adults) for each species.

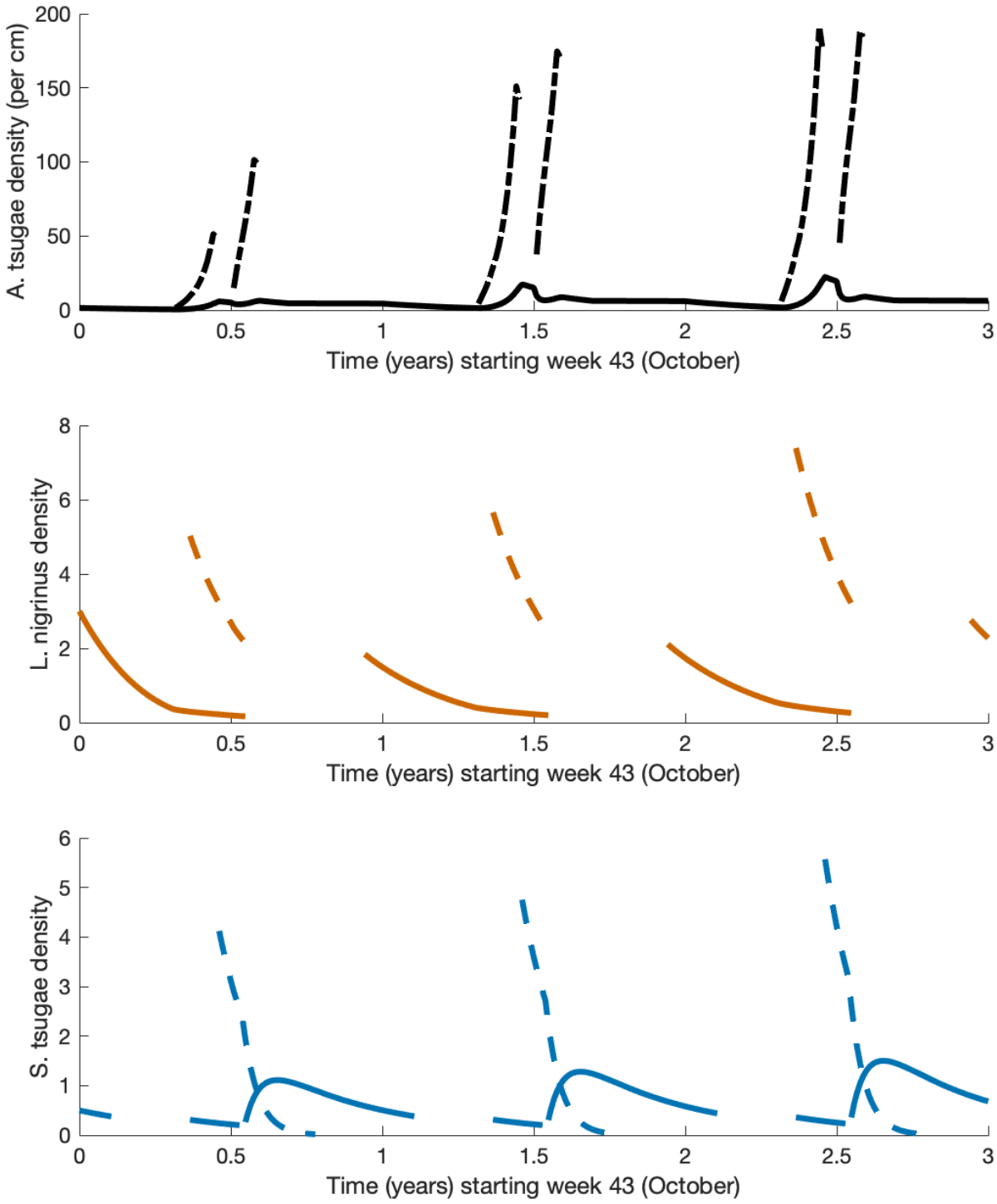


Figure 3.10: Simulation results with proportion tips alive set at $z = 0.95$. Dashed curves represent the immature life stage (*A. tsugae* eggs, predator larvae) and solid curves represent the mature class (non-egg *A. tsugae*, predator adults) for each species.

example $z = 0.45$, as shown in Figure 3.7, the increased mortality rate of *A. tsugae* produces lower *A. tsugae* densities which do not support predator populations and the density of all three species decreases over the three years studied. At lower values of z, representing unhealthy trees, the decline in densities of *A. tsugae*, *L. nigrinus*, and *S. tsugae* occurs more quickly. At higher z values, for example $z = 0.65$ proportion tips alive, as shown in Figure 3.8, *A. tsugae* densities increase over the three years, as do *S. tsugae* densities, but *L. nigrinus* densities decline. At the parameter values and initial conditions tested here within the first three years, a higher density of *A. tsugae* is necessary to allow the *L. nigrinus* density to increase. Whereas, a lower *A. tsugae* density will support growth in *S. tsugae* densities. At higher *T. canadensis* proportion tips alive, all three species increase in density over the 3 years studied here. For example, at $z = 0.80$ proportion tips alive, as shown in Figure 3.9, despite a decline in the *L. nigrinus* adult density, by the third year, the *L. nigrinus* larval density is larger than in the previous years. At high proportion tips alive, like $z = 0.95$, close to the estimated z value of 0.9499, as shown in Figure 3.10, all species are increasing in density, and *L. nigrinus* densities are higher than the *S. tsugae* densities.

3.6 Conclusions

We develop a novel model of the interaction of *A. tsugae* and two biological control organisms, *L. nigrinus* and *S. tsugae*. The model includes organism specific seasonality, *A. tsugae* density dependence, *A. tsugae* density dependent mortality of the *L. nigrinus* classes and *A. tsugae* density dependent reproduction of *S. tsugae*. Through parameter estimation, we achieve a good fit to the data and the model results exhibit biologically reasonable population dynamics. The maximum densities of both classes of *L. nigrinus* are higher than the maximum densities of the *S. tsugae* classes, but the model results have a lower *L. nigrinus* adult density than most of *L. nigrinus* adult density data in the third year. The *L. nigrinus* adult class in the model in the third year appears to be the most different from the corresponding density data when the data and model results are plotted together. The high minimum morality rate of the *L. nigrinus* larvae $m_{ll} = 0.087$ (with the total mortality rate being a decreasing function of *A. tsugae* density) combined with the small number of

L. nigrinus larval density data may be contributing to the low *L. nigrinus* adult densities. We determined the minimum *L. nigrinus* larval mortality rate from a lab study, which may not represent the conditions or true mortality rate in the field. Little is known about the coexistence behavior of *L. nigrinus* and *S. tsugae* or the joint impact of these two predators on *A. tsugae* populations in natural settings [23]. Based on scenarios of the presence or absence of the predators, according to our model results, *L. nigrinus* appear to be a more effective predator than *S. tsugae*. However, as the study by Wiggins et al. focused on the presence and seasonality of predators, we have only two *A. tsugae* density data, within the first year of the study [68, 67]. Thus, we place more emphasis on the coexistence of the predators and the population dynamics of *L. nigrinus* and *S. tsugae* established on the same tree, instead of the joint impact of predation by these two species. Further study of multiple biological control predators in the field and of the numerical impact on *A. tsugae* densities would be useful in evaluating our model results to assess if we have underestimated predation rates.

To our knowledge this is the first mathematical model to represent the interacting population dynamics of *A. tsugae* densities and multiple biological control organisms with the mechanisms thought to be biologically important including seasonality. This work makes significant progress from existing models of biocontrol predators and *A. tsugae* densities. Moore et al. included a biological control organism in their modified three species logistic predator prey system of differential equations model that was a part of their hierarchical bioeconomic model, but did they did not represent species specific mechanism, stage structure, or seasonality [53]. The Elkinton et al. difference equation model includes the impact of predation by *L. nigrinus* on *A. tsugae* eggs using field data from Jubb et al. as described by Crandall et al [13, 29, 9]. This model includes a time step for each generation but not more specific seasonality details. Elkinton et al. do not represent the density of *L. nigrinus* or the impact of a changing *A. tsugae* density on *L. nigrinus* or the predation rate of *L. nigrinus*, but instead use a single predation rate, the mean proportion of progrediens generation ovisacs predated by *L. nigrinus* larvae, as determined by a large scale field study by Jubb et al. [9]. They report that *A. tsugae* density dependence counteracts the impact of *L. nigrinus* predation on *A. tsugae* eggs, in both the model and field results

and argue that multiple predators acting on both generation of *A. tsugae* may be necessary to effectively control *A. tsugae* and limit damage to *T. canadensis*. Our work includes the density dependence and seasonality necessary to further study the result of the interaction of predation by multiple predator species active at different times of the year and *A. tsugae* density dependence.

Future research could include connecting our Hemlock-Adelgid model and Adelgid-Predator model to develop a four species model of *T. canadensis* proportion tips alive, and the densities of *A. tsugae*, *L. nigrinus*, and *S. tsugae*. With a four species model, we would be able to assess how effective biological control efforts may be by determining their impact of *T. canadensis* health. The Adelgid-Predator model could also be adapted to other biological control species by modifying the species specific seasonality and mechanisms in the model. Current rearing and releasing efforts have moved away from *S. tsugae* to include another *Laricobius* species, *Laricobius osakensis* as well as *Leucopis* species [39].

Bibliography

[1] S. T. Brantley, A. E. Mayfield III, R. M. Jetton, C. F. Miniat, D. R. Zietlow, C. L. Brown, and J. R. Rhea, *Elevated light levels reduce hemlock woolly adelgid infestation and improve carbon balance of infested eastern hemlock seedlings*, Forest Ecology and Management, 385 (2017), pp. 150–160. 4

[2] E. E. Butin, N. P. Havill, J. S. Elkinton, and M. E. Montogomery, *Feeding preference of three lady beetle predaotrs of the hemlock woolly adelgid (Homoptera: Adelgidae)*, Journal of Economic Entomology, 97(5) (2004), pp. 1635–1641. 49

[3] C. Cheah, *Sasajiscmnus (=Pseudoscymnus) tsugae, a ladybeetle from Japan*, in Implementation and Status of Biological Control of the Hemlock Woolly Adelgid, Tech. Rep. FHTET-2011-04, B. Onken and R. Reardon, eds., United States Department of Agriculture, Forest Service, Forest Health Technology Enterprise Team, 180 Canfield Street, Morgantown, WV 26505, December 2011, pp. 43–52. 49

[4] C. A. S.-J. Cheah, *Predicting hemlock woolly adelgid winter mortality in connecticut forests by climate divisions*, Northeastern Naturalist, 24(Special Issue 7) (2017), pp. B90–B118. 60

[5] C. A. S.-J. Cheah and M. S. McClure, *Life history and development of Pseudoscymnus tsugae (Coleoptera: Coccinellidae), a new predator of the hemlock woolly adelgid (Homoptera: Adelgidae)*, Environmental Entomology, 27(6) (1998), pp. 1532–1536. 19, 64

[6] C. A. S.-J. Cheah and M. S. McClure, *Seasonal synchrony of life cycles between the exotic predator, Pseudoscymnus tsugae (Coleoptera: Coccinellidae) and its prey, the hemlock woolly adelgid Adelges tsugae (Homoptera: Adelgidae)*, Agricultural and Forest Entomology, 2 (2000), pp. 241–251. 63

[7] J. Colbert and B. Onken, *Hemlock woolly adelgid impact assessment: How big of a threat is this critter?*, in Proceedings U.S. Department of Agriculture Interagency Research Forum on Gypsy Moth and Other Invasive Species 2001, S. L. C. Fosbroke and K. W. Gottschalk, eds., United States Department of Agriculture, Forest Service, Northeastern Research Station, pp. 33–38. 19

[8] J. Colbert, M. Seese, and B. Onken, *Hemlock woolly adelgid impact assessment survey*, in Symposium on the Hemlock Woolly Adelgid in Eastern North America, B. Onken, R. Reardon, and J. Lashomb, eds., N. J. Agricultural Experiment Station, Rutgers- The State University of New Jersey, pp. 323–328. 16

[9] R. S. Crandall, C. S. Jubb, A. E. Mayfield III, B. Thompson, T. J. McAvoy, S. M. Salom, and J. S. Elkinton, *Rebound of Adelges tsugae spring generation following predation on overwintering generation ovisacs by the introduced predator Laricobius nigrinus in the eastern United States*, Biological Control, 145 (2020), p. 104264. 46, 94

[10] I. K. Deal, *Life history of hemlock woolly adelgid, Adelges tsugae Annand, on eastern hemlock, Tsuga canadensis (L.) Carriere, in the southern Appalachians and assessment of egg releases of Sasajiscymnus tsugae (Sasaji and Mcclure) for its management*, Master's thesis, University of Tennessee, Knoxville, Tennessee, May 2016. 22, 57, 59, 60

[11] J.-C. Domec, L. N. Rivera, J. S. Kind, I. Peszlen, F. Hain, B. Smith, and J. Frampton, *Hemlock woolly adelgid (Adelges tsugae) infestation affects water and carbon relations of eastern hemlock (Tsuga canadensis) and Carolina hemlock (Tsuga caroliniana)*, New Phytologist, 199 (2013), pp. 452–463. 46

[12] J. S. Elkinton. Personal communication, 2020. 46

[13] J. S. Elkinton, R. T. Trotter, and A. F. Paradis, *Simulations of population dynamics of hemlock woolly adelgid and potential impact of biological control agents*, in Implementation and Status of Biological Control of the Hemlock Woolly Adelgid, Tech. Rep. FHTET-2011-04, B. Onken and R. Reardon, eds., United States Department of Agriculture, Forest Service, Forest Health Technology Enterprise Team, 180 Canfield Street, Morgantown, WV 26505, December 2011, pp. 15–24. 46, 94

[14] A. M. Ellison, D. A. Orwig, M. C. Fitzpatrick, and E. L. Preisser, *The past, present, and future of the hemlock woolly adelgid (Adelges tsugae) and its ecological*

interactions with eastern hemlock (Tsuga canadensis) forests, Insects, 9(4) (2018), p. 172. 46

[15] A. K. Eschtruth, N. L. Cleavitt, J. J. Battles, R. A. Evans, and T. J. Fahey, *Vegetation dynamics in declining eastern hemlock stands: 9 years of forest respondse to hemlock woolly adelgid infestation*, Canadian Journal of Forest Research, 36 (2006), pp. 1435–1450. 16

[16] R. A. Evans, E. Johnson, J. Shreiner, A. Ambler, J. Battles, N. Cleavitt, T. Fahey, J. Sciascia, and E. Pehek, *Potential impacts of hemlock woolly adelgid (Adelges tsugae) on eastern hemlock (Tsuga canadensis) ecosystems*, in Proceedings of the First Hemlock Woolly Adelgid Review, S. M. Salom, T. C. Tigner, and R. C. Reardon, eds., U.S. Department of Agriculture Forest Service, Forest Health Technology Enterprise Team,, pp. 42–57. 3

[17] M. J. Fischer, N. P. Havill, C. C. Brewster, G. A. Davis, S. M. Salom, and L. T. Kok, *Field assessment of hybridization between Laricobius nigrinus and L. rubidus, predators of adelgidae*, Biological Control, 82 (2015), pp. 1–6. 50

[18] R. W. Flowers, S. M. Salom, and L. T. Kok, *Competitive interactions among two specialist predators and a generalist predator of hemlock woolly adelgid, Adelges tsugae (Homoptera: Adelgidae), in the laboratory*, Biological Control– Parasitoids and Predators, 34(3) (2005), pp. 664–675. 50, 60

[19] R. W. Flowers, S. M. Salom, and L. T. Kok, *Competitive interactions among two specialist predators and a generalist predator of hemlock woolly adelgid, Adelges tsugae (Hemiptera: Adelgidae) in south-western Virginia*, Agricultural and Forest Entomology, 8 (2006), pp. 253–262. 50, 60, 61, 64

[20] H. W. Garris, T. H. Settle, J. E. Crossman, G. Stephen J, and S. L. Michaels, *Combined effects of hemlock woolly adelgid (Adelges tsugae) infestation and treatment with imidacloprid on eastern hemlock (Tsuga canadensis) leaf radiometry*, Journal of Forestry, 117(4) (2019), pp. 340–350. 7

[21] R. M. Godman and K. Lancaster, *Tsuga canadensis (L.) Carr. eastern hemlock*, Tech. Rep. Agriculture Handbook 654., United States Department of Agriculture, Forest Service, Washington, DC, 1990. 3

[22] D. R. Gray and S. M. Salom, *Biology of the hemlock woolly adelgid in the southern Appalachians*, in Proceedings of the First Hemlock Woolly Adelgid Review, S. M. Salom, T. C. Tigner, and R. C. Reardon, eds., U.S. Department of Agriculture Forest Service, Forest Health Technology Enterprise Team,, pp. 26–35. 19, 59

[23] A. Hakeem, J. F. Grant, G. J. Wiggins, P. L. Lambdin, and J. R. Rhea, *Establishment and coexistence of two predators, Laricobius nigrinus and Sasajiscymnus tsugae, introduced against hemlock woolly adelgid on eastern hemlock*, Biocontrol Science and Technology, 21(6) (2011), pp. 687–691. 50, 94

[24] N. Havill, M. Montgomery, and M. Keena, *Hemlock woolly adelgid and its hemlock hosts: A global perspective*, in Implementation and Status of Biological Control of the Hemlock Woolly Adelgid, Tech. Rep. FHTET-2011-04, B. Onken and R. Reardon, eds., United States Department of Agriculture, Forest Service, Forest Health Technology Enterprise Team, 180 Canfield Street, Morgantown, WV 26505, December 2011, pp. 3–14. 4, 59

[25] N. P. Havill, G. Davis, D. L. Mausel, J. Klein, R. McDonald, C. Jones, M. Fischer, S. Salom, and A. Caccone, *Hybridization between a native and introduced predator of adelgidae: An unintended result of classical biological control*, Biological Control, 63 (2012), pp. 359–369. 50, 53

[26] N. P. Havill, L. C. Vieira, and S. M. Salom, *Biology and control of hemlock woolly adelgid*, Tech. Rep. FHTET-2014-05, United States Department of Agriculture, Forest Service, Forest Health Technology Enterprise Team, 180 Canfield Street, Morgantown, WV 26505, April 2014. 3, 4, 5, 6, 16, 19, 49, 50, 57

[27] P.-F. Hsieh and Y. Sibuya, *Basic Theory of Ordinary Differential Equations*, Springer Science+Business Media, New York, NY, 1999. 23

[28] S. V. Joseph, A. E. Mayfield III, M. J. Dalusky, C. Asaro, and C. W. Berisford, *Phenology of the hemlock woolly adelgid (Hemiptera: Adelgidae) in northern Georgia*, Journal of Entomological Science, 46(4) (2011), pp. 315–324. 59

[29] C. S. Jubb, A. R. Heminger, A. E. Mayfield III, J. S. Elkinton, G. J. Wiggins, J. F. Grant, J. A. Lombardo, T. J. McAvoy, R. S. Crandall, and S. M. Salom, *Impact of the introduced predator, Laricobius nigrinus, on ovisacs of the overwintering generation of hemlock woolly adelgid in the eastern United States*, Biological Control, 143 (2030), p. 104180. 60, 94

[30] T. Kantola, J. L. Tracy, P. Lyytikäinen-Saarenmaa, H. Saarenmaa, R. N. Coulson, A. Trabucco, and M. Holopainen, *Hemlock woolly adelgid niche models from the invasive eastern North American range with projections to native ranges and future climates*, iForest, 12 (2019), pp. 149–159. 46

[31] M. A. Lewis, S. V. Petrovskii, and J. R. Potts, *The Mathematics Behind Biological Invasions*, Springer International Publishing, Switzerland, 2016. 1

[32] S. Limbu, M. A. Keena, and M. C. Whitmore, *Hemlock woolly adelgid (Hempitera: Adelgidae): A non-native pest of hemlocks in eastern north america*, Journal of Integrated Pest Management, 9(1) (2018), pp. 1–16. 57

[33] MathWorks, *Constrained nonlinear optimization algorithms*. https://www.mathworks.com/help/optim/ug/constrained-nonlinear-optimization-algorithms.html, 2021. Accessed: 2021-04-04. 2

[34] MathWorks, *fmincon*. https://www.mathworks.com/help/optim/ug/fmincon.html, 2021. Accessed: 2021-04-04. 2

[35] MathWorks, *How GlobalSearch and MultiStart work*. https://www.mathworks.com/help/gads/how-globalsearch-and-multistart-work.html, 2021. Accessed: 2021-04-04. 2

[36] MathWorks, *RandomStartPointSet*. https://www.mathworks.com/help/gads/randomstartpointset.html, 2021. Accessed: 2021-04-04. 2

[37] D. L. Mausel, G. A. Davis, A. S. Lamb, G. M. G. Zilahi-Balogh, L. T. Kok, and S. M. Salom, *Laricobius nigrinus fender (Coleoptera: Derodontidae)*, in Implementation and Status of Biological Control of the Hemlock Woolly Adelgid, Tech. Rep. FHTET-2011-04, B. Onken and R. Reardon, eds., United States Department of Agriculture, Forest Service, Forest Health Technology Enterprise Team, 180 Canfield Street, Morgantown, WV 26505, December 2011, pp. 77–89. 54

[38] D. L. Mausel, S. M. Salom, L. T. Kok, and J. G. Fidgen, *Propagation, synchrony, and impact of introduced and native Laricobius spp, (Coleoptera: Derodontidae) on hemlock woolly adelgid in Virginia*, Biological Control–Parasitoids and Predators, 37(6) (2008), pp. 1498–1507. 19, 62

[39] A. E. Mayfield III, S. M. Salom, K. Sumpter, T. McAvoy, N. F. Schneeberger, and R. Rhea, *Integrating chemical and biological control of the hemlock woolly adelgid: A resource manager's guide*, Tech. Rep. FHAAST-2018-04, United States Department of Agriculture, Forest Service, Forest Health Assessment and Applied Sciences Team, 180 Canfield Street, Morgantown, WV 26505, January 2020. 5, 7, 47, 49, 50, 95

[40] T. McAvoy. Unpublished data, 2015. 1, 7

[41] T. McAvoy. Personal communication, 2021. 7

[42] T. McAvoy, W. T. Mays, S. M. Salom, and L. T. Kok, *Impact of imidacloprid on hemlock woolly adelgid (Adelges tsugae) and water quality at Mt. Lake, Virginia*, in Third Symposium on Hemlock Woolly Adelgid in the Eastern United States, B. Onken and R. Reardon, eds., Forest Health Technology Enterprise Team, pp. 324–334. 1, 7, 16

[43] T. McAvoy, R. Saint-Amant, J. Foley, R. Mays, A. Dechaine, and S. M. Salom, *Laricobius species (Coleoptera: Derodontidae) predation, fecundity, and impact on hemlock wooley adelgid (in preparation)*. 2021. 54

[44] M. S. McClure, *Biology and control of hemlock woolly adelgid*, Tech. Rep. Bulletin 851, Connecticut Agricultural Experiment Station, Box 1106 New Haven, CT 06504, December 1987. 59

[45] M. S. McClure, *Evidence of a polymorphic life cycle in the hemlock woolly adelgid, Adelges tsugae (Homoptera: Adelgidae)*, Annals of the Entomological Society of America, 82(1) (1989), pp. 50–54. 4, 59, 60

[46] M. S. McClure, *Role of wind, birds, deer, and humans in the dispersal of hemlock woolly adelgid (Homoptera: Adelgidae)*, Environmental Entomology, 19(1) (1990), pp. 34–43. 4

[47] M. S. McClure, *Density-dependent feedback and population cycles in Adelges tsugae (Homoptera: Adelgidae) on Tsuga canadensis*, Environmental Entomology, 20(1) (1991), pp. 258–264. 3, 4, 6, 19, 31, 49

[48] M. S. McClure, *Using natural enemies from Japan to control hemlock woolly adelgid*, Environmental Entomology, 47(2) (1995), pp. 5–7. 60

[49] M. S. McClure and C. A. S.-J. Cheah, *Released Japanese ladybugs are multiplying and killing hemlock woolly adelgids*, Frontiers of Plant Science, 50(2) (1998), pp. 6–8. 49

[50] M. S. McClure and C. A. S.-J. Cheah, *Reshaping the ecology of invading populations of hemlock woolly adelgid, Adelges tsugae (Homoptera:Adelgidae), in eastern North America*, Biological Invasions, 1 (1999), pp. 247–254. 4

[51] A. M. Mech, *Abiotic and biotic factors influencing eastern hemlock (Tsuga canadensis) health and hemlock wooly adelgid (Adelges tsugae) success in the southern Appalachian mountains*, PhD thesis, University of Georgia, Athens, Georgia, May 2015. 3, 17, 24

[52] M. E. Montgomery, S. E. Bentz, and R. T. Olsen, *Evaluation of hemlock (Tsuga) species and hybirds for resistance to Adelges tsugae (Hemiptera: Adelgidae) using artificial infestation*, Journal of Economic Entomology, 102(3) (2009), pp. 1247–1254. 4

[53] C. C. Moore, D. J. Phaneuf, and W. N. Thurman, *A Bayesian bioeconometric model of invasive species control: The case of the hemlock woolly adelgid*, Environmental and Resource Economics, 50 (2011), pp. 1–26. 46, 94

[54] W. W. Murdoch, C. J. Briggs, and T. R. Collier, *Biological control of insects: implications for theory in population ecology*, in Insect Populations: In theory and in practice, J. P. Dempster and I. F. G. McLean, eds., Kluwer Academic Publishers, Dordrecht, 1998, pp. 167–186. 1, 3

[55] B. Onken and R. Reardon, *Implementation and status of biological control of the hemlock woolly adelgid*, Tech. Rep. FHTET-2011-04, United States Department of Agriculture, Forest Service, Forest Health Technology Enterprise Team, 180 Canfield Street, Morgantown, WV 26505, December 2011. 5

[56] A. F. Paradis, *Population dynamics of the hemlock woolly adelgid (Hemiptera, Adelgidae)*, PhD thesis, University of Massachusetts, Amherst, Massachusetts, September 2011. 3, 6, 24, 31

[57] P. Parkman. Personal communication, 2018. 62

[58] J. W. Quimby, *Value and importance of hemlock ecosystems in the eastern united states*, in Proceedings of the First Hemlock Woolly Adelgid Review, S. M. Salom, T. C. Tigner, and R. C. Reardon, eds., U.S. Department of Agriculture Forest Service, Forest Health Technology Enterprise Team,, pp. 1–8. 3

[59] H. Sasaji and M. S. McClure, *Description and distribution of Pseudoscymnus tsugae sp. nov. (Coleoptera: Coccinellidae), an important predator of hemlock woolly adelgid in Japan*, Annals of the Entomological Society of America, 90(5) (1997), pp. 563–568. 49

[60] M. E. Schomaker, S. J. Zarnoch, W. A. Bechtold, D. J. Latelle, W. G. Burkman, and S. M. Cox, *Crown-condition classification: A guide to data collection and analysis*, Tech. Rep. SRS-102, United States Department of Agriculture, Forest

Service, Southern Research Station, 200 W.T. Weaver Blvd. Asheville, NC 28804, May 2007. 8, 16

[61] H. L. Smith, *Monotone Dynamical Systems: An Introduction to the Theory of Competitive and Cooperative Systems*, American Mathematical Society, Providence, RI, 1995. 23

[62] E. M. Sussky and J. S. Elkinton, *Density-dependent survival and fecundity of hemlock woolly adelgid (Hemiptera: Adelgidae)*, Environmental Entomology, 43(5) (2014), pp. 1157–1167. 19

[63] E. M. Sussky and J. S. Elkinton, *Survival and near extinction of hemlock woolly adelgid (Hemiptera: Adelgidae) during summer aestivation in a hemlock plantation*, Environmental Entomology, 44(1) (2015), pp. 153–159. 19

[64] P. C. Tobin, R. M. Turcotte, and D. A. Snider, *When one is not necessarily a lonely number: Initial colonization dynamics of Adelges tsugae on eastern hemlock Tsuga candensis*, Biological Invasions, 15 (2013), pp. 1925–1932. 19

[65] R. E. Webb, J. R. Frank, and R. Michael J, *Eastern hemlock recovery from hemlock woolly adelgid damage following imidacloprid therapy*, Journal of Arboriculture, 45(6) (2016), pp. 298–302. 7

[66] A. S. Weed, J. S. Elkinton, and N. K. Lany, *Density-dependent recruitment and diapause in the spring-feeding generation of hemlock woolly adelgid (Hemiptera: Adelgidae) in western North America*, Environmental Entomology, 45(6) (2016), pp. 1352–1359. 19

[67] G. Wiggins. Unpublished data, 2013. 1, 50, 80, 94

[68] G. J. Wiggins, J. F. Grant, J. R. Rhea, A. E. Mayfield III, A. Hakeem, P. L. Lambdin, and A. B. L. Galloway, *Emergence, seasonality, and hybridization of Laricobius nigrinus (Coleoptera: Derodontidae), an introduced predator of hemlock woolly adelgid (Hemiptera: Adelgidae), in the Tennessee Appalachians*, Environmental Entomology, 45(6) (2016), pp. 1371–1378. vii, 1, 50, 51, 52, 53, 62, 80, 94

[69] G. M. G. Zilahi-Balogh, C. D. Broeckling, L. T. Kok, and S. M. Salom, *Comparison between a native and exotic adelgid as hosts for Laricobius rubidus (Coleoptera: Derodontidae)*, Biocontrol Science and Technology, 15(2) (2005), pp. 165–171. 50

[70] G. M. G. Zilahi-Balogh, L. M. Humble, A. B. Lamb, S. M. Salom, and L. T. Kok, *Seasonal abundance and synchrony between Laricobius nigrinus (Coleoptera: Derodontidae) and its prey, the hemlock woolly adelgid (Hemiptera: Adelgidae)*, The Canadian Entomologist, 135 (2003), pp. 103–115. 50, 54

[71] G. M. G. Zilahi-Balogh, L. T. Kok, and S. M. Salom, *Host specificity of Laricobius nigrinus Fender (Coleoptera: Derodontidae), a potential biological control agent of the hemlock woolly adelgid, Adelges tsugae Annand (Hemiptera: Adelgidae)*, Biological Control, 24 (2002), pp. 192–198. 50, 60, 62

[72] G. M. G. Zilahi-Balogh, S. M. Salom, and L. T. Kok, *Development and reproductive biology of Laricobius nigrinus, a potential biological control agent of Adelges tsugae*, BioControl, 48 (2003), pp. 293–306. 54, 62, 63

Vita

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