

Flexibility of the spruce budworm – parasitoid food web

by

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**A Thesis
presented to
The University of Guelph**

**In partial fulfilment of requirements
for the degree of
Master of Science
in
Integrative Biology**

Guelph, Ontario, Canada

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ABSTRACT

FLEXIBILITY OF THE SPRUCE BUDWORM – PARASITOID FOOD WEB

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The reduction in diversity is reducing the capacity of food webs to respond to variability. Two potentially important food web mechanisms are flexible food web structure and spatiotemporal coupling. To date, little research has examined flexibility and spatiotemporal coupling at the community scale. The large variation in spruce budworm densities every 35 years likely causes the community of parasitoids to shift from spruce budworm on balsam fir (a softwood) to other caterpillars on hardwood trees. We examined whether the parasitoid community flexibly responded to the changing relative abundances of spruce budworm and other caterpillars and exhibited spatiotemporal coupling of balsam fir and hardwoods. We found that the parasitoid community tracked the changing relative abundances of spruce budworm and other caterpillars and spatiotemporally coupled balsam fir and hardwoods. Community-level flexibility and spatiotemporal coupling could mute large oscillations. Therefore, maintaining hardwood tree diversity could similarly mute the large spruce budworm density fluctuations.

Acknowledgments

With the nature of the dataset used in my dataset, many thanks go to the technicians and scientists who created and cleaned the data. For the fantastic guidance in writing, I want to thank the University of Guelph Writing Centre staff. Tim Bartley deserves special recognition for inspiring me to further my writing skills. I learned new design skills from the design wizard Monica Granados. I want to thank Marie Gutgesell, Sarah Dolson, and Carling Bieg for being thesis buddies. I also wish to thank my fellow graduate students and lab members who gave me fantastic feedback. Thanks go to the administrative staff of the University of Guelph Integrative Biology department for ensuring a smooth graduate degree. Special thanks go to my committee for constantly testing and pushing me. Eldon's punny nature definitely left me groaning on many a occasion. Finally, I want to thank my partner for her loving support and her wonderful, funny nature.

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Chapter 1

Prologue

Species are disappearing at alarming rates worldwide (Ceballos *et al.* 2015), and yet the consequences of these losses remain largely unknown. Current ecological understanding suggests that fewer species decreases the ability of an ecosystem to persist in the face of natural or human-caused change (defined here as ecosystem stability) (McCann 2000; Mori *et al.* 2013). Although superficially, diversity could be considered a pivotal factor in ecosystem stability, in fact diversity is a product of important ecological mechanisms, and it is these ecological mechanisms that determine ecosystem stability (McCann 2000). Thus, researching these stabilizing mechanisms is critical to understanding the consequences of global environmental and ecosystem change.

One such stabilizing ecological mechanism is flexible responses, produced when consumers alter their feeding patterns in response to changing resource abundances (also known as smart or adaptive responses, see Kondoh (2003) and Valdovinos *et al.* (2010)). These responses cause non-random changes in the arrangement of interactions (the topology) and interaction strengths because a consumer usually shifts from foraging on a low density resource to a high density resource (Winemiller 1990; Polis 1991; Kondoh 2003). Individuals and species have long been known to exhibit these flexible responses (Murdoch *et al.* 1975; Elliott 2004; Armstrong *et al.* 2016). Whole communities could also exhibit a flexible response, but so far flexible responses at a community-level has received less research attention (but see Bartley (2017)). Importantly, if flexible responses are found at the scale of whole communities within an ecosystem, the collective shifting from low density resources

to high density resources could dampen population variation at lower trophic levels by reducing the growth rates of the rapidly growing populations of lower trophic levels (Rooney & McCann 2012). The muting of population variation at lower trophic levels imparts stability to the whole ecosystem.

One mechanism that could be classed within community-level flexibility is if communities couple resource compartments. Coupling of resource compartments is when a community (or a species) feeds within two or more separated subgroups of an entire food web with greater interactions within the subgroup than between the subgroups (Blanchard *et al.* 2011; McMeans *et al.* 2015). These separated resource compartments can either be separated in space, in which case the community would act as a spatial coupler, or in time, in which case the community would act as a temporal coupler (Schindler & Scheuerell 2002; McMeans *et al.* 2015). The spatial or temporal separation in resource compartments is thought to be created by lower trophic level species being more restricted in space and/or time than higher trophic level species (McMeans *et al.* 2016). In all likelihood, there is a continuum of coupling spatially and temporally separated resource compartments by communities and species (McCann *et al.* 2005). Consequently, in this thesis we use the term spatiotemporal coupling to acknowledge this continuum. Although coupling has been examined in single species, identifying communities exhibiting coupling has been relatively unexplored (but see Bartley 2017). Furthermore, the temporal axis of resource compartment separation is similarly unexplored (McMeans *et al.* 2015).

Spruce budworm is an excellent system to examine community-level flexibility and spatiotemporal coupling because spruce budworm densities exhibit large fluctuations. Spruce budworm, a moth species, have six larval stages (instars) where the second instar overwinters and the following four instars forage on new balsam fir (a softwood) foliage before they pupate. Every 35 years, spruce budworm have regular massive outbreaks across eastern North America. The cause of these regular outbreaks is thought to be a predator-prey cycle but where the predator is a collection of natural enemies including pathogens, birds, and parasitoids (Royama *et al.* 2017). Approximately, 50 parasitoid species kill 50% of spruce budworm caterpillars every year (Royama *et al.* 2017). When spruce budworm densities increase, there is a subsequent increase in parasitoid diversity at all trophic levels on balsam firs (Eveleigh *et al.* 2007). The increasing spruce budworm densities act like a birdfeeder; first, consumers of spruce budworm arrive and then consumers of the first consumers arrive. Implicit in this birdfeeder effect is that there are other resources which

the consumers have arrived from or will leave for. These other resources are likely other caterpillar species because many parasitoid species are generalist consumers (Krombein *et al.* 1979). The potential collective response of all parasitoids shifting from other caterpillar species to spruce budworm is an example of flexible responses at the community-level. However, in the spruce budworm system, quantification of the capacity of the parasitoid community to exhibit flexibility remains scarce. Specifically, we do not know the relative parasitism of spruce budworm and other caterpillar species as spruce budworm densities change. Furthermore, these other caterpillar species are likely found on both balsam fir and on hardwood trees, including red maple. If the parasitoids of spruce budworm collectively switch from attacking spruce budworm on balsam fir to other caterpillar species on hardwoods, then the spruce budworm – parasitoid food web is an example of spatiotemporal coupling.

In this thesis, we empirically tested for community-level flexibility and spatiotemporal coupling in the spruce budworm – parasitoid food web. In Chapter 2, we examined whether the parasitoid community collectively exhibited flexibility in response to changing spruce budworm densities using a multi-year food web data set. We found that the parasitism rates of the parasitoid community tracked the changing relative abundances of spruce budworm and other caterpillars on balsam fir. Furthermore, this pattern was found to be driven by the aggregated responses of all parasitoid species. In Chapter 3, we examined whether the spruce budworm – parasitoid system exhibited spatiotemporal coupling using stable isotope analysis of parasitoids sampled over four years spanning a spruce budworm outbreak. We found that the extent of spatiotemporal coupling depended on the parasitoid group, but generally we found indications of spatiotemporal coupling. Overall, our study highlighted the importance of flexibility generally and spatiotemporal coupling specifically as mechanisms for ecosystems to respond to and persist in the face of human caused global environmental and ecosystem change.

Chapter 2

Flexibility of the spruce budworm – parasitoid food web on balsam fir.

2.1 Abstract

The world is astoundingly variable, and individuals to whole communities must respond to variability to survive. One potent example of nature's variability is the massive fluctuations in spruce budworm (*Choristoneura fumiferana* Clemens) populations that occur over long temporal scales (approximately 35 years). Here, we examined whether the parasitoid community predictably altered its parasitism of spruce budworm and other caterpillars in response to these fluctuations. Using a long-term dataset, we found that the parasitoid community exhibited flexible parasitism in response to the changing relative abundances of spruce budworm and other caterpillars on balsam fir. This flexible parasitism appeared to be an aggregated response by the parasitoid community and caused the distribution of interaction strengths to change. Finally, we found that parasitoids left balsam fir stands likely for hardwood stands as spruce budworm densities declined (the birdfeeder effect when resources decrease). Overall, the parasitoid community's flexible response likely mutes spruce budworm population cycles.

2.2 Introduction

Ecologists have long used equilibrium assumptions to study the complex suite of interactions that make up food webs (May 1973b; Allesina & Tang 2012). Although a reasonable first approach, in fact, both abiotic and biotic conditions are notoriously variable (Levin 1998; Guichard & Gouhier 2014). Despite this, our understanding of how organisms respond to variation remains surprisingly limited. In light of human-driven impacts including climate change that promise to significantly alter this variation (Cotton 2003; Ims *et al.* 2008), it behooves ecologists to embrace variation and to ask how individuals to whole communities respond to both natural variation and changes in this natural variation caused by human modifications.

Community-level responses to variability are a function of individual-level responses and recent work has found compelling evidence that individuals behave to take advantage of strong changing conditions, defined here as flexible responses (also known as smart or adaptive responses, see Kondoh 2003 and Valdovinos *et al.* 2010). As an example, Armstrong *et al.* (2016) showed evidence of grizzly bears “surfing” the asynchronous pulses of variation in yearly salmon runs in Alaska. The bears tracked the peaking out-of-phase salmon densities in a manner that maximized their energy intake over a long period of time. Individuals can also switch their diet depending on the abundances of different resource items, where an individual preferentially consumes whichever resource is at the highest abundance (Murdoch *et al.* 1975; Elliott 2004). Again, this behaviour maximizes the individual’s energy intake. These individual responses can add together to produce a community-level response. One known example of a community-level response to variability is the impressive convergence of parasitoids on the periodic spruce budworm *Choristoneura fumiferana* Clemens outbreaks, similar to how many species of birds converge on a birdfeeder (Eveleigh *et al.* 2007). The individual parasitoids all respond to the changing densities of spruce budworm in order to maximise their fecundity and collectively they converge on high densities of spruce budworm during outbreaks. This convergence leads to a diversity cascade across trophic levels suggesting that such strong changes as spruce budworm outbreaks may produce seemingly unified community responses as a function of all individual responses.

Because of the possibility of unified behaviour within the parasitoid community, the spruce budworm – parasitoid food web provides an excellent system to examine community-level responses to variability. Spruce budworm have massive and relatively predictable

outbreaks every thirty five years, followed by periods of spruce budworm rarity (Royama *et al.* 2005). This cycle is considered to be a predator – prey cycle, where the predator is a complex of natural enemies including insects that parasitize and then kill a caterpillar host (parasitoids) (Royama *et al.* 2017). Although spruce budworm are consumed by many invertebrate predators and birds, about 50% of spruce budworm caterpillars are killed by 50 species of parasitoid, principally by tachinid flies, and ichneumonid and braconid wasps (Royama *et al.* 2017). Furthermore, this community of parasitoids likely has the strongest response to changing spruce budworm densities because invertebrate predators and birds are more generalist than parasitoids, and birds are also limited in numbers due to territory competition (Renault & Miller 1972; Royama *et al.* 2017). Therefore, we expect to find a community-level response in this parasitoid community. From Eveleigh *et al.* (2007), which showed a birdfeeder effect, we know the parasitoid community response when spruce budworm are plentiful, but we do not know the parasitoid community response when spruce budworm are rare. In effect, we have not observed what happens when the “bird feed” has gone.

For the birdfeeder effect to occur, either parasitoids remain dormant when spruce budworm are rare, or move between patches of outbreaking spruce budworm, or find alternative sources of caterpillar hosts when spruce budworm are rare. We can immediately discount parasitoids remaining dormant as a hypothesis for maintaining the birdfeeder effect because no parasitoid of spruce budworm is known to enter dormancy longer than a year (Thireau & Régnière 1995; O’Hara 2005), and due to metabolic costs, most insects are thought not to be capable of entering dormancy for longer than 3 years (Ellers & Van Alphen 2002; Corley *et al.* 2004). Within the relatively short duration of a spruce budworm outbreak (5 - 10 years), parasitoids are moving between patches of high density spruce budworm and so there are effectively many birdfeeder effects happening simultaneously across the patchwork of spruce budworm outbreaks. However, we can assume that the birdfeeder effect, solely with spruce budworm, is not occurring throughout the longer periods when spruce budworm are rare because spruce budworm are uniformly rare over their whole range for these longer periods. When spruce budworm are rare, parasitoid populations decrease, but a reserve population of parasitoids could be maintained by attacking other caterpillar species. Parasitoids attacking other caterpillar species is a possibility because we know that there are generalist parasitoids that attack spruce budworm and other caterpillar species and also specialist parasitoids that attack only spruce budworm (Krombein *et al.* 1979; Eveleigh *et al.*

2007; Smith *et al.* 2011). If a reserve population of parasitoids are attacking other caterpillar species, then the birdfeeder effect occurs over the whole population cycle of spruce budworm where parasitoids converge on high spruce budworm densities and then leave to attack other caterpillars when spruce budworm densities decline. The full birdfeeder effect, including other caterpillar species, has as yet not been examined. Specifically, we do not know the relative attack rates of the parasitoid community on spruce budworm and other caterpillar species as spruce budworm densities change. There is the potential for the whole parasitoid community to respond in a flexible manner to fluctuating spruce budworm densities by collectively altering the relative parasitism rates of spruce budworm and other caterpillar species. These are fundamental questions because scaling this community-level response to the landscape scale has the potential to moderate the amplitude and severity of spruce budworm outbreaks.

In this study, we examined whether the foraging patterns of a parasitoid community were fundamentally altered by the large relative change in spruce budworm densities that unfold against the densities of other potential hosts in time and space. We tested our hypothesis that the parasitoid community collectively altered its relative parasitism rates of spruce budworm and other caterpillar species (the flexible parasitism hypothesis) by examining four aspects. First, we determined whether the parasitoid community collectively attacked spruce budworm in proportion to the abundance of spruce budworm relative to other caterpillars on balsam fir (community-level resource tracking). Second, we evaluated whether any community-level resource tracking was an aggregate response and not a single species response (aggregate response). Third, we evaluated whether the distributions of interaction strengths between parasitoids and the different caterpillars changed (fluctuating interaction strength distributions). Fourth, with the addition of more years to the dataset used by Eveleigh *et al.* (2007), we examined the full extent of the birdfeeder effect by determining whether decreasing spruce budworm densities caused a reversal of the cascading increases in parasitoid species diversity that Eveleigh *et al.* (2007) noted (parasitoid exodus). Not finding any one of these four aspects would suggest that community-level flexibility can not be found in the spruce budworm – parasitoid food web. The four aspects of the flexible parasitism hypothesis were tested by analyzing rearing data of spruce budworm and other caterpillar species collected from balsam fir branches sampled between 1982 to 1995. During this time period, balsam fir branches were collected from three plots and a representative sample of spruce budworm and all other caterpillar species were put into feeding

vials. Parasitoids emerged from these spruce budworm and other caterpillar species, and the parasitoids were subsequently morphologically identified. Importantly, the whole parasitoid community tracked the changing relative abundances of spruce budworm and other caterpillars on balsam fir illustrating the flexibility of the spruce budworm – parasitoid food web.

2.3 Materials and Methods

2.3.1 Study sites

Three plots in balsam fir forests in New Brunswick were established. Plot 1 was in the Acadia Research Forest near Fredericton (66°25'W, 46°00'N). Balsam fir branches were sampled in this plot from 1982 to 1989. Because spruce budworm caused 60% tree mortality in plot 1 by the mid-1980s, plot 2 was added, which was also in the Acadia Research Forest. Balsam fir branches were sampled in this plot from 1986 to 1995. In the late 1980s, the spruce budworm populations in both plots were so low that plot 3 was added, which was situated near Saint-Quentin (67°15'W, 47°29'N). Balsam fir branches were sampled in plot 3 from 1988 until 1994 when spruce budworm populations also declined to a low level. All plots were outside areas of biopesticide application. Full details of the three plots and all sampling and rearing procedures can be found in Lucarotti *et al.* (2004), Eveleigh *et al.* (2007) (SI Materials and Methods) and Royama *et al.* (2017). Here, we present only a brief synopsis.

2.3.2 Sampling

At the beginning of each season, a group of codominant balsam fir trees were selected in 20 random locations within each plot. Every year and for each plot, before larval emergence from winter diapause, one balsam fir branch from each of the 20 locations was collected. As soon as second instar larvae in the field began emerging from diapause, balsam fir branches were sampled approximately every day until the end of spruce budworm adult eclosion. On each sampling day during the earlier years when spruce budworm populations were high, one foliated mid-crown balsam fir branch from one of the trees in each of the 20 locations was collected. During the later years when spruce budworm populations were low, two or

more branches were collected from each location to increase the number of collected spruce budworm larvae at each sample date and location

2.3.3 Laboratory work

All spruce budworm caterpillars found on branches sampled before spruce budworm emergence from winter diapause were collected. For branches sampled after spruce budworm emergence from winter diapause, a minimum of 100 spruce budworm individuals on each sampling day were collected. If there were more than 100 spruce budworm individuals on a branch, all individuals were collected to avoid selecting easy-to-find individuals. Where there were fewer than 100 on a branch, all spruce budworm individuals from another branch were added to the collection. When spruce budworm populations were low, obtaining more than 100 spruce budworm individuals became difficult. As a result, all spruce budworm that were found on the sampled branches were collected. All individuals of other caterpillar species were collected from the sampled branches. All collected caterpillars (spruce budworm and other caterpillar species) were individually reared on artificial diet (McMorran 1965). All reared caterpillars were inspected every weekday for mortality and the causes of mortality. All parasitoids that emerged from any reared caterpillars were identified to the lowest taxonomic rank possible.

2.3.4 Statistical Analyses

Because we are interested in quantifying the trophic interactions of parasitoids that attack both spruce budworm and other caterpillars, we excluded all parasitoid taxa (at the level of species or the lowest taxonomic rank that was identifiable) that attacked only spruce budworm or only other caterpillars. Out of a total of 69 parasitoid taxa reared from spruce budworm and other caterpillars in all years, 34 parasitoid taxa (listed in Figure 2.3) were found to attack both spruce budworm and other caterpillars. These 34 parasitoid taxa formed 90% of all trophic interactions with spruce budworm and 84% of all trophic interactions with all other caterpillar species.

Because spruce budworm populations peaked in different years in the three different plots (plot 1 and 2 peaked in 1985 and plot 3 peaked in 1991), we created a new time variable called Years before/after peak. In this variable, zero was set as the relative year at which spruce budworm populations peaked in each plot. For all analyses, plots were compared

using this relative variable. Hereafter, *year* refers to the relative year of this created Years before/after peak variable.

Using the same data, Eveleigh *et al.* (2007) established through rarefaction that changes in diversity of parasitoid taxa was not due to sampling artefacts. Consequently, we too are confident that any patterns found by the analyses below are not due to changes in sampling intensity but due to underlying ecological interactions.

All of the following analyses were done using R version 3.4.3 (R Core Team 2012). The data used here can be found on the Dryad Digital Repository (To be uploaded later) and the R script can be found on GitHub (Greyson-Gaito *et al.* 2018).

2.3.4.1 Community-level resource tracking

To examine whether the parasitoid community attacks spruce budworm in proportion to the relative abundances of spruce budworm and other caterpillars on balsam fir, we calculated two values for every combination of *year* and plot: the ratio of parasitoid emergence from spruce budworm to other caterpillars for all parasitoid taxa combined, and the ratio of abundances of spruce budworm to other caterpillars. Out of a total of 25 data points, we removed four data points where no spruce budworm, nor other caterpillars, nor parasitoid emergence from either spruce budworm or other caterpillar was found. We ran a generalized least squares regression with the log₁₀ of the ratio of emergence as the response variable and the log₁₀ of the ratio of the abundances of spruce budworm to other caterpillars, plot, and their interaction as the explanatory variables (function `gls`, R package `nlme`, version 3.1-137, Pinheiro *et al.* 2018). We fitted the full model using maximum likelihood estimation (ML) and then used backwards selection with log likelihood ratio tests to select the final fixed effects. We refitted the final model using restricted maximum likelihood estimation (REML) to give unbiased ML predictors (Zuur *et al.* 2009). We tested whether the average slope for all plots was significantly different from zero using a one sample t-test. A slope of zero would indicate that the parasitoid community does not track the relative abundances of spruce budworm and other caterpillars. Any other slope would indicate tracking, with the slope quantifying the community “preference” for spruce budworm and other caterpillars.

To unpack the relationship between the ratio of abundances of spruce budworm to other caterpillars with the ratio of parasitoid emergence from spruce budworm to other caterpillars, we examined how the abundances of spruce budworm and other caterpillars changed

over time and compared this to the absolute number of parasitoid emergences from spruce budworm and other caterpillars over time. For every combination of *year* and plot, we calculated two values: the abundances of spruce budworm and other caterpillars sampled from balsam fir branches, and the average number of emergences from spruce budworm and other caterpillars for all parasitoid taxa. We ran generalised least squares regressions to test the effects of *year*, caterpillar type (spruce budworm or other caterpillars), plot, and their interactions on each value. We added a varIdent correlation structure in both models to account for residual heterogeneity. We added a corAR1 autocorrelation structure to account for temporal autocorrelation for the abundances of spruce budworm and other caterpillars model only. We fitted the full models using ML, used backwards selection with log likelihood ratio tests to select the final fixed effects, and refitted the final model using REML.

2.3.4.2 Aggregate response

To identify whether the response to the changing relative abundances of spruce budworm to other caterpillars was driven by a single species or by the whole community, we found the three parasitoid taxa that emerged from all caterpillars the most, which included two species and one taxon not taxonomically tractable under Ichneumonidae. We then removed in turn the top parasitoid taxon, the top two parasitoid taxa, and the top three parasitoid taxa from the data and ran generalized least squares regressions with the log₁₀ of the ratio of emergence as the response variable and the log₁₀ of the ratio of the abundances of spruce budworm to other caterpillars, plot and their interaction as the explanatory variables (same final model as for the first analysis in the flexible parasitism hypothesis). Using one-sample t-tests, we compared the average slopes for all plots of each of these models with the average slope for all plots produced in the model with all parasitoid taxa included. Finding a different slope after dropping the dominant parasitoid taxa would indicate that there is no aggregate response. To examine turnover in parasitoid taxa over time, we ran an nMDS analysis where the abundances of individual species were divided by the total number of parasitoid emergences (all species) for each *year* and plot (function metaMDS, R package vegan, version 2.4.2, Oksanen *et al.* 2018). We used the Bray-Curtis dissimilarity measure, assessed the dimensionality of the data by examining the change in stress with decreasing dimensions, and assessed the stability of the final solution by calculating the standard deviation of the stress values for the ten preceding iterations. We ran a perMANOVA between three groups (function adonis, R package vegan): three and two years before the peak; one

year before and after the peak, and the peak; and two to ten years after the peak. In this perMANOVA, we used the Bray-Curtis dissimilarity measure, constrained permutations within each plot, and maintained the temporal order of permutations. Finding no species turnover would indicate that there is no aggregate response.

2.3.4.3 Fluctuating interaction strength distributions

Much of food web ecology has operated from constant interaction strength matrices (e.g., May 1973a; Allesina & Tang 2012). Although clearly of value, the notion of flexible foraging suggests that these interaction strength distributions may change predictably in time. Given the potential for flexible foraging in the spruce budworm – parasitoid food web, we examined how these interaction strength distributions changed with respect to the relative distribution of weak and strong interactions (e.g. skewed or uniform) by calculating the number of emergences of each parasitoid taxa from either spruce budworm or other caterpillars for every *year*, where the number of emergences is a proxy of interaction strength. From these numbers of emergences, we produced visual bipartite food webs (R package bipartite, version 2.07, Dormann *et al.* 2008) and calculated the ratio of the median to maximum interaction strength for every *year*. By examining the bipartite graphs and the change in ratio of median to maximum interaction strength, we qualitatively assessed how the distributions of interactions strengths changed over time. No change in median to maximum interaction strength over time would indicate that interaction strengths distributions are not fluctuating.

2.3.4.4 Parasitoid exodus

To establish whether the richness of parasitoid taxa emerging from spruce budworm and other caterpillars declined with decreasing spruce budworm densities, we calculated the number of parasitoid taxa that emerged from spruce budworm and other caterpillars for every combination of *year* and plot. We ran a generalised least squares regression to test the effects of *year*, caterpillar type (spruce budworm or other caterpillars), plot, and their interactions on the numbers of parasitoid taxa emerging from spruce budworm and other caterpillars. We added a corAR1 autocorrelation structure to account for temporal autocorrelation. We fitted the full model using ML, used backwards selection with log likelihood ratio tests to select the final fixed effects, and refitted the final model using REML. Assuming that the parasitoid taxa populations do not become tiny, if the richness of parasitoid taxa

did not decrease from spruce budworm and other caterpillars, then we would conclude that parasitoids are not leaving balsam fir stands.

2.4 Results

2.4.1 Community-level resource tracking

The final model explaining the log₁₀ ratio of parasitoid emergence from spruce budworm to other caterpillars included the explanatory variables of the log₁₀ ratio of abundances of spruce budworm to other caterpillars, plot, and their interaction (Figure 2.1 A). The average slope for all plots, signifying whether or not the parasitoid community attacked spruce budworm in proportion to the relative abundances of spruce budworm and other caterpillars, was significantly different from 0 (0.966 ± 0.247 , $df=15$, $P < 0.00001$, one-sample t-test).

The final model explaining the abundances of spruce budworm and other caterpillars included the variables of *year*, caterpillar type, and their interaction (interaction: $L = 10.813$, $P = 0.001$, $df = 1$, log likelihood ratio test, Figure 2.1 B). On average, there were 22 times as many spruce budworm caterpillars as there were other caterpillars ($\beta = 8503.821$, $t = 4.882$, $P < 0.0001$, $N = 50$, coefficient t-test). The abundance of spruce budworm decreased to zero over time; however, the abundance of other caterpillars on balsam fir was mostly constant over time (interaction: $\beta = -91.097$, $t = -3.349$, $P < 0.01$, $N = 50$, coefficient t-test).

The final model explaining the number of parasitoid emergences from spruce budworm and other caterpillars included the variables of *year*, caterpillar type, and their interaction (interaction: $L = 20.346$, $P < 0.001$, $df = 1$, log likelihood ratio test, Figure 2.1 C). Although the number of parasitoid emergences from spruce budworm decreased markedly, the number of parasitoid emergences from other caterpillars decreased only slightly (interaction: $\beta = -4.702$, $t = -4.457$, $P < 0.001$, $N = 50$, coefficient t-test).

2.4.2 Aggregate response

When the parasitoid taxon with the most emergences from all caterpillars (*Apanteles fumiferanae*) was dropped, the average slope was 9% smaller (0.880 ± 0.258 , $df = 15$, $P = 0.526$, one-sample t-test) than the slope with all parasitoid taxa (original slope was 0.966). With the two most abundant parasitoid taxa dropped (*Apanteles fumiferanae* and *Glypta*

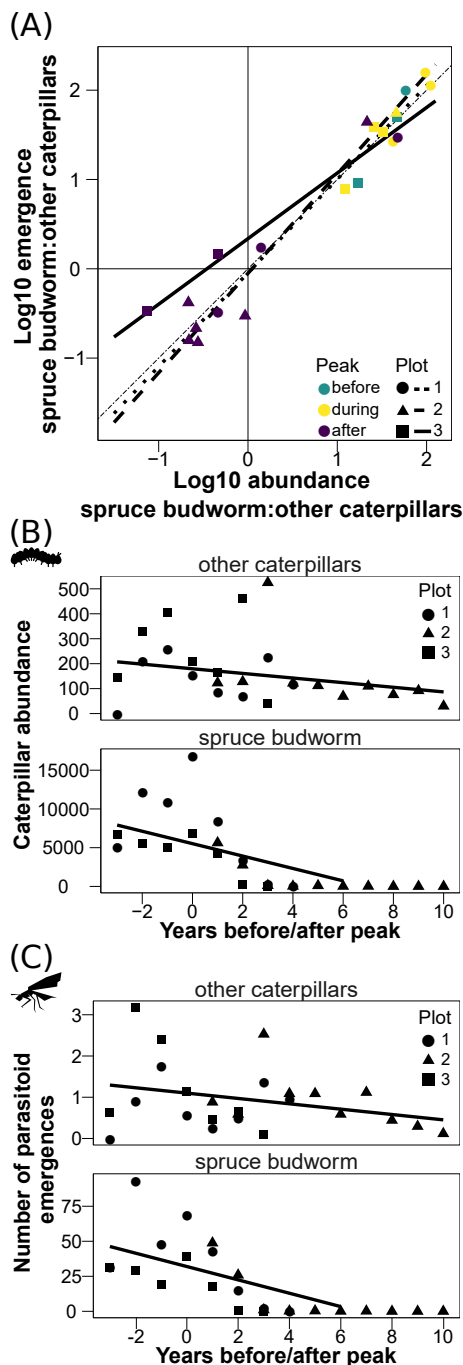


Figure 2.1: (A) Log_{10} ratio of parasitoid emergences from spruce budworm to other caterpillars for all parasitoid taxa used in our analysis as a function of the log_{10} ratio of all sampled spruce budworm and other caterpillars. Each point is a single year and a single plot. The thin dashed line is the $y = x$ line. (B) Spruce budworm and other caterpillar abundances over time. Each point is a single year and a single plot. Zero is the peak of the spruce budworm population in each plot. (C) Number of emergences of parasitoids from spruce budworm and other caterpillars over time. Each point is an average across all parasitoid taxa used in our analysis for each year and for each plot. Zero is the peak of the spruce budworm population in each plot. Caterpillar by Juraj Sedlák from the Noun Project - <https://creativecommons.org/licenses/by/3.0/us/legalcode>. Parasitoid by m. turan ercan from the Noun Project - <https://creativecommons.org/licenses/by/3.0/us/legalcode>.

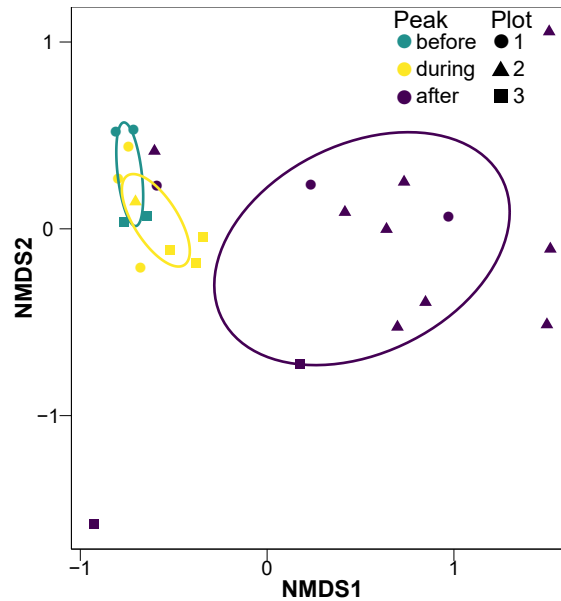


Figure 2.2: nMDS of parasitoid community over time. The colour of each point corresponds to the three temporal groups: three and two *years* before the peak (before); one *year* before and after the peak, and the peak (during); and two to ten *years* after the peak (after). Each point is a single *year* and a single plot. 20 iterations. Final stress of 0.0954. Instability for preceding 10 iterations was 0.0141.

fumiferanae), the slope decreased by 18% (0.796 ± 0.309 , $df = 15$, $P = 0.300$, one-sample t-test). With the three most abundant parasitoid taxa dropped (*Apanteles fumiferanae*, *Glypta fumiferanae*, and Und Ichneumonoidea), the slope decreased by 22% (0.754 ± 0.323 , $df = 15$, $P = 0.219$, one-sample t-test). The community of parasitoid taxa differed over time ($F = 5.111$, $P < 0.001$, 999 permutations, perMANOVA, Figure 2.2).

2.4.3 Fluctuating interaction strength distributions

The distribution of interactions strengths for spruce budworm and other caterpillars changed from a skewed distribution dominated by weak interactions towards a uniform distribution, though the variation in the median:maximum interaction strengths between sequential years is greater for other caterpillars than for spruce budworm (Figure 2.4).

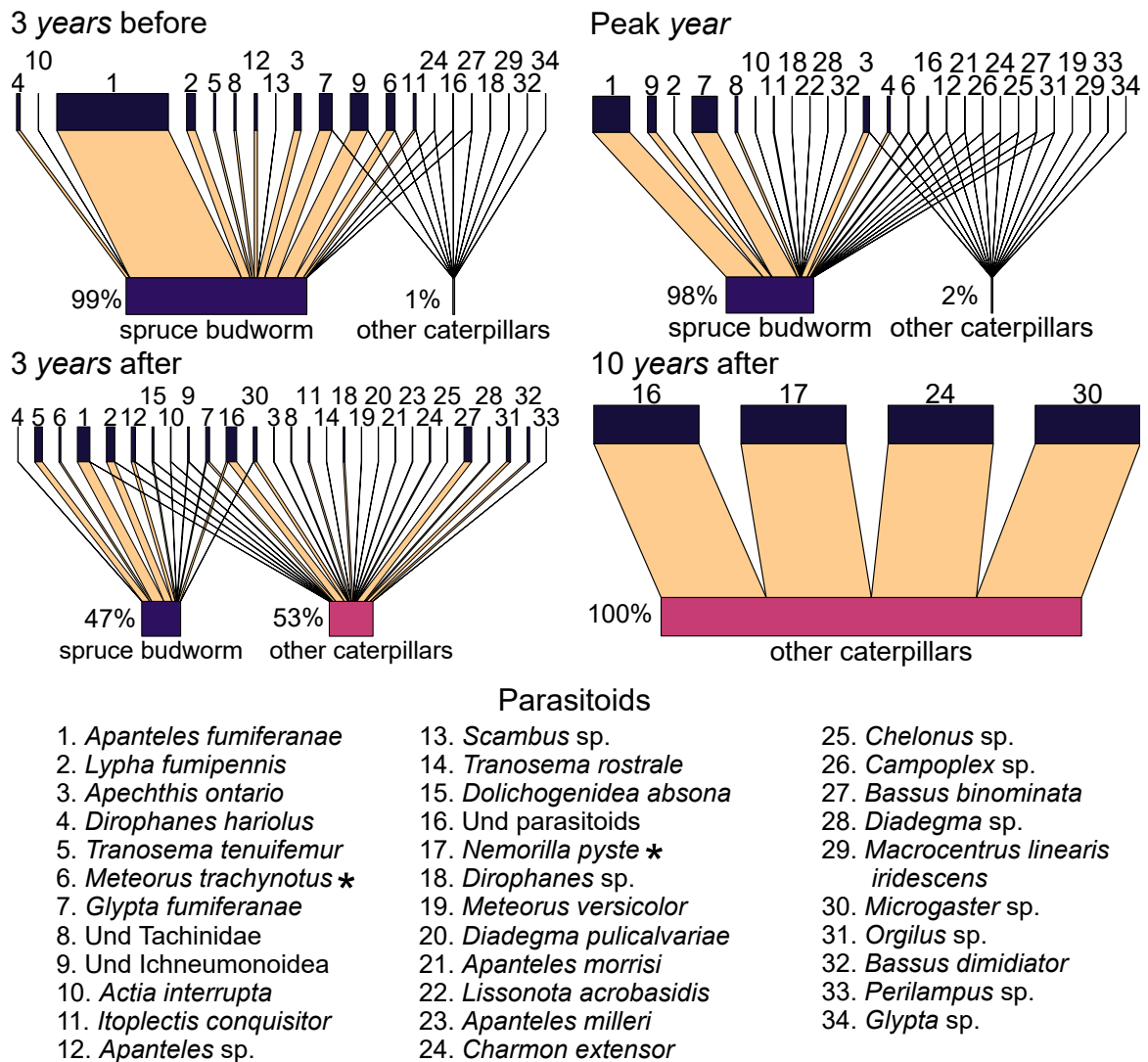


Figure 2.3: Graphical representations of the number of emergences of each parasitoid taxon (top boxes) from spruce budworm and other caterpillars (bottom boxes) over time. The width of links is proportional to the fraction of emergences of each parasitoid taxon from either spruce budworm or other caterpillars. The width of the bottom boxes are proportional to the number of emergences from spruce budworm versus other caterpillars, and the percentages show this quantitatively. Four different *years* are shown, where all plots were combined within a *year*: (A) three *years* before the peak, (B) peak *year*, (C) three *years* after the peak, and (D) ten *years* after the peak. All other *years* can be found in Figures A.1 & A.2. Und is a group of unidentified parasitoids within the stated taxonomic group. A star denotes a species that requires an alternate caterpillar host to overwinter in. To find the corresponding species in Eveleigh *et al.* (2007), see Table A.1.

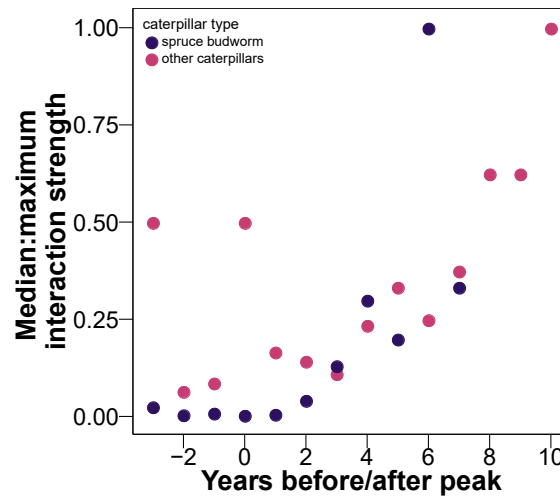


Figure 2.4: Median:maximum interaction strength over time and for each caterpillar type. Parasitoid emergence was used as a proxy for interaction strengths. Figure inspired by the median:maximum interaction strength figure in Ushio *et al.* (2018).

2.4.4 Parasitoid exodus

The final model explaining the number of parasitoid taxa emerging from spruce budworm and other caterpillars included the explanatory variables of *year*, caterpillar type, plot, *year:caterpillar type*, and *year:plot* (Figure 2.5). Graphically, we see that the number of parasitoid taxa that emerged from spruce budworm decreased at a faster rate than the number of parasitoid taxa that emerged from other caterpillars (log likelihood ratio test of *year:caterpillar type*, $L = 10.349$, $P = 0.0013$, $df = 1$, Figure 2.5).

2.5 Discussion

In our study, we have shown that this boreal insect food web is highly responsive and flexible in time to changing spruce budworm densities. We used long-term data of host/parasitoid abundance and diversity to assess how parasitism rates changed over the course of a large budworm cycle. We found a dramatic aggregated whole community correspondence of parasitism rates with caterpillar relative abundance (spruce budworm:other caterpillar abundance) and a sharp decline in parasitoid taxa richness on balsam fir as spruce budworm densities decreased.

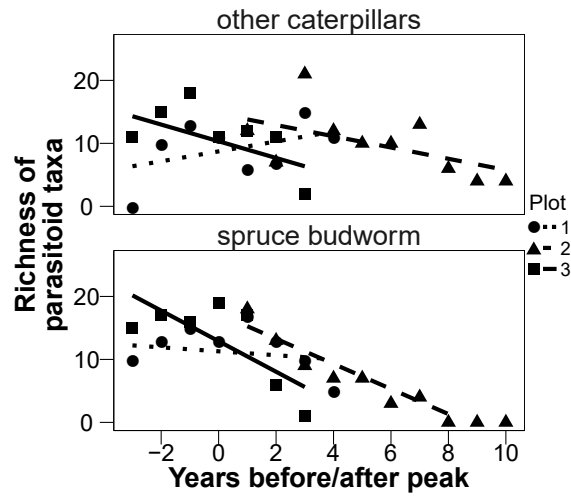


Figure 2.5: Number of parasitoid taxa that emerged from spruce budworm and other caterpillars over time. Each point is for a single *year* and a single plot. Zero is the peak of the spruce budworm populations in each plot.

One aspect of flexible food webs is that consumers often shift from feeding on a low abundance resource to a high abundance resource (Kondoh 2003). We found this pattern on balsam fir where the parasitoid community attacked spruce budworm and other caterpillars in proportion to their relative abundances. Interestingly, this pattern likely occurred because the flexible responses of the parasitoids happen over scales larger than individual balsam fir stands. Essentially, Eveleigh *et al.* (2007) found this issue of scale too when they observed that parasitoids congregated on balsam fir stands as spruce budworm density increased. For parasitoids to congregate on balsam fir, there must be a separate source of parasitoids. Our results support this conjecture for three reasons. First, we know that although the abundance of other caterpillars and parasitoid emergence from other caterpillars stayed relatively constant over time, the abundance of spruce budworm and parasitoid emergence from spruce budworm decreased during our study period (Figure 2.1B & C). Second, parasitoid emergence from other caterpillars on balsam fir could never produce enough parasitoid individuals to match our observed parasitoid emergence from spruce budworm. Third, if the only parasitoids on balsam fir emerged from either spruce budworm or other caterpillars on balsam fir, then the slope of the line in Figure 2.1A would be shallower because the “balsam fir” parasitoid population could never produce enough parasitoid individuals to match the observed ratio of abundances of spruce budworm and other caterpillars. Therefore, the best explanation for not finding this shallower slope is a source of parasitoids separate from the

“balsam fir” population. Consequently, an important aspect of the flexibility of the spruce budworm – parasitoid food web is that the response occurs across larger scales than balsam fir stands and that there is a source of parasitoids.

There is the possibility that this flexible response is a community-level phenomenon created by the flexible responses of all of the individual parasitoid taxa combined. If so, then the parasitoid community’s pattern of attacking spruce budworm and other caterpillars in proportion to their relative abundances should be an aggregate response of all parasitoid taxa and should not be a response by a few dominant parasitoid taxa. By excluding from the dataset the three most abundant parasitoid taxa and finding that the parasitoid community still tracked the changing relative abundances of spruce budworm and other caterpillars, we concluded that this flexible response was an aggregate community response. Furthermore, there was high turnover in parasitoid taxa suggesting that in any given year the dominant parasitoid taxa were replaced in later years. Similarly, Royama *et al.* (2017) found that no single parasitoid functional group determined the yearly spruce budworm cycle. Instead, as spruce budworm densities changed, there was turnover in the parasitoid functional group that attacked spruce budworm the most, which produced a relatively constant overall parasitism rate of spruce budworm. As a possible mechanism for this constant parasitism rate, Royama *et al.* (2017) posited that the profitability of spruce budworm and other caterpillar species changes in time differently for each parasitoid species. Consequently, different parasitoid species will attack spruce budworm at different time periods during the spruce budworm cycle. Theoretical work supports this supposition where two consumers attack a common resource at different rates during the cycling of the resource (Armstrong & McGehee 1980; Xiao & Fussmann 2013). Furthermore, our finding of a likely aggregate response and the suggestion by Royama *et al.* (2017) that parasitoids individually respond to the profitability of the relative densities of spruce budworm and other caterpillar species are in line with complex adaptive systems theory. Complex adaptive systems theory posits that patterns at lower levels of organization (at the level of individuals or species) produce patterns at higher levels of organization (the community or the ecosystem) (Levin 1998). Overall, our results and the results of Royama *et al.* (2017) suggest that the flexibility in the spruce budworm – parasitoid food web is produced from synchronized changes in parasitism rates on spruce budworm and other caterpillar species by the whole parasitoid community.

By definition, flexible responses change interaction strengths because a shift in resource use necessitates a change in interactions strengths. Therefore within a food web, changing

interaction strengths likely alters the distribution of interactions strengths. Indeed from our study, the collective change in parasitism rates led to dramatic shifts in the distribution of interaction strengths over the spruce budworm cycle. When spruce budworm were at high densities, the distribution of interaction strengths showed a dichotomy of strong-weak interaction strengths but skewed with a preponderance of weak interactions. As spruce budworm densities declined, the distribution of interaction strengths became uniform. Similarly, Ushio *et al.* (2018) found that interaction strengths distributions in a marine fish community were dominated by weak interactions in the summer and were more uniform in the winter. Both Ushio *et al.* (2018) and theoretical studies have found that skewed distribution dominated by weak interaction strengths stabilizes foods webs (Neutel *et al.* 2002; Emmerson & Raffaelli 2004). However, apart from Ushio *et al.*'s (2018) study, the pattern of fluctuating interaction strength distributions has not been well explored in the theoretical or empirical literature. Ushio *et al.* (2018) posited a few drivers for these fluctuations including higher productivity in the summer months leading to higher fish abundance (Masuda *et al.* 2010) and behavioural or physiological responses that vary over time (Kondoh 2003; Reynolds & Bruno 2013; McMeans *et al.* 2015). We agree with Ushio *et al.*'s (2018) assessment. Greater spruce budworm densities could be thought of as the same as high fish abundance in the summer. We suggest too that the behavioural responses by the parasitoid individuals that produces a unified community response over several years and generations of parasitoids is integral to the fluctuations in interaction strength distributions.

Theory may help to further explain this unified community response. One theoretical model proposes that higher trophic level generalist consumers react to variation in their resources by either starting consumer interactions with a species in one separated subgroup of an entire food web (coupling to a resource compartment) or stopping consumer interactions with a different species in another separate subgroup of the entire food web (decoupling from a resource compartment) (McCann *et al.* 2005; McMeans *et al.* 2016). This coupling and decoupling of different resource compartments can mute large population variation in lower trophic level organisms and so can stabilize food webs. In the spruce budworm – parasitoid food web, although individual parasitoid species may be specialists or generalists, the collective parasitoid community acts as a generalist consumer and can couple or decouple the resource compartment with balsam fir as the basal resource (hereafter referred to as balsam fir resource compartment). This theoretical model suggests multiple resource compartments, more than the single balsam fir resource compartment that we have examined in

this study. Consequently, a separate resource compartment from balsam fir is likely what contributes to the flexibility of the parasitoid community in response to changing spruce budworm densities.

The analogy of the birdfeeder suggests that when spruce budworm densities decrease, parasitoids should leave balsam fir. In support of our parasitoid exodus prediction, the diversity of parasitoids emerging from spruce budworm dropped precipitously in comparison to parasitoids emerging from other caterpillars. Combined with Eveleigh *et al.*'s (2007) study, the full extent of the birdfeeder effect can be seen. As spruce budworm densities increased, parasitoid diversity on balsam fir increased (Eveleigh *et al.* 2007). Then, as spruce budworm densities decreased, parasitoid diversity on balsam fir decreased. Implicit in this birdfeeder effect is a source of parasitoids when spruce budworm densities increase and a destination for the parasitoids when spruce budworm densities decrease. Effectively, there is a "hidden diversity" of parasitoid species not usually found in, and therefore not sampled from, balsam fir stands that quickly congregate on spruce budworm and then subsequently leave. The coupling/decoupling theoretical model suggests that the source, destination, and where the "hidden diversity" can be found are likely one resource compartment separate from balsam fir stands. We suggest that the separate resource compartment has hardwood trees as the basal resource (hereafter referred to as hardwood resource compartment), where balsam fir is a softwood tree species, and white birch (*Betula papyrifera*) and red maple (*Acer rubrum*) are hardwood tree species. Our suggestion stems from two observations. First, we know that parasitoids do attack other caterpillar species, so logically parasitoids attacking other caterpillar species on hardwoods is plausible. Second, there have been several observations that spruce budworm densities in stands that contained a mixture of softwoods and hardwoods, otherwise known as mixed forest stands, were lower than spruce budworm densities in balsam fir dominated stands during an outbreak, even after accounting for the different tree densities (Su *et al.* 1996; Eveleigh *et al.* 2007). Consequently, these researchers hypothesized that there must be greater diversity and abundances of parasitoids in mixed forest stands, maintained by the greater diversity and abundances of caterpillar hosts in mixed forest stands over the full duration of a spruce budworm population cycle.

This hypothesis is essentially the Enemies Hypothesis where greater abundances and diversity of natural enemies are maintained in more diverse plant communities (Root 1973; Letourneau 1987; Jactel *et al.* 2002). Researchers have examined the Enemies Hypothesis in forest plantations (spruce budworm detrimentally impacts forest plantations in eastern

North America and so comparisons with other forest plantation studies is useful) but have found a range of responses of natural enemies to tree diversity. These responses range from no effect of tropical tree species diversity on parasitoid species and abundance (Schuldt *et al.* 2011; Abdala-Roberts *et al.* 2016) to increased abundances of insect predators in diverse forest plots (Sobek *et al.* 2009). We acknowledge the mixed results of the Enemies Hypothesis in forest plantations, but due to the findings from Eveleigh *et al.* (2007) and Su *et al.* (1996), we believe that the Enemies Hypothesis is the likely mechanism behind lower spruce budworm densities in mixed forest stands. We hypothesize that hardwood trees are an important part of the spruce budworm system by providing alternative caterpillar hosts for the parasitoids that attack spruce budworm. Consequently, parasitoids are likely attacking other caterpillar species on hardwoods when spruce budworm are rare and attacking spruce budworm on balsam fir when spruce budworm are abundant. Hardwoods are likely how the “hidden diversity” of parasitoids and the flexibility of the food web are maintained, but further research is required to evaluate this hypothesis.

The parasitoid community response to changing spruce budworm populations illustrates the fantastic flexibility of food webs. As spruce budworm densities increase on balsam fir, the diversity of parasitoid species found on balsam fir increase at all trophic levels. In times of spruce budworm rarity, parasitoid species diversity drops and yet this “hidden diversity” must be maintained by some mechanism otherwise the swift parasitoid community response to increased spruce budworm abundance could not occur. Our study has shown that the parasitoid community responded to changing densities of spruce budworm by altering its relative parasitism rate of and interaction strengths with spruce budworm and other caterpillars on balsam fir. The other caterpillar species that these parasitoids attack are not solely found on balsam fir, and in fact, many researchers have suggested that caterpillars on hardwoods should be the dominant resource while spruce budworm are rare. We have corroborated this suggestion by observing that there must be net immigration of parasitoids into balsam fir as spruce budworm densities are increasing. Consequently, further research should include caterpillars on hardwoods in a food web analysis of the spruce budworm system. Specifically, further research could identify whether the parasitism rates of spruce budworm on balsam fir compared to the parasitism rates of caterpillars on hardwoods change as spruce budworm densities peak and ebb away. Such a response, which appears to be created by the combined actions of all parasitoid species, is an excellent example of a complex adaptive system and of community ecology driving the population ecology of a dominant species.

For spruce budworm management, we have highlighted the importance of other caterpillar species and the potential use of these caterpillars by parasitoids to the population dynamics of spruce budworm. The other caterpillar species are possible resources that maintain the “hidden diversity” of parasitoids. Therefore, increasing the abundance and diversity of these other caterpillar species has the potential to mute the amplitude of spruce budworm outbreaks, thus helping to reduce the defoliation and destruction of balsam fir forests in eastern North America.

Chapter 3

Spatiotemporal coupling of the balsam fir and hardwood resource compartments by the parasitoids of spruce budworm

3.1 Abstract

One potential method of community-level flexibility is coupling of spatially or temporally separated resources compartments. To date, most research on coupling has examined spatial coupling in single species. Relatively little research has examined coupling by a community and coupling of temporally separated resource compartments. The parasitoids of spruce budworm are thought to shift from attacking spruce budworm on balsam fir to other caterpillars on hardwood trees. Because of this shift in resource use over time, the spruce budworm – parasitoid food web presents an opportunity to examine community-level coupling of temporally separated resource compartments. Using stable isotope analysis of parasitoids sampled over four years spanning a spruce budworm outbreak, we found indications of spatiotemporal coupling at the scales of multiple years and within a season. Even with our limited dataset, we still found spatiotemporal coupling trends providing an impetus to fully examine spatiotemporal coupling in the spruce budworm – parasitoid food web.

3.2 Introduction

Flexibility has been found to be an important stabilising mechanism that can counteract variability in abiotic and biotic conditions (Kondoh 2003; Bartley 2017). Often, empirical studies on flexibility examine a single consumer species (Tunney *et al.* 2012; Guzzo *et al.* 2017; but see Bartley 2017). In Chapter 2, we explored flexibility of a parasitoid community in response to the massive fluctuations of spruce budworm densities. Indeed, we did find flexibility at the community-level. On balsam fir, the aggregated response of all parasitoid taxa tracked the changing relative abundances of spruce budworm and other caterpillars, causing changes in the interaction strength distributions. Furthermore, when spruce budworm populations decreased, parasitoid diversity on balsam fir decreased. This flexible response of using other caterpillar species to offset the lack of spruce budworm most of the time appears integral to the functioning of the spruce budworm – parasitoid food web. Other caterpillar species are clearly important, yet here we have explored parasitism of other caterpillar species solely on balsam fir. A more thorough understanding of the flexible response by the parasitoids requires an examination of parasitism of other caterpillar species on hardwood trees, the trees that, when spruce budworm are rare, support a persistent reservoir population of caterpillars (Barbosa *et al.* 2000).

If the parasitoid community shifts from attacking caterpillars on hardwoods to attacking spruce budworm on balsam fir, then the spruce budworm system exhibits coupling, an important stabilising ecological mechanism. The parasitoids could be coupling two separate resource compartments: the hardwood trees and other caterpillar species, and the balsam fir trees and spruce budworm. To date, most coupling studies have focused on coupling of spatially separated resource compartments (spatial coupling) (e.g. Schindler & Scheuerell 2002; Baskerville *et al.* 2011). However, McCann *et al.* (2005), McMeans *et al.* (2015), and Humphries *et al.* (2017) suggested that resource compartments can also be separated in time, and any consumer that accumulates resources from these different resource compartments would exhibit temporal coupling. We suggest that not only are the parasitoids of spruce budworm coupling balsam fir and hardwood resource compartments in space but also couple in time. Overall, we hypothesize that the parasitoids of spruce budworm are spatiotemporally coupling the balsam fir and hardwood resource compartments. Because coupling of spatially separated resource compartments has been relatively well explored,

using the spruce budworm system to examine coupling of temporally separated resource compartments is important to understand the full extent of coupling in ecosystems.

One factor suggested to temporally separate resource compartments is periodic variation in resources (McMeans *et al.* 2015). Seasonality is the most conspicuous example of resources periodically varying over time. An example of seasons causing periodic resource variation is phytoplankton dominating Arctic marine carbon flux in summer and detritus dominating Arctic marine carbon flux in winter (McMeans *et al.* 2015). Periodic variation is not restricted to seasons but can be found at other scales including diurnal and multi-year cycles. Drivers of this periodic variation include abiotic (e.g. temperature changes) or biotic (e.g. insect outbreaks) factors. Therefore, the temporal periodicity of the spruce budworm population cycle presents a fantastic opportunity to examine whether a community of consumers can temporally couple resource compartments.

Interestingly, the spruce budworm – parasitoid food web is similar to the example of temporal coupling in an Arctic food web suggested by McMeans *et al.* (2015). In McMeans *et al.*'s (2015) example, the detritus is constantly available but at low levels. Instead, the phytoplankton abundance increases every summer and decreases every winter. In the spruce budworm – parasitoid food web, the other caterpillar species on hardwood species are constantly available but at low levels (see Figures 3.1 & 3.2 for illustrations of the temporal coupling in the spruce budworm – parasitoid food web). Spruce budworm, though, increase every 35 years and then decrease to obscurity. Over the 35 years, the mechanism creating periodic variation is a predator – prey cycle. However within a year, seasons cause spruce budworm to be periodically available as caterpillars (in May/June) and then unavailable as moths or when they are overwintering in balsam fir foliage (any months apart from May/June).

We may expect to find temporal coupling at multiple temporal scales because some parasitoid species have a single generation in a year and other parasitoid species have multiple generations within a year. Therefore, there is a gradient of some parasitoid species attacking only spruce budworm within a single year (single generation within a year) to other parasitoid species attacking spruce budworm at the beginning of the summer and then attacking different caterpillar species in which to overwinter (multiple generations within a year) (Hébert *et al.* 1989; Maltais *et al.* 1989; O'Hara 2005). Even the parasitoid species that

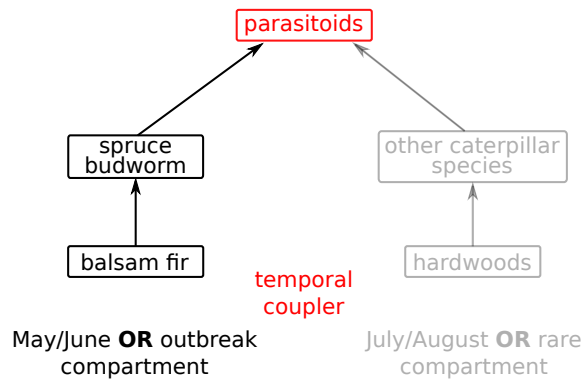


Figure 3.1: Illustration of the spruce budworm – parasitoid food web that includes the basal resources of balsam fir and hardwood trees. Balsam fir and spruce budworm are one resource compartment occurring in May/June or when spruce budworm are outbreaking. Hardwoods and other caterpillar species are another resource compartment occurring in July/August or when spruce budworm are rare. The community of parasitoids spatiotemporally couples these two resource compartments. Figure inspired by the Arctic marine food web figure in McMeans *et al.* (2015)

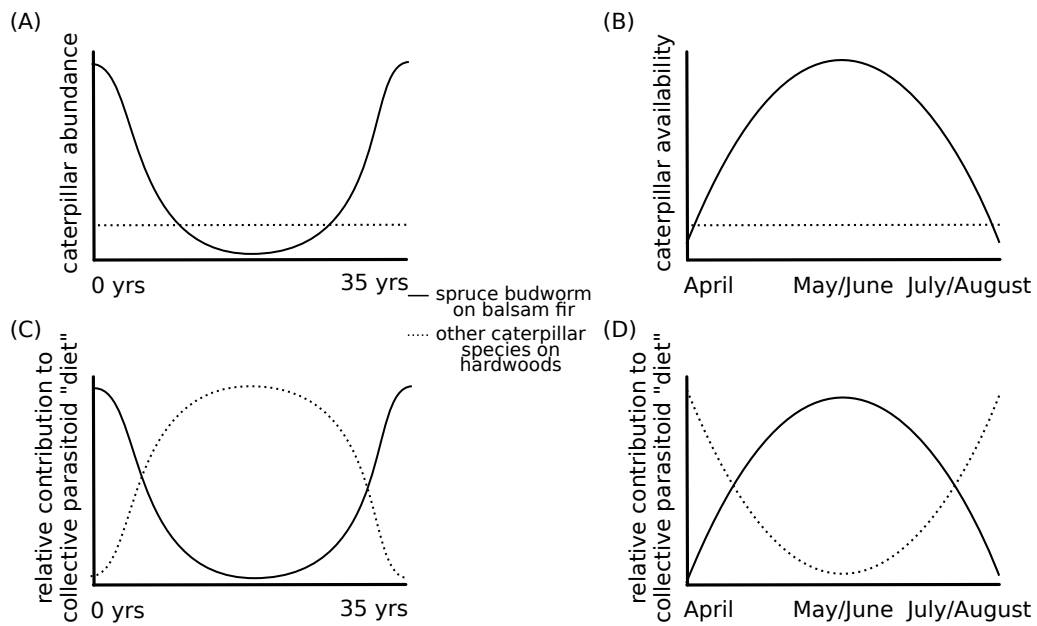


Figure 3.2: Hypothetical illustration of temporal separation of balsam fir and hardwood resource compartments. (A) Caterpillar abundance over 70 years and (B) caterpillar availability within a summer for spruce budworm on balsam fir and other caterpillar species on hardwoods. (C) Relative contribution of spruce budworm on balsam fir and other caterpillar species on hardwoods to the collective parasitoid “diet” over 70 years and (D) within a summer.

attack only spruce budworm within one year do attack other caterpillar species over multiple years due to different generations being able to attack different hosts (O'Hara 2005; Cossentine *et al.* 2007). Consequently depending on the parasitoid functional group, we would expect spatiotemporal coupling to occur over the length of the spruce budworm population cycle and within a year.

To examine whether the spruce budworm parasitoids exhibited spatiotemporal coupling, we used stable isotope analysis of parasitoids caught in the 1980s. With stable isotope analysis, we were effectively examining the relative contributions of spruce budworm on balsam fir and other caterpillars on hardwoods to the “diet” of the parasitoid community. We predicted that (1) the parasitoids that attack only spruce budworm within a year should exhibit the least change in relative contributions of spruce budworm and other caterpillars over multiple years, (2) the parasitoids that attack spruce budworm and likely attack other caterpillars within a year should exhibit a medium amount of change in relative contributions of spruce budworm and other caterpillars over multiple years, and (3) the parasitoids that are forced to alternate between spruce budworm and other caterpillars within a year should exhibit a change in the relative contributions of spruce budworm and other caterpillars within a year but should not exhibit any change in relative contributions over multiple years.

3.3 Materials and Methods

All sampling was done in the Acadia Research Forest near Fredericton (66°25'W, 46°00'N). We sampled fourteen parasitoid Dipteran species and three parasitoid Ichneumonid and Braconid species using three Malaise traps each at low, mid, and high crown heights in a single balsam fir dominated plot in the summers of 1982, 1983, 1986, and 1987. The plot was outside areas of spruce budworm insecticide application and was heavily defoliated by 1985 (60% tree mortality). The Malaise traps were separated by approximately 100 metres and were placed on the same trees every year beginning in May until September. The parasitoids were collected daily and were stored in 70% ethanol at -7°C (except the parasitoids from 1982, which were stored without ethanol but still in the freezer). In 2017, these parasitoids were separated into three functional groups: group one attack only spruce budworm within a year, group two attack spruce budworm and likely caterpillars on hardwoods within a year, and group three alternate between attacking spruce budworm and caterpillars on hardwoods within a single year. These three groups were then further split into two seasons: May/June

(spruce budworm present), and July/August/September (spruce budworm absent). When there were fewer than 50 total individuals in a group and season, we took all legs and wings off all individuals. When there were more than 50 total individuals in a group and season, we randomly selected 50 individuals and ensured the proportions of selected individuals of each species matched the proportions of total number of individuals for each species within each group and season (see Figures A.3, A.4, & A.5 for the abundances of all parasitoids). For these individuals, legs and wings were removed and the approximate mass of legs and wings was kept constant for all individuals. Legs and wings were combined for each group and season and were dried at 60°C for at least 48 hours. We used only legs and wings for stable isotope analysis because many adult parasitoids consume non-host nutrient sources (Benelli *et al.* 2017). Legs and wings have a slower turnover rate compared to other body parts, and consequently stable isotope ratios from the legs and wings will reflect the diet of the immature parasitoid (Gratton & Forbes 2006). We also sampled new foliage from balsam fir and a variety of hardwoods and any spruce budworm and other caterpillar species found on the foliage from nine plots during the summer of 2017. All samples were analysed for carbon and nitrogen stable isotopes by the University of Windsor Great Lakes Institute for Environmental Research (Windsor, ON, Canada) laboratories.

Balsam fir foliage $\delta^{13}\text{C}$ was less negative than hardwood foliage $\delta^{13}\text{C}$ by 2.4% ($t = 2.183$, $df = 40.219$, $P < 0.01$, Welch two sample t-test). Similarly, $\delta^{13}\text{C}$ for caterpillars sampled from balsam fir trees were less negative by 4.1% than caterpillars sampled from hardwood trees ($t = 3.161$, $df = 39.161$, $P < 0.01$, t-test). However, likely due to the parasitoids being stored in ethanol for over 30 years, the $\delta^{13}\text{C}$ values for the parasitoids were completely different from the foliage and caterpillar $\delta^{13}\text{C}$ values (less negative by 16.3%). Furthermore, we did not find any statistical differences in $\delta^{15}\text{N}$ between foliage and caterpillars of balsam fir and hardwood trees. Consequently, we were not able to use mixing models to determine the percentage of balsam fir or hardwood caterpillars that the parasitoids were attacking. Because we know there is a difference in $\delta^{13}\text{C}$ between the tree types and between the caterpillars, instead, we compared the relative change in $\delta^{13}\text{C}$ over time for each parasitoid group.

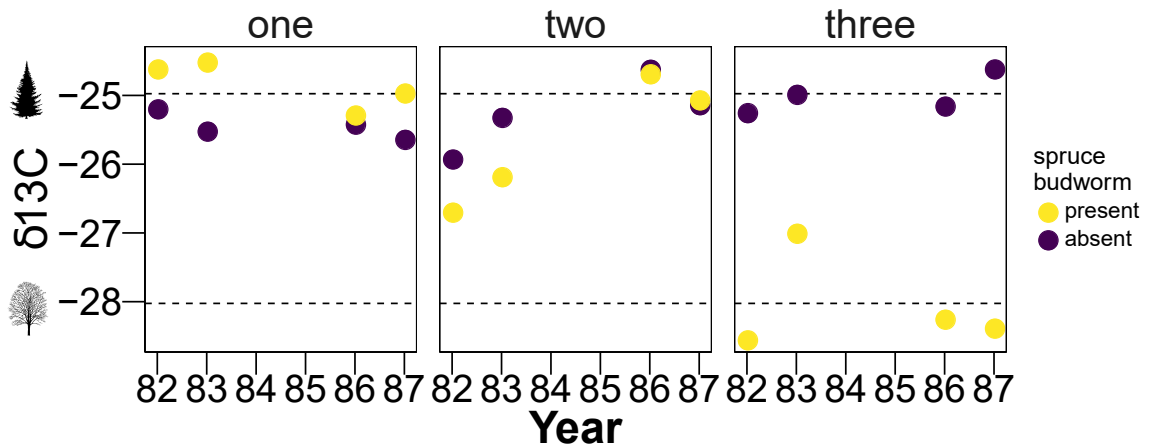


Figure 3.3: $\delta^{13}\text{C}$ for three groups of parasitoid species: group one attack only spruce budworm within a year, group two attack spruce budworm and likely caterpillars on hardwoods within a year, and group three alternate between attacking spruce budworm and caterpillars on hardwoods within a single year. Spruce budworm populations peaked in 1985. $\delta^{13}\text{C}$ was measured on parasitoids captured in May and June when spruce budworm were present and in July, August, and September when spruce budworm were absent. Dashed lines depict the average $\delta^{13}\text{C}$ value for the group three parasitoids when spruce budworm were present and absent (used as estimates for the balsam fir and hardwood foliage $\delta^{13}\text{C}$ values). Balsam fir and red maple by Natural Resources Canada, Canadian Forest Service - publicly available.

3.4 Results and Discussion

The parasitoids in group three showed a clear difference of 12.2% in $\delta^{13}\text{C}$ between when spruce budworm were present and absent (Season: $L = 19.681$, $P < 0.0001$, $df = 1$, log likelihood ratio test, Figure 3.3). When spruce budworm were present, group three parasitoids had more negative $\delta^{13}\text{C}$ values similar to hardwood trees. When spruce budworm were absent, group three parasitoids had less negative $\delta^{13}\text{C}$ values similar to balsam fir trees. Between years, $\delta^{13}\text{C}$ did not change significantly (Year: $L = 0.00187$, $P = 0.965$, $df = 1$, log likelihood ratio test). These findings match our prediction because the results suggest that group three parasitoids emerged from caterpillars on hardwood trees when spruce budworm were present and emerged from spruce budworm on balsam fir trees to attack other caterpillars when spruce budworm were absent. Because we found a difference in $\delta^{13}\text{C}$ values between when spruce budworm were present and absent for group three parasitoids, matching our prediction, we can be confident that similar changes in $\delta^{13}\text{C}$ for the other

groups were due to the parasitoids changing their attack rates on spruce budworm on balsam fir and other caterpillars on hardwoods. Furthermore, we can use the average $\delta^{13}\text{C}$ for when spruce budworm are present and absent as estimates for the balsam fir and hardwood foliage $\delta^{13}\text{C}$ values.

We found that $\delta^{13}\text{C}$ values for group one parasitoids became slightly more negative by approximately 0.5% each year (Year: $\beta = -0.0879$, $L = 6.417$, $P = 0.0113$, $df = 1$, log likelihood ratio test, Figure 3.3), and group one parasitoids caught when spruce budworm were absent had more negative $\delta^{13}\text{C}$ values by 2.4% compared to group one parasitoids caught when spruce budworm were present (Season: $\beta = -0.598$, $L = 11.762$, $P < 0.001$, $df = 1$, log likelihood ratio test, Figure 3.3). Although statistically significant, we are skeptical that the changes in $\delta^{13}\text{C}$ values over the four years of sampling and within a year are biologically important because the changes are significantly smaller than the changes exhibited by the group three parasitoids. Furthermore, for all years and within a year the $\delta^{13}\text{C}$ values were close to the balsam fir value estimated using the group three parasitoids. If not biologically important, then we could conclude that the group one parasitoids exhibited little spatiotemporal coupling and stayed on balsam fir over the four years that were sampled supporting our first prediction. The studies to date on the parasitoids in this group generally conclude that the parasitoids attack spruce budworm more than other caterpillars (O'Hara 2005; Cossentine *et al.* 2007). Therefore, the small change in $\delta^{13}\text{C}$ is unsurprising. However, this suggests that group one parasitoids do not attack other caterpillars on hardwoods as much as we think, and thus we still know little about how their populations are supported when spruce budworm are rare. Clearly, sampling of these parasitoids at least ten years after a peak of spruce budworm is required to ascertain what caterpillar species are supporting their populations.

We found that the $\delta^{13}\text{C}$ values for group two parasitoids became less negative over time by approximately 1% each year (Year: $\beta = 0.275$, $L = 8.797$, $P < 0.01$, $df = 1$, log likelihood ratio test, Figure 3.3). In contrast to the group one parasitoids, this change is larger and likely biologically important. Consequently, these parasitoids likely attacked other caterpillars on hardwoods and then attacked spruce budworm on balsam fir. There is the qualitative suggestion that group two parasitoids attacked spruce budworm the most around 1986 after the spruce budworm peak in 1985, but without more years of sampling, we cannot equivocally conclude this. However, Royama *et al.* (2017) corroborates this supposition by stating that these parasitoid taxa increase their parasitism rates on spruce budworm after group one

parasitoids decrease their parasitism rates (see Table A.2 to compare the parasitoid groups in this study and in Royama *et al.*'s (2017) study).

Remarkably, despite our limited data and the parasitoids stored in ethanol for 30 years, we found a pattern in $\delta^{13}\text{C}$ for the different parasitoid groups. We found indications of spatiotemporal coupling over multiple years and within a year in the spruce budworm – parasitoid food web. Spruce budworm populations are increasing again in eastern North America (Bouchard *et al.* 2018), presenting a rare opportunity to explicitly test the spatiotemporal coupling hypothesis in this system with more years and more plots. Furthermore, adding fatty acid analysis alongside the use of $\delta^{13}\text{C}$ would strengthen future analyses because the fatty acid compositions differ between softwoods and hardwoods more than $\delta^{13}\text{C}$ (Mueller *et al.* 2012; Visser *et al.* 2013). We have shown that hardwoods are important for this example of spatiotemporal coupling to occur and therefore are integral in sustaining the flexible response of the parasitoid community. Coupling is known to confer stability to ecosystems because the coupling mutes the oscillations of the populations of lower trophic levels. In the spruce budworm system, spatiotemporal coupling could mute the spruce budworm oscillations, leading to less severe outbreaks. Consequently, to reduce the impact of spruce budworm on the forestry industry, we recommend increasing the hardwood diversity in eastern North America to maintain the flexibility and spatiotemporal coupling in the spruce budworm – parasitoid food web. Overall, our study has deepened our understanding of the mechanisms that enable individuals, species, and food webs to respond to variability. Species loss threatens these mechanisms, and consequently, maintaining these mechanisms is imperative to enable ecosystems to persist in spite of human-caused global environmental and ecosystem change.

Chapter 4

Epilogue

Because of the variation in resources and abiotic conditions found at many scales in nature, animals must respond to this variation to survive and reproduce. Individual animals may respond to resource variation with behavioural or evolved diet shifts called adaptive responses (Kondoh 2003). Potentially, many species could be exhibiting these adaptive responses, and when measuring a whole community, we could find a whole community flexible response to changing resources. In Chapter 2, we identified a flexible response by a parasitoid community in response to changing spruce budworm densities. We did not identify the specific mechanism for how the flexibility is produced, but from our study and previous knowledge we suspect that a combination of species composition turnover over time and species diet switching produces this community-level flexibility. The fluctuating interaction strength distributions that we found has unexplored consequences for the stability of the spruce budworm – parasitoid system and food webs in general. The example of community-level flexibility found by Bartley (2017) and our example suggest that community-level flexibility is an important aspect of many systems and we should continue to identify more examples of flexibility, the mechanisms producing flexibility, and any beneficial consequences of flexibility.

Arguably, one method of flexibility is coupling of resource compartments separated in space and/or time. Temporal coupling is relatively unexplored compared to spatial coupling, and yet the mechanisms producing temporal coupling and the consequences of temporal coupling should be similar to spatial coupling (McCann *et al.* 2005; McMeans *et al.* 2015, 2016). In all likelihood, there is a continuum of coupling of resource compartments

separated in space and time, thus we used the term spatiotemporal coupling. In Chapter 3, we found indications of coupling of the balsam fir and hardwood resource compartments by the parasitoids of spruce budworm. The extent of coupling differed depending on the parasitoid group which supports our suggestion above that the community-level flexibility is likely caused by a mixture of species turnover and diet switching. Again, the lack of carbon isotope change for the group one parasitoids begs the question of how these parasitoids are supported when spruce budworm are rare. Regardless, we found spatiotemporal coupling at the scale of multiple years and within a year. Amazingly with such little data, we still found trends which bodes well for future research to fully examine this hypothesis with increased sampling of balsam fir and hardwoods and by using a combination of stable isotopes and fatty acids.

Spruce budworm is a pest species of balsam fir, a financially important wood resource in Eastern North America. Consequently, our research contributes to identifying methods to reduce spruce budworm outbreaks. In this thesis, there are indications that spatiotemporal coupling of the balsam fir and hardwood resource compartments is important to produce the flexibility found in the parasitoid community. This coupling and flexibility likely mutes spruce budworm population cycles, thus reducing the severity of spruce budworm outbreaks. To aid in reducing spruce budworm outbreaks, further research is required to exactly ascertain the extent of spatiotemporal coupling in the spruce budworm system and then to ascertain the spatial scales at which hardwood trees should be placed to aid this coupling. Systematic sampling of hardwood trees to compare the caterpillars and parasitoids on hardwoods versus softwoods combined with stable isotope and fatty analysis over the peak and decline of spruce budworm populations would help answer the extent of spatiotemporal coupling. Experimental manipulations of hardwood diversity within stands and surrounding stands, again combined with stable isotope and fatty acid analysis would help to answer the spatial scale of the coupling.

In light of human-caused change impacting the world's ecosystems, understanding the mechanisms by which organisms and communities respond to variability is integral to conserving our ecosystems. Community-level flexibility is one such mechanism that we believe is important for communities to respond to variability. Finding multiple examples of community-level flexibility could suggest that food webs can recombine up to an unknown extent to respond to human-caused variability. Community-level flexibility is a relatively

new concept and more work is required to understand the specific mechanisms behind flexibility and how flexibility can transfer to communities responding to human-caused variability. Communities and ecosystems are amazingly complicated and likely have a myriad methods to respond to variation. As ecologists and conservationists, we must tap these myriad methods in order to preserve our bounteous biodiversity.

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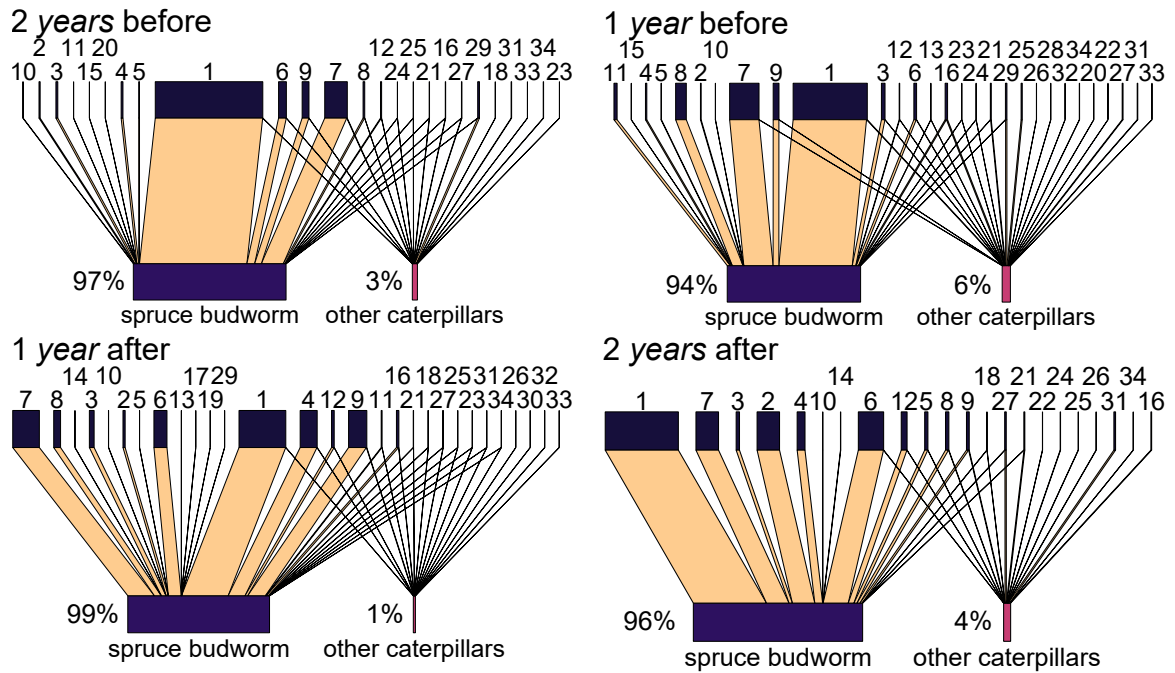
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Appendix



Parasitoids

- | | | |
|-----------------------------------|-----------------------------------|---|
| 1. <i>Apanteles fumiferanae</i> | 13. <i>Scambus</i> sp. | 25. <i>Chelonus</i> sp. |
| 2. <i>Lypha fumipennis</i> | 14. <i>Tranosema rostrale</i> | 26. <i>Campoplex</i> sp. |
| 3. <i>Apechthis ontario</i> | 15. <i>Dolichogenidea absona</i> | 27. <i>Bassus binominata</i> |
| 4. <i>Dirophanes hariolus</i> | 16. Und parasitoids | 28. <i>Diadegma</i> sp. |
| 5. <i>Tranosema tenuifemur</i> | 17. <i>Nemorilla pyste</i> * | 29. <i>Macrocentrus linearis iridescens</i> |
| 6. <i>Meteorus trachynotus</i> * | 18. <i>Dirophanes</i> sp. | 30. <i>Microgaster</i> sp. |
| 7. <i>Glypta fumiferanae</i> | 19. <i>Meteorus versicolor</i> | 31. <i>Orgilus</i> sp. |
| 8. Und Tachinidae | 20. <i>Diadegma pulicalvariae</i> | 32. <i>Bassus dimidiator</i> |
| 9. Und Ichneumonoidea | 21. <i>Apanteles morrissi</i> | 33. <i>Perilampus</i> sp. |
| 10. <i>Actia interrupta</i> | 22. <i>Lissonota acrobasisis</i> | 34. <i>Glypta</i> sp. |
| 11. <i>Itoplectis conquisitor</i> | 23. <i>Apanteles milleri</i> | |
| 12. <i>Apanteles</i> sp. | 24. <i>Charmon extensor</i> | |

Figure A.1: Graphical representations of the number of emergences of each parasitoid taxon (top boxes) from spruce budworm and other caterpillars (bottom boxes) over time. The width of links is proportional to the fraction of emergences of each parasitoid taxon from either spruce budworm or other caterpillars. The width of the bottom boxes are proportional to the number of emergences from spruce budworm versus other caterpillars, and the percentages show this quantitatively. Four different *years* are shown, where all plots were combined within a *year*: two *years* before the peak, one *year* before the peak, one *year* after the peak, and two *years* after the peak. Und is a group of unidentified parasitoid within the stated taxonomic group. A star denotes a species that requires an alternate caterpillar host to overwinter in. To find the corresponding species in Eveleigh *et al.* (2007), see Table A.1.

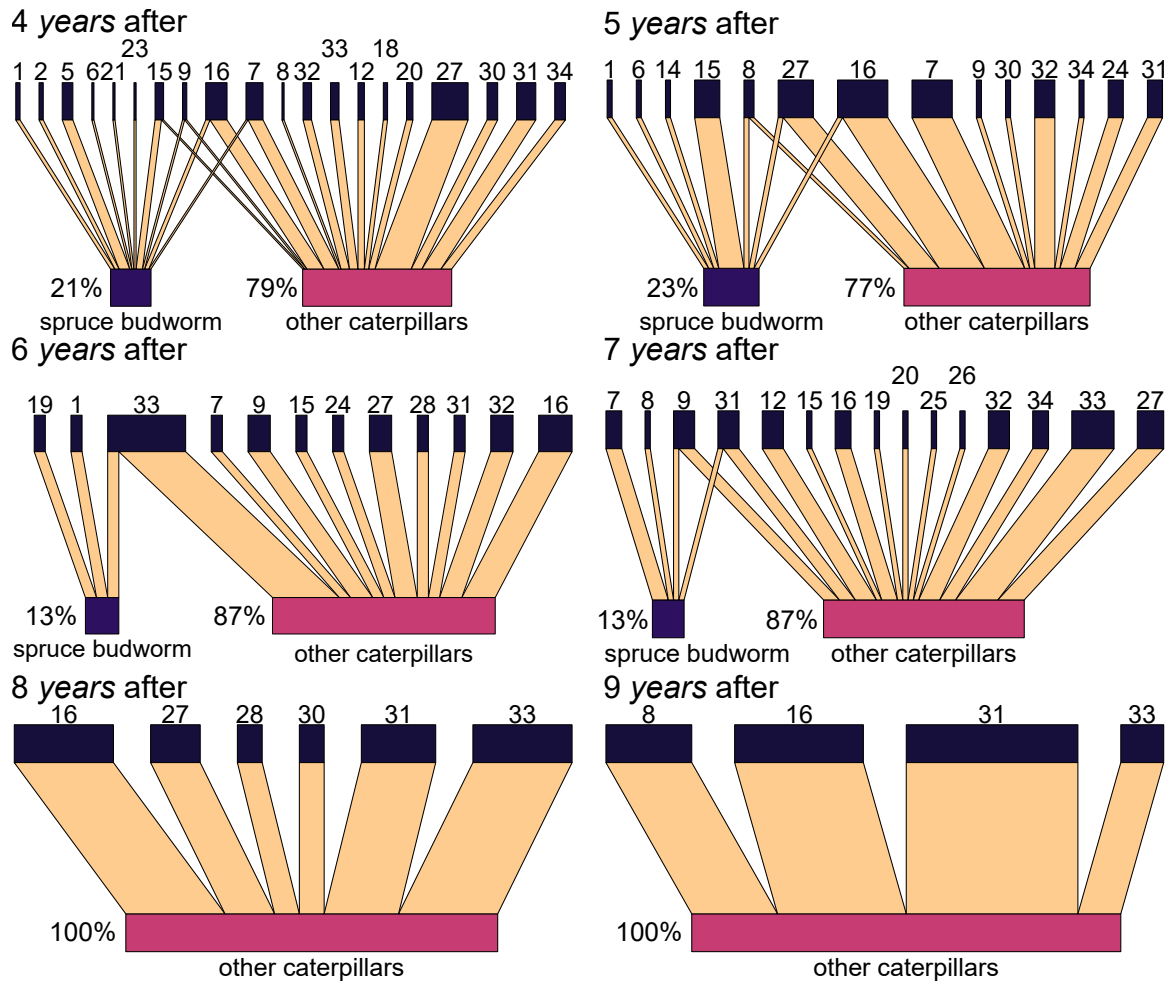


Figure A.2: Graphical representations of the number of emergences of each parasitoid taxon (top boxes) from spruce budworm and other caterpillars (bottom boxes) over time. Four different *years* are shown: four *years* after the peak, five *years* after the peak, six *years* after the peak, seven *years* after the peak, eight *years* after the peak, and nine *years* after the peak.

Our parasitoids	Eveleigh <i>et al.</i> (2007) PNAS parasitoids
1. <i>Apanteles fumiferanae</i>	9. <i>Apanteles fumiferanae</i>
2. <i>Lypha fumipennis</i>	2. <i>Lypha fumipennis</i>
3. <i>Apechthis ontario</i>	15. <i>Apechthis ontario</i>
4. <i>Dirophanes hariolus</i>	14. <i>Dirophanes hariolus</i>
5. <i>Tranosema tenuifemur</i>	66. <i>Synetaeris</i> sp.
6. <i>Meteorus trachynotus</i>	11. <i>Meteorus trachynotus</i>
7. <i>Glypta fumiferanae</i>	10. <i>Glypta fumiferanae</i>
8. Und Tachinidae	65. Tachinid sp.
9. Und Ichneuemoidea	No corresponding taxonomic group
10. <i>Actia interrupta</i>	6. <i>Actia interrupta</i>
11. <i>Itoplectis conquisitor</i>	16. <i>Itoplectis conquisitor</i>
12. <i>Apanteles</i> sp.	67. <i>Apanteles</i> sp.
13. <i>Scambus</i> sp.	80. <i>Scambus</i> sp.
14. <i>Tranosema rostrale</i>	45. <i>Tranosema rostrale</i>
15. <i>Dolichogenidea absona</i>	18. <i>Dolichogenidea absona</i>
16. Und parasitoids	No corresponding taxonomic group
17. <i>Nemorilla pyste</i>	5. <i>Nemorilla pyste</i>
18. <i>Dirophanes</i> sp.	48. <i>Phaeogenes</i> sp.
19. <i>Meteorus versicolor</i>	60. <i>Meteorus</i> sp. (versicolor?)
20. <i>Diadegma pulicalvariae</i>	50. <i>Diadegma pulicalvariae</i>
21. <i>Apanteles morrissi</i>	19. <i>Apanteles morrissi</i>
22. <i>Lissonota acrobasis</i>	62. <i>Lissonota acrobasis</i>
23. <i>Apanteles milleri</i>	38. <i>Apanteles milleri</i>
24. <i>Charmon extensor</i>	22. <i>Charmon extensor</i>
25. <i>Chelonus</i> sp.	29. <i>Chelonus</i> sp.
26. <i>Campoplex</i> sp.	24. <i>Campoplex</i> sp.
27. <i>Bassus binominata</i>	20. <i>Bassus binominata</i>
28. <i>Diadegma</i> sp.	39. <i>Diadegma</i> sp.
29. <i>Macrocentrus linearis iridescens</i>	41. <i>Macrocentrus linearis iridescens</i>
30. <i>Microgaster</i> sp.	49. <i>Microgaster</i> sp. & 74. <i>Microgasterinae</i>
31. <i>Orgilus</i> sp.	21. <i>Orgilus</i> sp.
32. <i>Bassus dimidiator</i>	40. <i>Bassus dimidiator</i>
33. <i>Perilampus</i> sp.	54. <i>Perilampus</i> sp.
34. <i>Glypta</i> sp.	56. <i>Glypta</i> sp.

Table A.1: Parasitoid taxa found to attack spruce budworm and other caterpillars on balsam fir from this study compared to the corresponding parasitoid taxa found to attack spruce budworm in Eveleigh *et al.* (2007).

Group	Parasitoid Species	Group in Royama <i>et al.</i> (2017)
1	<i>Apanteles fumiferanae</i>	1
	<i>Glypta fumiferanae</i>	1
	<i>Smidtia fumiferanae</i>	2b
	<i>Lypha fumipennis</i>	2b
2	<i>Actia interrupta</i>	2b
	<i>Eumea caesar</i>	2b
	<i>Sarcophaga aldrichi</i>	NA
	<i>Nilea erecta</i>	NA
	<i>Hemisturmia parva</i>	NA
	<i>Agria affinis</i>	2b
	<i>Compsilura concinnata</i>	NA
	<i>Tachinomyia nigricans</i>	NA
3	<i>Meteorus trachynotus</i>	2a
	<i>Ceromasia auricaudata</i>	NA
	<i>Nemorilla pyste</i>	2b
	<i>Phryxe pecosensis</i>	2b
	<i>Madremyia saundersii</i>	2b
	<i>Tranosema rostrale</i>	2a

Table A.2: List of parasitoid species in each group used in the $\delta^{13}\text{C}$ analysis along with corresponding groups in Royama *et al.* (2017).

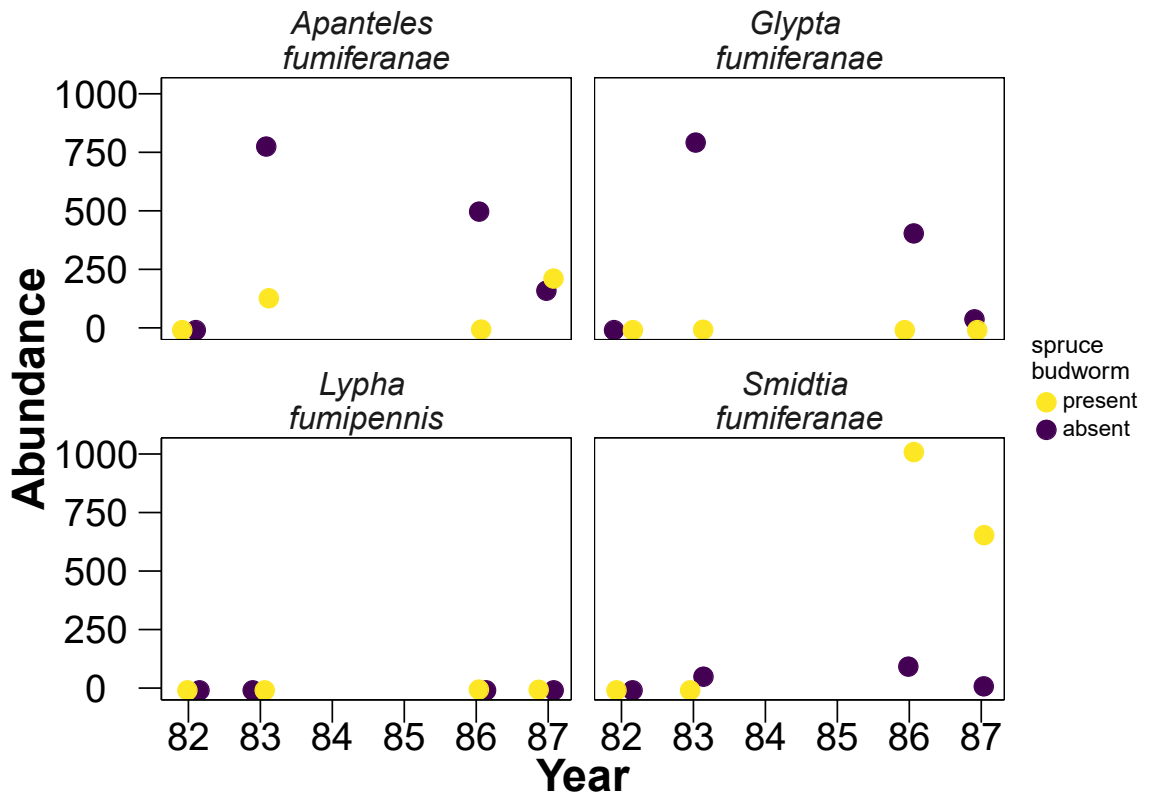


Figure A.3: Abundance of group one parasitoids caught by malaise traps in four years spanning either side of a spruce budworm population peak in 1985. Group one parasitoids attack only spruce budworm within a single year. Between years, group one parasitoids are capable of attacking other caterpillars but are not generally known to substantially attack other caterpillars.

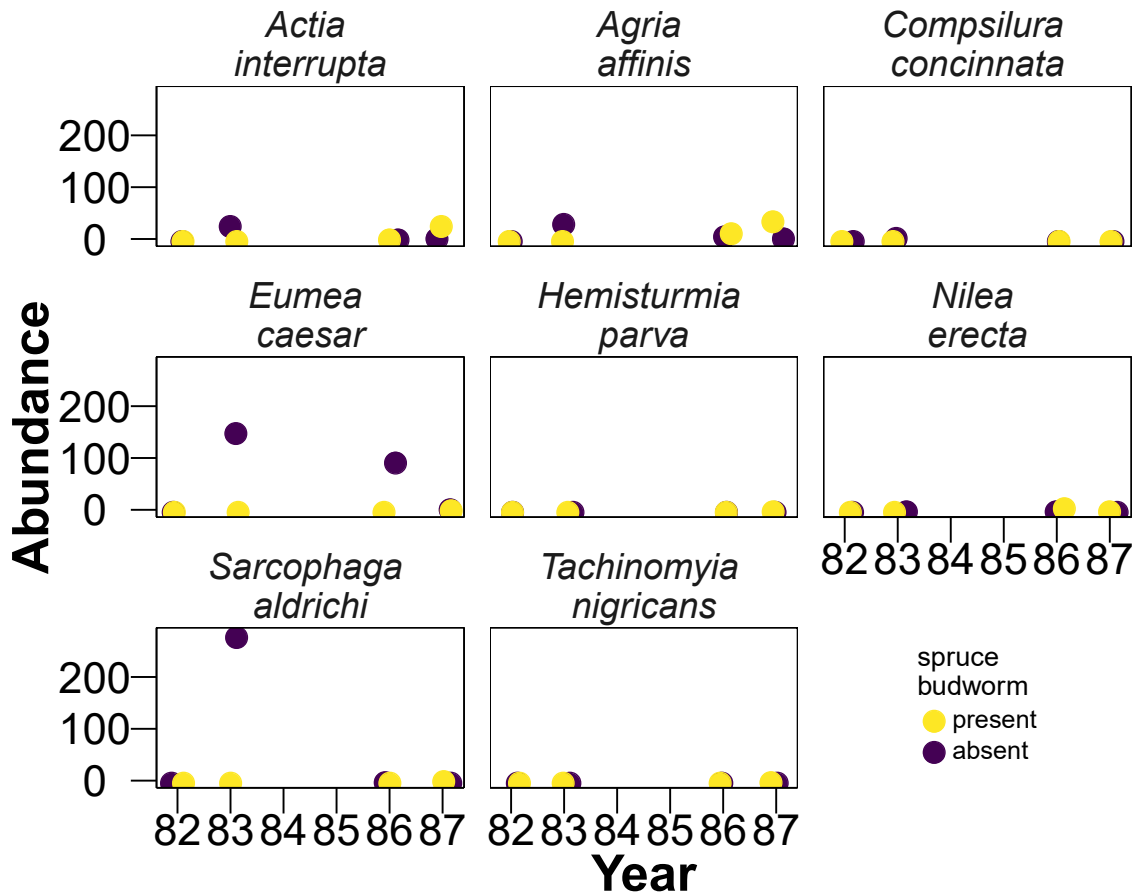


Figure A.4: Abundance of group two parasitoids caught by malaise traps in four years spanning either side of a spruce budworm population peak in 1985. Group two parasitoids attack spruce budworm and likely attack other caterpillars within a year. Between years, group two parasitoids are capable of attacking other caterpillars.

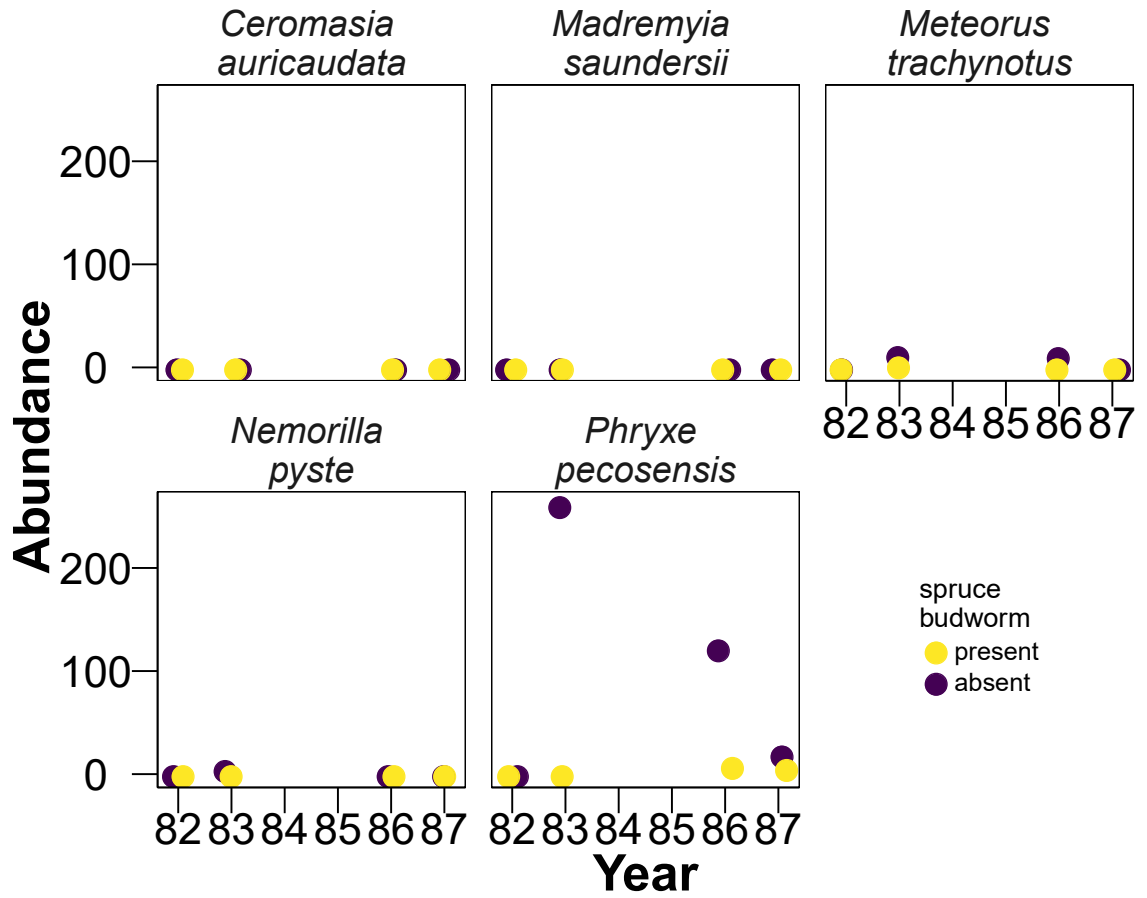


Figure A.5: Abundance of group three parasitoids caught by malaise traps in four years spanning either side of a spruce budworm population peak in 1985. Group three parasitoids alternate between attacking spruce budworm and other caterpillars within a year.