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ARTICLE

Parasitoid community responds indiscriminately to fluctuating spruce budworm (Lepidoptera: Tortricidae) and other caterpillars on balsam fir (Pinaceae)

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Abstract

The world is astoundingly variable, and organisms – from individuals to whole communities – must respond to variability to survive. One example of nature's variability is the fluctuations in populations of spruce budworm, *Choristoneura fumiferana* Clemens (Lepidoptera: Tortricidae), which cycle every 35 years. In this study, we examined how a parasitoid community altered its parasitism of budworm and other caterpillar species in response to these fluctuations. Budworm and other caterpillar species were sampled from balsam fir (Pinaceae) in three plots for 14 years in Atlantic Canada, then were reared to identify any emerging parasitoids. We found that the parasitoid community generally showed an indiscriminate response (*i.e.,* no preference, where frequencies dictated parasitism rates) to changes in budworm frequencies relative to other caterpillar species on balsam fir. We also observed changes in topology and distributions of interaction strengths between the parasitoids, budworm, and other caterpillar species as budworm frequencies fluctuated. Our study contributes to the hypothesis that hardwood trees are a critical part of the budworm–parasitoid food web, where parasitoids attack other caterpillar species on hardwood trees when budworm populations are low. Taken together, our results show that a parasitoid community collectively alters species interactions in response to variable budworm frequencies, thereby fundamentally shifting food-web pathways.

Introduction

Ecologists have long used equilibrium or steady-state assumptions to examine ecological patterns (Guichard and Gouhier 2014). Furthermore, food-web ecologists have routinely assumed fixed interaction strengths (May 1972; Allesina and Tang 2012). Although these are reasonable first approaches, nature is highly variable and provides many examples of nonequilibrium ecological patterns and flexible interactions (Levin 1998; Guichard and Gouhier 2014). However, human-driven impacts promise to significantly alter natural variation, and our understanding of how organisms and communities respond to natural variation remains limited (Cotton 2003; Ims *et al.* 2008). Examining how organisms, from individuals to whole communities, respond to both natural variation and changes in this

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natural variation caused by human modifications is therefore integral to the future management and conservation of our natural world.

Individual and species-level responses to variability – including behavioural and population changes (Armstrong *et al.* 2016) – can combine to produce community-level responses, which include species richness, species evenness, and total biomass changes (Keitt 2008; Supp and Ernest 2014). These individual and species-level responses can combine in a compensatory manner, maintaining constant community metrics, or in a synchronous manner, causing synchronous changes in community metrics (Keitt 2008). For example, Supp and Ernest (2014) found compensatory dynamics ensured the maintenance of constant community richness and evenness in terrestrial animal communities exposed to a disturbance. In contrast, Stephens *et al.* (2017) found that, although several sympatric small mammal species exhibited varying abundance responses to forest type, the whole community exhibited synchronous abundance and diversity changes over time. Regardless of the mechanisms, these community-level responses can have large implications on food-web dynamics and on ecosystem function (Kent *et al.* 2007; Gouhier *et al.* 2010).

One example of a community-level response to variability that has implications for the management of a major forest pest is the convergence of parasitoids on the periodic outbreaks of spruce budworm, *Choristoneura fumiferana* Clemens (Lepidoptera: Tortricidae) on balsam fir, *Abies balsamea* Miller (Pinaceae) (Eveleigh *et al.* 2007). Budworm has massive and relatively predictable outbreaks every 35 years, followed by periods of budworm rarity (Royama *et al.* 2005). This cycle is considered to be a predator–prey cycle, in which the predator is a complex of natural enemies, including insects that parasitise, then kill, caterpillar hosts (parasitoids; Pureswaran *et al.* 2016; Royama *et al.* 2017). These parasitoids collectively cause 30–90% mortality, depending on the surrounding forest composition and the point in the budworm cycle (Dowden *et al.* 1950; Cappuccino *et al.* 1998; Seehausen *et al.* 2014; Royama *et al.* 2017). When budworm densities increase, the parasitoid species collectively converge on those high densities, and that convergence can be measured as an increasing parasitoid diversity on balsam fir ("the birdfeeder effect"; Eveleigh *et al.* 2007). Because the parasitoid community has such a strong response to changing budworm populations, the budworm–parasitoid food web presents an excellent system to examine community responses to variability in host densities. Furthermore, an improved understanding of the parasitoid community response to budworm-density fluctuations could help forest managers act to better moderate the severity of budworm outbreaks.

What remains largely unknown about this budworm–parasitoid food web is how the parasitoid community interacts with other caterpillar species in relation to the fluctuations of budworm. We know that some budworm parasitoids are generalists that attack multiple species and that other parasitoid species are specialists that either exclusively or primarily attack budworm (Krombein *et al.* 1979; Eveleigh *et al.* 2007; Smith *et al.* 2011). The question that remains is: How are the parasitoid populations maintained when budworm is rare? Parasitoid populations very likely decrease when budworm densities decline, but depending on the parasitoid species, a reserve population of parasitoids might be maintained if it attacked other caterpillar species. As with the community-level response whereby parasitoids converge on high budworm densities, a community-level response whereby parasitoids attack other caterpillars when budworm densities decline could also be expected. Specifically, there is limited research on the relative attack rates of the parasitoid community on budworm and other caterpillar species as budworm densities change.

Whereas Eveleigh *et al.* (2007) provided a qualitative examination of the entire budworm food web on balsam fir, and Royama *et al.* (2017) examined the impact of parasitoids on budworm only, in the present exploratory study, we aimed to quantify the changing trophic interactions of parasitoids with both budworm and other caterpillar species on balsam fir as budworm densities changed from high to low. We analysed rearing data of budworm and other

caterpillar species collected from balsam fir branches that were sampled from 1982 to 1995. During this period, balsam fir branches were collected from three plots, and a representative sample of budworm and all other caterpillar species was placed into feeding vials so that mortality causes, including parasitoids, could be identified.

Using this dataset, we examined the parasitoid community's response to changing relative frequencies of budworm and other caterpillar species on balsam fir. Firstly, we examined patterns of host preference at the parasitoid community scale. Host preference was established by testing the relationship between the relative abundances of caterpillars and the relative abundances of parasitoid emergences from each caterpillar type. The underlying causes of the parasitoid community host–preference response were tested in two ways: by excluding the most abundant species and reevaluating community host preference and by testing for temporal species-diversity turnover.

Secondly, because parasitism rates and species turnover impact the structure and dynamics of food webs, we examined how the topology and interaction strengths of the budworm food web on balsam fir changed with fluctuating budworm frequencies. Overall, we found that the parasitoid community indiscriminately tracked changes in relative densities of budworm and other caterpillar species on balsam fir, exhibiting a collective response akin to a generalist consumer.

Materials and methods

Study sites

Three plots of approximately one hectare each were established in balsam fir forests in New Brunswick, Canada. Plot 1 was in the Acadia Research Forest, near Fredericton (46° 00′ N, 66° 25′ W). Balsam fir branches were sampled from this plot from 1982 to 1989. Because 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 from this plot from 1986 to 1995. In the late 1980s, the budworm populations in plots 1 and 2 were so low that plot 3 was added. Plot 3 is located approximately 170 km north of plots 1 and 2, near Saint-Quentin (47° 29′ N, 67° 15′ W). Balsam fir branches were sampled from plot 3 from 1988 until 1994, when budworm populations there also declined to a low level. All plots contained mostly balsam fir, but they also contained spruces (Pinaceae) and a variety of hardwood trees (Eveleigh *et al.* 2007). All plots were located outside areas of biopesticide application. Full details of the three plots and of 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.

Branch sampling

At the beginning of each season, a group of co-dominant balsam fir trees was selected in 20 random locations within each plot. Co-dominant trees were selected because the majority of balsam fir trees in the plots were co-dominant trees (Royama *et al.* 2017). 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 began emerging from diapause in the field, balsam fir branches were sampled approximately daily until the end of budworm adult eclosion (approximately 50 days). On each sampling day during the earlier years when 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 budworm populations were low, two or more branches were collected from each location to increase the number of collected budworm larvae at each sample date and location.

Caterpillar and parasitoid sampling

Overall, all caterpillars (budworm and other caterpillar species) were sampled from a subset of the collected branches, with the goal of sampling at least 100 budworm individuals. For branches sampled before budworm emergence from winter diapause, all caterpillars were collected for rearing from all 20 branches sampled. For branches sampled after budworm emergence from winter diapause, all caterpillars from one of the 20 sampled branches were reared. If at least 100 budworm were obtained for rearing from this branch, no more branches were selected for collection of caterpillars for rearing. If fewer than 100 budworm were obtained from the first branch selected, another branch was selected, and all caterpillars from that branch were collected and reared, even if the final total number of budworm collected exceeded 100. When budworm populations were low, obtaining more than 100 budworm individuals became difficult. As a result, all caterpillars that were found on all the sampled branches were collected for rearing.

All collected caterpillars were individually reared on artificial diet (McMorran 1965) and inspected every weekday for mortality. Rearing success of both budworm and other caterpillar species was high because all of these hosts feed on balsam fir and therefore readily feed on the artificial diet (see Supplementary material, Table S1 for the total number of budworm and other caterpillars reared in each relative year and plot). All parasitoids that emerged from any reared caterpillars were morphologically identified to genus and, where possible, to species. Any parasitoids unidentifiable to at least genus were excluded from our analysis. Eleven per cent of the total number of emergences from budworm or other caterpillars were excluded, due to this reason. It is important to note that budworm was implanted in plot 2 between 1990 and 1995 for manipulative experiments that are unrelated to the present study (see Eveleigh *et al.* 2007, SI Methods). These implanted budworms were not collected during sampling of budworm and other caterpillars for the present study.

Dataset preparation

Because we were interested in quantifying the trophic interactions of parasitoids that attack budworm, we excluded all parasitoid taxa that attacked only other caterpillar species. The 48 parasitoid taxa (listed in Fig. 3) found to attack budworm formed 81% of all recorded trophic interactions with other caterpillar species. Using Chao2 (function specpool, R package vegan, version 2.5.2; Oksanen *et al.* 2018), we checked how the exclusion of parasitoid taxa that attacked only other caterpillar species impacted our sampling of the total potential number of interactions between parasitoids and budworm or other caterpillar species. This subsetted dataset captured 74% of the potential interactions between parasitoids and budworm and 63% of the potential interactions between parasitoids and other caterpillar species. Furthermore, using the full original dataset, Eveleigh *et al.* (2007) established through rarefaction that changes in diversity of parasitoid species were not due to sampling artefacts. As a result, we are confident that any patterns identified in the analyses below are not due to changes in branch sampling intensity but are due to underlying ecological mechanisms.

Parasitoid community host preference

To examine how the parasitoid community uses budworm or other caterpillar species on balsam fir, we calculated two values for every combination of relative year and plot: the ratio of parasitoid emergence from budworm to other caterpillar species for all parasitoid taxa combined and the ratio of abundances of budworm to other caterpillar species. For this relationship, we use the term "preference". Here, preference is applied to the community level, similarly to how preference is applied to the population level in Krebs (2014). It should also be noted that "relative year" (and years before and after peak; see Fig. 4) refers to a created

variable, where zero was set as the relative year at which budworm populations peaked in each plot (budworm peaked in 1985, 1985, and 1991 for plots 1, 2, and 3, respectively). We ran a generalised least squares regression with the log10 of the ratio of emergence (hereafter referred to as "relative budworm utilisation") as the response variable and with the log10 of the ratio of the abundances of budworm to other caterpillar species (hereafter referred to as "relative budworm frequency"), plot, and their interaction as the explanatory variables (function gls, R package nlme, version 3.1-145; Pinheiro *et al.* 2018). We fitted the full model using maximum likelihood estimation, then used backwards selection with likelihood ratio tests to select the final fixed effects. We refitted the final model using restricted maximum likelihood estimation to give unbiased maximum likelihood estimation predictors (Zuur *et al.* 2009). Following the methods in Greenwood and Elton (1979), we assessed whether the parasitoid community host preference was frequency dependent, where a slope that differs from "1" indicates frequency-dependent host preference and an intercept that differs from "0" indicates frequency-independent preference. The interaction of relative budworm frequency and plot was significant (see the Results section); therefore, we performed separate linear regressions for each plot, using relative budworm frequency as the explanatory variable and relative budworm utilisation as the response variable. From these linear regressions, we used one-sample *t*-tests to test whether the slopes differed from "1" and the intercepts differed from "0".

We wanted to test two underlying causes of the parasitoid community host preference: (1) whether the parasitoid community host preference was driven by a single parasitoid taxon or whether it was driven by the whole community and (2) whether community composition changes over time. To test whether a single parasitoid taxon or the whole community drove preference, we first determined the three most frequently emerging parasitoid taxa. We determined only these three parasitoid taxa because they comprised 73% of the total number of emergences from budworm and other caterpillars. We then removed, in turn, the top parasitoid taxon, the top two parasitoid taxa, and the top three parasitoid taxa from the data. Then, using these three datasets, we ran linear regressions for each plot, with relative budworm frequency serving as the explanatory variable and relative budworm utilisation serving as the response variable. Using one-sample *t*-tests, we compared the slopes and intercepts for each plot when the one, two, and three most abundant parasitoid taxa were excluded, with the corresponding plot slopes and intercepts produced in the linear regression with all parasitoid taxa included. To examine community composition in parasitoid taxa over time, we ran a nonmetric multidimensional scaling analysis using the Bray–Curtis dissimilarity measure (function metaMDS, R package vegan, version 2.5.2; Oksanen *et al.* 2018). The community matrix for calculating the Bray–Curtis dissimilarities consisted of the abundances of individual taxa divided by the total number of parasitoid emergences (all taxa) for each relative year and plot. We ran a permutational multivariate analysis of variance between four groups that described the phase of the budworm population cycle that each year was in (function adonis, R package, vegan, version 2.5-6). The four groups were "before the peak" (three and two relative years before the peak), "during the peak" (one relative year before the peak, the peak, and one relative year after the peak), "after the peak" (two and three relative years after the peak), and "endemic" (4 to 10 relative years after the peak). In this permutational multivariate analysis of variance, we used the Bray–Curtis dissimilarity measure, constrained permutations within each plot, and maintained the temporal order of permutations.

Food-web topology and interaction strengths

Because parasitism rates and species turnover impact the structure and dynamics of food webs, we assessed how the topology and interaction strengths of the budworm food web on balsam fir changed with fluctuating budworm densities. To examine changes in topology, we produced visual

bipartite food webs, using the number of emergences of each parasitoid taxon from either budworm or other caterpillar species for every relative year (R package bipartite, version 2.15; Dormann *et al*. 2008). To examine changes in interaction strengths, we calculated the ratio of the median to maximum interaction strengths for every relative year, where the number of emergences was used for interaction strengths. We note that using the number of emergences or the per capita emergences for calculating the ratio of median to maximum interaction strengths yields the same answer. To reduce the biasing of the median to maximum interaction strength ratio by low caterpillar frequencies, we removed any median:maximum value where fewer than 50 caterpillars were collected (budworm and other caterpillars were counted separately). To assess how the distribution of weak to strong interaction strengths changed over time, we ran separate linear models for budworm and other caterpillars with the response variable of the ratio of median to maximum interaction strengths and the explanatory variables of relative year, relative year^2, and plot. To simplify the model, four was added to each relative year to make negative relative years positive (–3 relative year became 1, and 10 relative year became 14).

All analyses were done using R, version 3.6.3 (R Core Team 2012).

Results

Parasitoid community host preference

The final model explaining relative budworm utilisation included the explanatory variables of relative budworm frequency, plot, and their interaction (relative budworm frequency:plot interaction, $L = 11.429$, $P = 0.0033$, df = 1, log-likelihood ratio test; Fig. 1).

The slopes of plots 1 and 2 did not significantly differ from "1", nor did their intercepts significantly differ from "0" (Table 1). Plot 3 had a slope that significantly differed from "1" and an intercept that significantly differed from "0" (Table 1).

Excluding the most abundant parasitoid taxon with the most emergences from all caterpillars (*Apanteles fumiferanae* Viereck) (Hymenoptera: Braconidae), the two most abundant parasitoid taxa (*Apanteles fumiferanae* and *Glypta fumiferanae* Viereck) (Hymenoptera: Ichneumonidae), and the three most abundant taxa (*Apanteles fumiferanae*, *Glypta fumiferanae*, and *Smidtia fumiferanae* Tothill) (Diptera: Tachinidae) did not cause the slopes and intercepts for plots 1 and 2 to significantly differ from the plot 1 and 2 slopes and intercepts that resulted when all parasitoid taxa were included (Table 2). However, the opposite occurred with plot 3: excluding the most abundant, two most abundant, and three most abundant parasitoid taxa in plot 3 caused the slopes and intercepts to differ compared to when all parasitoid taxa were included (Table 2). The parasitoid community did not differ between before and during the peak, but the parasitoid community in these two periods differed from after the peak and during the endemic periods ($F = 5.918$, $P = 0.003$, 999 permutations, permutational multivariate analysis of variance; Fig. 2).

Table 1. Slopes and intercepts with corresponding *t* statistics, *P* values, and degrees of freedom for each plot. The explanatory variable in the linear models for each plot was relative budworm frequency. The response variable was relative budworm use.

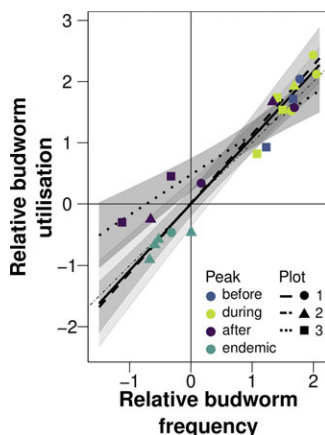| Plot	Slope	Slope *t*	Slope *P*	Intercept	Intercept *t*	Intercept *P*	df
1	1.082	0.823	0.448	0.002	0.011	0.992	5
2	1.128	0.997	0.365	0.014	0.113	0.914	5
3	0.656	−3.035	0.029	0.477	3.345	0.020	5

Fig. 1. With some differences between plots, generally the parasitoid community did not show a preference for budworm or other caterpillar species by either frequency or type. Relative budworm utilisation (log10 ratio of parasitoid emergences from budworm to other caterpillar species) for all parasitoid taxa used in our analysis as a function of the relative budworm frequency (log10 ratio of all sampled budworm and other caterpillars). Each point is a single relative year and a single plot. Shaded areas are 95% confidence intervals. The thin dashed line is the $y = x$ line.

Food-web topology and interaction strengths

Some parasitoid taxa (*e.g.*, *Diadegma pulicalvariae* Walley) (Hymenoptera: Ichneumonidae) were found throughout the sampling period but not in every year (Fig. 3 and Supplementary material, Figs. S4 and S5). Parasitoid taxa that were found in the food web consistently through time (*e.g.*, *Apanteles fumiferanae*) often changed between years from emerging from both budworm and other caterpillar species to emerging from just one caterpillar type (Fig. 3 and Supplementary material, Figs. S4 and S5). The distribution of interaction strengths for budworm changed from a skewed distribution dominated by weak interactions when budworm frequencies were high towards a uniform distribution when budworm frequencies were low (Year: $\beta = -0.040$, $t = -1.592$, $P = 0.132$; Year^2: $\beta = 0.008$, $t = 2.920$, $P = 0.011$; Fig. 4). The distribution of interaction strengths for other caterpillar species remained constant over time (Year: $\beta = -0.022$, $t = -0.526$, $P = 0.605$; Year^2: $\beta = 0.002$, $t = 0.951$, $P = 0.353$; Fig. 4)

Discussion

In our study, we have shown that this boreal spruce budworm–parasitoid food web is highly responsive and flexible in time to changing budworm frequencies. We used a 14-year dataset of host–parasitoid abundance to assess how parasitism rates and trophic interactions changed over the course of a budworm cycle. We found an aggregated whole-community correspondence of parasitism rates with caterpillar relative frequency (budworm:other caterpillar species frequency) and a change in topology and interaction strength distributions on balsam fir as budworm frequencies fluctuated.

We found that the parasitoid community's preference for budworm or other caterpillar species by either frequency or type depended on the plot (Fig. 1). The parasitoid community in plot 3 appeared to prefer budworm regardless of the relative densities of budworm and other caterpillars. In contrast, the parasitoid communities in plots 1 and 2 did not prefer budworm or other caterpillars by either frequency or type. This discrepancy may be explained by two possible explanations: (1) unlike plots 1 and 2, plot 3 was not sampled during the budworm endemic time period, and its slope therefore may be smaller without those multiple years of very low budworm populations having been sampled, and (2) there could be parasitoid

Table 2. Slopes and intercepts with corresponding *t* statistics, *P* values, and degrees of freedom when the three most abundant parasitoid taxa were dropped consecutively. The explanatory variables in this model were relative budworm frequency, plot, and their interaction. The response variable was relative budworm use.

| Dropped taxa	Plot	Slope	Slope *t*	Slope *P*	Intercept	Intercept *t*	Intercept *P*	df
A. fumiferanae	1	0.995	−0.0.716	0.506	−0.120	−0.644	0.548	5
	2	1.052	−0.757	0.779	−0.117	−1.384	0.264	5
	3	0.545	−0.765	0.014	0.349	−0.698	0.114	5
A. fumiferanae and *G. fumiferanae*	1	0.820	−1.703	0.149	−0.107	−0.456	0.667	5
	2	1.073	−0.388	0.953	−0.206	−1.647	0.180	5
	3	0.519	−0.923	0.012	0.321	−0.843	0.145	5
A. fumiferanae and *G. fumiferanae* and *S. fumiferanae*	1	0.712	−1.978	0.104	−0.121	−0.421	0.691	5
	2	1.054	−0.517	0.856	−0.246	−1.715	0.165	5
	3	0.503	−1.000	0.013	0.304	−0.903	0.175	5
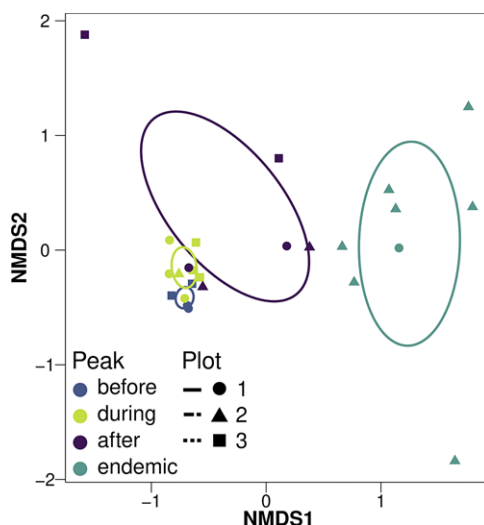
Fig. 2. The parasitoid communities before and during the peak were significantly different from after the peak. Nonmetric multidimensional scaling analysis of parasitoid community emerging from budworm and other caterpillar species on balsam fir over time. The colour of each point and ellipse corresponds to the four temporal groups: three and two relative years before the peak (before – average budworm abundance 7296); one relative year before and after the peak, and the peak (during – average budworm abundance 8067); two and three relative years after the peak (after – average budworm abundance 1128); and four to 10 relative years after the peak (endemic – average budworm abundance 29). Each point is a single relative year and a single plot. Each ellipse is a covariance ellipse. Twenty iterations were run with a final stress of 0.087 and instability for the preceding 10 iterations of 0.0196.

community differences due to plot differences. Whereas plots 1 and 2 were within 10 km of each other, plot 3 was 170 km distant. Plot 3 also had the lowest percentage cover of balsam fir (Eveleigh *et al.* 2007). Although at smaller scales, we found heterogeneity in parasitoid community responses to relative budworm and other caterpillar frequencies, it could be argued that, at larger scales, the parasitoid emergences followed the relative frequencies of budworm and other caterpillar species; that is, the parasitoid community may have indiscriminately attacked budworm and other caterpillar species on balsam fir. The major implication of these results for biological control of budworm is that they show that other caterpillars are an important resource for the parasitoid community, potentially maintaining higher populations of parasitoids and increasing the parasitism of budworm.

The indiscriminate response by the whole parasitoid community could either be caused by a few dominant parasitoid taxa or could be a summation of all parasitoid taxa responses. When we excluded the three most abundant parasitoid taxa from our dataset, the resulting parasitoid communities in plots 1 and 2 still largely exhibited no host preference by frequency or by type (Table 2). When we excluded the three most abundant parasitoid taxa in plot 3, the resulting parasitoid community exhibited reduced preference for the most abundant caterpillar (smaller positive slope; Table 2). This change in slope was probably caused by the exclusion of *Apanteles fumiferanae*, the most abundant parasitoid taxa: excluding the two most and three most abundant parasitoid taxa resulted in slopes similar to that which resulted when only *Apanteles fumiferanae* was excluded. Overall, the less common parasitoids exhibited a greater preference for other caterpillar species than the common parasitoids did. This is corroborated by the identified preferences of each of the three most common parasitoids: *Apanteles fumiferanae* emerged from budworm more often than from other caterpillar species, regardless of the relative frequencies of budworm and other caterpillar species (Supplementary material, Fig. S1); *Glypta fumiferanae* emerged from caterpillars (both budworm and other caterpillars) when
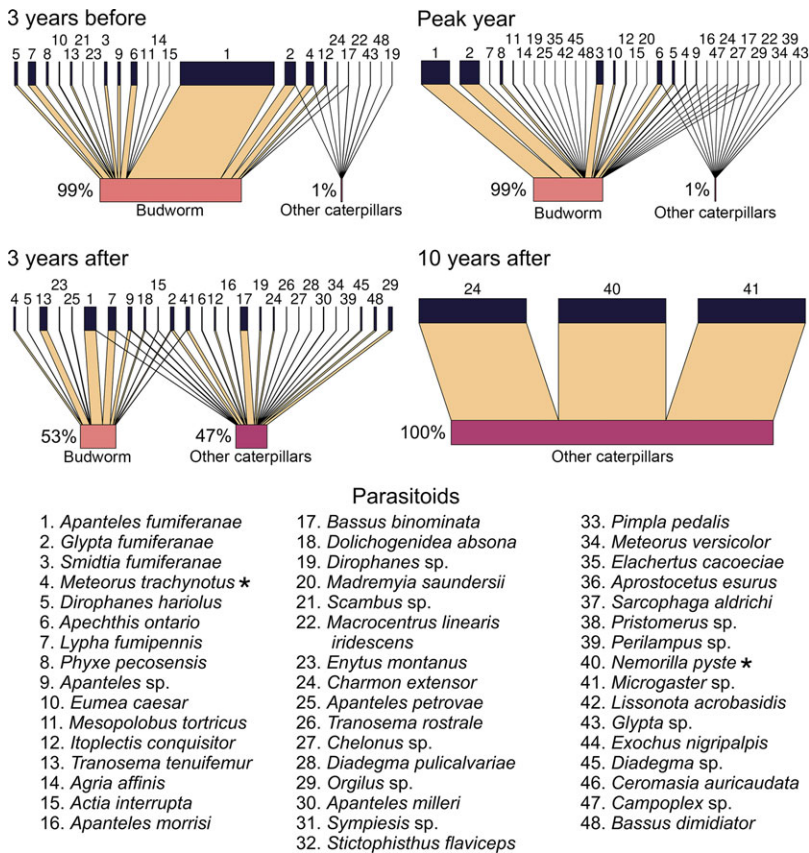
Fig. 3. Graphical representations of the number of emergences of each parasitoid taxon (top boxes) from budworm and other caterpillar species (bottom boxes) over time. The width of links is proportional to the fraction of emergences of each parasitoid taxon from either budworm or other caterpillars. The width of the bottom boxes is proportional to the number of emergences from budworm versus other caterpillars, and the percentages show this quantitatively. Four different relative years are shown, where all plots were combined within a relative year: **A**, three relative years before the peak; **B**, peak relative year; **C**, three relative years after the peak; and **D**, 10 relative years after the peak. All other relative years can be found in Supplementary material, Figs. S4 and S5. A star denotes a taxon that requires an alternate caterpillar host to overwinter in. To find the corresponding taxon in Eveleigh *et al*. (2007), see Supplementary material, Table S2.

budworm was abundant but were generally not found when budworm was rare (Supplementary material, Fig. S2); and *Smidtia fumiferanae* emerged from only budworm (Supplementary material, Fig. S3). This indicates that parasitoid taxa have differing preferences for budworm and other caterpillars, but collectively, the community exhibited little to no preference, depending on the plot. The differing preferences of each parasitoid taxon could produce species turnover over time, and we did indeed find species turnover (Fig. 2). Further support for the effect of parasitoid taxons' differing preferences on species turnover comes from Royama *et al*. (2017), who found that, as budworm densities changed, turnover occurred in the parasitoid functional group that attacked budworm the most, which produced a relatively constant overall parasitism rate of budworm. As a possible mechanism, Royama *et al*. (2017) posited that the relative profitability of budworm and other caterpillar species changes differently over time for each parasitoid species, where profitability is defined as the relative energy content plus the number of caterpillars that can be attacked for a given amount of hunting effort. As a result, different parasitoid species would attack budworm at different time periods during the
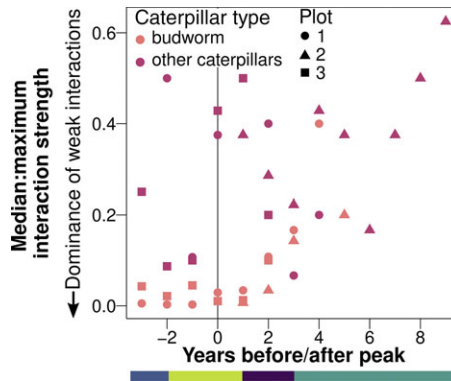
Fig. 4. As budworm frequencies decreased, the distribution of interaction strengths shifted from a dichotomy of strong and weak interaction strengths but skewed with a preponderance of weak interactions to a uniform distribution of interaction strengths. Median:maximum interaction strength over time, for each plot and for each caterpillar type, where the number of emergences was used for interaction strengths. Bar at bottom depicts the peak variable level each year is in: (going from left to right) before, during, after, and endemic.

budworm cycle. Overall, our results suggest that the parasitoids act individually but produce a compensatory response to fluctuating budworm frequencies.

The observed large changes in parasitism rates and species turnover appeared to translate into fluctuating topology and interaction strengths of the food web. We found large changes in topology with many parasitoid taxa emerging from budworm and other caterpillar species in some years but not in others (Fig. 3). We also found shifts in the distribution of interaction strengths over the budworm cycle (Fig. 4). When budworm was at high frequencies, we found few strong interactions and many weak interactions. As budworm frequencies declined, the distribution of interaction strengths became uniform. We acknowledge that the likely cause behind this change in interaction strength distribution is declining budworm frequencies. By random chance alone, the parasitoids that rarely attack budworm (the parasitoids that form the weak interactions) would rarely be found by our sampling, leaving the parasitoids that often attack budworm (the parasitoids that form the strong interactions) to be found in our sampling, thus biasing the median:maximum interaction strength metric towards higher values (see Supplementary material, Table S1 for total number of budworm and other caterpillars sampled). Indeed, our observed pattern of increasing median:maximum interaction strength metric was not different from 10 000 simulations of a parasitoid community attacking declining budworm populations (see Supplementary material, Figs. S6 and S7). In contrast, Ushio *et al.* (2018) posited that behavioural and physiological responses or higher productivity in the summer months caused interaction strength distributions in a marine fish food web to skew towards weak interactions in the summer and towards being more uniform in the winter. In the present study, greater budworm densities could be considered similar to high fish productivity in the summer in Ushio *et al.*'s (2018) study. Thus, finding weak interactions dominating during high-productivity periods in both the budworm and marine fish food webs is intriguing because these high-productivity periods may be the temporal periods that most require stabilisation (Rosenzweig 1971; Mougi and Nishimura 2007), whereas weak interactions are thought to be a major stabilising mechanism in food webs (McCann *et al.* 1998; Gellner and McCann 2016). Regardless of the specific mechanism behind the shifting distribution of interaction strengths, a major proportion of budworm were parasitised by parasitoids that form weak interactions. All of these parasitoids must have other sources of caterpillars.

Theory centred on responses to variable resources may help to explain the observed aggregated indiscriminate community response and changes in interaction strength distributions. One theoretical model proposes that higher trophic-level generalist consumers react to variation in their resources by either increasing consumption of a resource in one separated subgroup of an entire food web (coupling to a resource compartment) or decreasing consumption of a different resource 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, thereby stabilising food webs. In the budworm–parasitoid food web, although individual parasitoid species may be specialists or generalists, the aggregate response suggests that the collective parasitoid community could be seen as a generalist consumer that couples and decouples the resource compartment with balsam fir as the basal resource (hereafter referred to as balsam fir resource compartment). However, this hypothesis for the parasitoid community response requires another resource compartment separate from the balsam fir resource compartment.

We suggest that the other resource compartment in the budworm–parasitoid food web has hardwood trees as the basal resource, where white birch, *Betula papyrifera* Marshall (Betulaceae), and red maple, *Acer rubrum* Linnaeus (Sapindaceae), are hardwood trees. This supposition derives from observations that, during an outbreak, budworm densities were lower and budworm parasitoid diversity was higher in stands that contained a mixture of softwoods and hardwoods (mixed forest stands) compared to balsam fir-dominated stands (Su *et al.* 1996; Cappuccino *et al.* 1998; Eveleigh *et al.* 2007; Smith *et al.* 2011). Consequently, these researchers hypothesised 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 those stands. Both the hardwood resource compartment hypothesis and this mixed stand hypothesis posit that hardwood trees provide an important alternative source of caterpillar hosts for the budworm parasitoid community. Indeed, our study shows that other caterpillar species are important to the parasitoid community that attacks budworm, suggesting that the mixed stand and hardwood resource compartment hypotheses are mechanistically feasible. However, our study undersamples the interactions between other caterpillar species on balsam fir and parasitoids (using Chao2 with interactions, 63% of the potential interactions between parasitoids and other caterpillar species were sampled in this study). In the wider budworm research, the interactions of parasitoids with other caterpillar species on hardwoods are even less well sampled, thus preventing a clear test of these interrelated hypotheses. Because the application of these hypotheses could reduce the severity of budworm outbreaks, future research should sample the interactions of parasitoids with other caterpillar species on balsam fir and hardwoods.

The parasitoid community response to changing budworm populations illustrates the fantastic flexibility of food webs. Previous research found that as budworm densities increase on balsam fir, the diversity of parasitoid species found on balsam fir increases at all trophic levels (Eveleigh *et al.* 2007). In times of budworm rarity, parasitoid species diversity on balsam fir drops – and yet the parasitoid community must be maintained by some mechanism or the swift parasitoid community response to increased budworm abundance could not occur (Eveleigh *et al.* 2007). The present study revealed that the parasitoid community responded to changing densities of budworm by largely indiscriminately following the relative frequencies of budworm and other caterpillar species on balsam fir. Changes in topology and interaction strengths in the budworm food web on balsam fir resulted from the changes in parasitism rates and species turnover. The other caterpillar species that these parasitoids attack are not found solely on balsam fir, and in fact, many researchers have suggested that caterpillars on hardwoods may be the dominant resource when budworm are rare (Su *et al.* 1996; Cappuccino *et al.* 1998; Eveleigh *et al.* 2007). Consequently, including consideration of caterpillars on hardwoods is

imperative in future budworm research; specifically, that research could identify whether the parasitism rates of budworm on balsam fir change in comparison to the parasitism rates of caterpillars on hardwoods as budworm densities peak and ebb. Such a response, which appears to be created by the combined actions of all parasitoid species, would be an excellent example of community ecology driving the population ecology of a dominant species. For budworm management, if other caterpillars on hardwoods are found to maintain budworm parasitoid populations, bolstering this mechanism could mute the amplitude of budworm outbreaks, helping to reduce the defoliation and destruction of balsam fir forests in eastern North America.

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Data accessibility. All data and code to reproduce the reported results are publicly available on GitHub (https://github.com/cgreysongaito/SpruceBudworm_Parasitoid_BalsamFir) and have been archived on Zenodo (https://doi.org/10.5281/zenodo.1305399) (Greyson-Gaito *et al.* 2020).

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