

1 Coherent whole food web responses to outbreaking
2 spruce budworm

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14 **Abstract**

15 The world is astoundingly variable, and individuals to whole communities must respond to
16 variability to survive. One potent example of nature's variability is the massive fluctuations
17 in spruce budworm (*Choristoneura fumiferana* Clemens) populations that occur over 35
18 years. We examined how the parasitoid community altered its parasitism of budworm and
19 other caterpillars in response to these fluctuations. Budworm and other caterpillar species
20 were sampled from balsam fir in three plots for 13 years in Atlantic Canada. These
21 caterpillars were reared to identify any emerging parasitoids. We found that the parasitoid
22 community showed a simple linear, and indiscriminate, response (i.e., no preference and so
23 densities purely dictated parasitism rates) to changes in budworm densities relative to other
24 caterpillar species on balsam fir. Furthermore, we observed strong changes in topology and
25 distributions of interaction strengths. These observations suggest parasitoid movement
26 between hardwood stands and balsam fir stands is integral to the population dynamics of
27 budworm. Furthermore, our study remarkably shows that species communities coherently
28 alter species interactions in response to variable resources, fundamentally shifting food web
29 pathways in a manner similar to generalist apex predators.

30 **Keywords**

31 coherent responses, community ecology, food webs, parasitoids, species interactions, variable
32 resources, spruce budworm (*Choristoneura fumiferana*), balsam fir (*Abies balsamea*)

33 Introduction

34 Ecologists have long used equilibrium assumptions to study the complex suite of
35 interactions that make up food webs [1, 2]. Although a reasonable first approach, in fact,
36 both abiotic and biotic conditions are notoriously variable [3, 4]. Despite this, our
37 understanding of how organisms respond to variation remains surprisingly limited. In light
38 of human-driven impacts including climate change that promise to significantly alter this
39 variation [5, 6], it behooves ecologists to embrace variation and to ask how individuals to
40 whole communities respond to both natural variation and changes in this natural variation
41 caused by human modifications.

42 Community-level responses to variability are a function of individual-level responses and
43 recent work has found compelling evidence that individuals and species behave to take
44 advantage of strongly changing conditions. An example of individuals taking advantage of
45 changing conditions is grizzly bears in Alaska following the ephemeral pulses of salmon
46 densities across the river and stream landscape [7]. The bears track the phenological
47 variation of salmon spawning across space and time, so maximising the bear's energy
48 intake. Another example is individuals switching their diet depending on the abundances of
49 different resource items, where an individual preferentially consumes whichever resource is
50 at the highest abundance [8, 9]. Again, diet switching can maximize the individual's energy
51 intake. These individual responses can add together to produce a community-level
52 response. One known example of a community-level response to variability is the impressive
53 convergence of parasitoids on the periodic spruce budworm (*Choristoneura fumiferana*
54 Clemens) outbreaks on balsam fir (*Abies balsamea* Miller) [10]. Similar to how many species
55 of birds converge on a full birdfeeder, parasitoid diversity sampled from balsam fir increases
56 when spruce budworm densities increase (the birdfeeder effect). The individual parasitoids
57 likely all respond to the changing densities of budworm in order to maximize their fitness
58 [11] and collectively they converge on high densities of budworm during outbreaks. This
59 convergence leads to a diversity cascade across trophic levels suggesting that such strong
60 changes as budworm outbreaks may produce seemingly coherent community responses as a
61 function of all individual responses.

62 Because of the possibility of coherent behavior within the parasitoid community, the
63 budworm – parasitoid food web provides an excellent system to examine community-level
64 responses to variability. Budworm have massive and relatively predictable outbreaks every
65 thirty five years, followed by periods of budworm rarity [12]. This cycle is considered to be
66 a predator – prey cycle, where the predator is a complex of natural enemies including
67 insects that parasitize and then kill a caterpillar host (parasitoids) [13]. Although budworm
68 are consumed by many invertebrate predators and birds, about 50% of budworm
69 caterpillars are killed by 50 species of parasitoids [13]. Furthermore, this parasitoid
70 community likely has the strongest response to changing budworm densities because
71 invertebrate predators and birds are more generalist than parasitoids, and birds are also
72 limited in numbers due to territory competition [13, 14]. Therefore, we expect to find a
73 community-level response in this parasitoid community. From Eveleigh et al. [10], which
74 showed a birdfeeder effect, we know the parasitoid community response when budworm are

75 plentiful, but we do not know the parasitoid community response when budworm are rare.
76 In effect, we have not observed what happens when the “bird feed” has gone.

77 For the birdfeeder effect to occur, the parasitoids either remain dormant when budworm are
78 rare, or move between patches of outbreaking budworm, or find alternative sources of
79 caterpillar hosts when budworm are rare. We can immediately discount parasitoids
80 remaining dormant as a hypothesis for maintaining the birdfeeder effect because no
81 parasitoid of budworm is known to enter dormancy longer than a year [15, 16]. We can also
82 discount parasitoids moving between patches of budworm when budworm are rare because
83 budworm are uniformly rare over their whole range for these longer periods. When
84 budworm are rare, parasitoid populations decrease, but a reserve population of parasitoids
85 could be maintained by attacking other caterpillar species. Parasitoids attacking other
86 caterpillar species is a possibility because we know that of the whole parasitoid community
87 that attacks budworm, some parasitoids are generalists that attack both budworm and
88 other caterpillar species [10, 17, 18]. Therefore, the parasitoid community could converge
89 on high budworm densities and then leave to attack other caterpillars when budworm
90 densities decline. The full birdfeeder effect, including other caterpillar species, has as yet
91 not been examined. Specifically, we do not know the relative attack rates of the parasitoid
92 community on budworm and other caterpillar species as budworm densities change. There
93 is the potential for the whole parasitoid community to flexibly and coherently respond to
94 fluctuating budworm densities by collectively altering the relative parasitism rates of
95 budworm and other caterpillar species. These are fundamental questions because scaling
96 this community-level response to the landscape scale has the potential to moderate the
97 amplitude and severity of budworm outbreaks.

98 Whereas Eveleigh et al. [10] provided a qualitative examination of the entire budworm food
99 web on balsam fir, and Royama et al. [13] examined the impact of parasitoids on budworm
100 only, in this exploratory study, we aimed to quantify the changing trophic interactions of
101 parasitoids with both budworm and other caterpillars. Here, we take the first step towards
102 this goal by examining the interactions on balsam fir solely. First, we extended the
103 birdfeeder effect pattern observed by Eveleigh et al. [10] to a longer dataset by evaluating
104 whether a reversal of the cascading increases in parasitoid species diversity occurred or not
105 when budworm densities decrease. Second, we examined whether the whole parasitoid
106 community exhibited host preference by caterpillar frequency or type. Third, we evaluated
107 whether the parasitoid community response was an aggregate response and not a single
108 species response by dropping the most abundant species and examining species turnover.
109 Fourth, because total diversity changes, parasitism rates, and species turnover all impact
110 the structure and dynamics of food webs, we examined how the topology and interaction
111 strengths of the budworm food web on balsam fir changed. We analyzed rearing data of
112 budworm and other caterpillar species collected from balsam fir branches sampled from
113 1982 to 1995. During this time period, balsam fir branches were collected from three plots
114 and a representative sample of budworm and all other caterpillar species were placed into
115 feeding vials to identify any parasitoids that emerged. Importantly, we found that the
116 parasitoid community coherently and indiscriminately tracked changes in relative densities
117 of budworm and other caterpillars. Furthermore, the observed changes in total diversity,
118 parasitism rates, and species turnover produced a rewiring of the budworm food web on

119 balsam fir.

120 **Materials and methods**

121 **Study sites**

122 Three plots in balsam fir forests in New Brunswick, Canada were established. Plot 1 was in
123 the Acadia Research Forest near Fredericton (46°00'N, 66°25'W). Balsam fir branches were
124 sampled in this plot from 1982 to 1989. Because budworm caused 60% tree mortality in
125 Plot 1 by the mid-1980s, Plot 2 was added, which was also in the Acadia Research Forest.
126 Balsam fir branches were sampled in this plot from 1986 to 1995. In the late 1980s, the
127 budworm populations in Plot 1 and 2 were so low that Plot 3 was added, approximately
128 170km farther north near Saint-Quentin (47°29'N, 67°15'W). Balsam fir branches were
129 sampled in Plot 3 from 1988 until 1994 when budworm populations also declined to a low
130 level. All plots had mostly balsam fir but also contained spruces and a variety of hardwood
131 trees [10]. Both the Acadia Research Forest and the Restigouche River watershed (where
132 Plot 3 is located) contained balsam fir dominated, mixed, and hardwood dominated stands
133 [19, 20]. All plots were outside areas of biopesticide application. Full details of the three
134 plots and all sampling and rearing procedures can be found in Lucarotti et al. [21], Eveleigh
135 et al. [10] (SI Materials and Methods) and Royama et al. [13]. Here, we present only a brief
136 synopsis.

137 **Sampling**

138 At the beginning of each season, a group of codominant balsam fir trees were selected in 20
139 random locations within each plot. Every year and for each plot, before larval emergence
140 from winter diapause, one balsam fir branch from each of the 20 locations was collected. As
141 soon as second instar larvae in the field began emerging from diapause, balsam fir branches
142 were sampled approximately every day until the end of budworm adult eclosion. On each
143 sampling day during the earlier years when budworm populations were high, one foliated
144 mid-crown balsam fir branch from one of the trees in each of the 20 locations was collected.
145 During the later years when budworm populations were low, two or more branches were
146 collected from each location to increase the number of collected budworm larvae at each
147 sample date and location

148 **Laboratory work**

149 All budworm and other caterpillars were collected for rearing from all 20 branches sampled
150 before budworm emergence from winter diapause. For branches sampled after budworm
151 emergence from winter diapause, one of the 20 sampled branches was selected and all
152 budworm and other caterpillars on that branch were reared. If a minimum of 100 budworm

153 were obtained for rearing from this branch, no more branches were selected for collection of
154 caterpillars for rearing. If less than 100 budworm were obtained from the first branch
155 selected, then another branch was selected and all budworm and all other caterpillars from
156 that branch were collected and reared, even if the final total number of budworm exceeded
157 100. When budworm populations were low, obtaining more than 100 budworm individuals
158 became difficult. As a result, all budworm and all other caterpillars that were found on the
159 sampled branches were collected for rearing. Overall, for every sampling day, all budworm
160 and all other caterpillars were reared from the subset of branches of the 20 collected each
161 sampling day. All collected caterpillars (budworm and other caterpillar species) were
162 individually reared on artificial diet [22] and inspected every weekday for mortality. There
163 was high rearing success of both budworm and other caterpillars because all of these hosts
164 feed on balsam fir and therefore readily feed on the artificial diet. On average, 317 other
165 caterpillars were collected each year. All parasitoids that emerged from any reared
166 caterpillars were morphologically identified to genus and where possible to species. Any
167 parasitoids unidentifiable to genus or species were excluded from our analysis (1.6% of the
168 total number of emergences from spruce budworm or other caterpillars).

169 **Statistical Analyses**

170 Because we were interested in quantifying the trophic interactions of parasitoids that attack
171 both budworm and other caterpillars, we excluded all parasitoid taxa that attacked only
172 budworm or only other caterpillars. The 31 parasitoid taxa (listed in Fig. 4) found to
173 attack both budworm and other caterpillars formed 89% of all trophic interactions with
174 budworm and 80% of all trophic interactions with all other caterpillar species. Using Chao2
175 (function specpool, R package vegan, version 2.5.2, [23]) to estimate the total potential
176 number of interactions between parasitoids and budworm or other caterpillars, this
177 subsetted dataset captures 50% of the potential interactions between parasitoids and
178 budworm and 63% of the potential interactions between parasitoids and other caterpillars.

179 Because budworm populations peaked in different years in the three different plots, we
180 created a new time variable called years before/after peak. In this variable, zero was set as
181 the relative year at which budworm populations peaked in each plot. For all analyses, plots
182 were compared using this relative variable. Hereafter, the phrase **relative year** refers to
183 this created variable "years before/after peak variable". Plot 1 peaked in 1985 and Plot 3
184 peaked in 1991. We do not know exactly when budworm populations peaked in plot 2 but
185 because population trends in plots 1 and 2 were nearly identical due to their close
186 proximity, we assumed budworm populations peaked in 1985.

187 Using the same data, Eveleigh et al. [10] established through rarefaction that changes in
188 diversity of parasitoid species were not due to sampling artefacts. Consequently, we are
189 confident that any patterns found by the analyses below are not due to changes in sampling
190 intensity but due to underlying ecological mechanisms.

191 All of the following analyses were done using R version 3.5.2 [24]. The data used here can
192 be found on the Dryad Digital Repository (presently, privately archived on Dryad) and the

193 R script can be found on GitHub [25].

194 **Parasitoid taxa diversity**

195 To establish whether the richness of parasitoid taxa emerging from budworm and other
196 caterpillars declined with decreasing budworm densities, we calculated the number of
197 parasitoid taxa that emerged from budworm and other caterpillars for every combination of
198 relative year and plot. We ran a generalized least squares (GLS) regression to test the
199 effects of relative year, caterpillar type (budworm or other caterpillars), plot, and their
200 interactions on the numbers of parasitoid taxa emerging from budworm and other
201 caterpillars (function `gls`, R package `nlme`, version 3.1-137, [26]). We added a `corAR1`
202 autocorrelation structure to account for temporal autocorrelation. We fitted the full model
203 using maximum likelihood estimation (ML) and then used backwards selection with log
204 likelihood ratio tests (LLRT) to select the final fixed effects. We refitted the final model
205 using restricted maximum likelihood estimation (REML) to give unbiased ML predictors
206 [27].

207 **Parasitoid community host preference**

208 To examine whether the parasitoid community exhibited preference for budworm or other
209 caterpillars on balsam fir, we calculated two values for every combination of relative year
210 and plot: the ratio of parasitoid emergence from budworm to other caterpillars for all
211 parasitoid taxa combined, and the ratio of abundances of budworm to other caterpillars.
212 We ran a GLS regression with the \log_{10} of the ratio of emergence as the response variable
213 and the \log_{10} of the ratio of the abundances of budworm to other caterpillars, plot, and
214 their interaction as the explanatory variables. We fitted the full model using ML, used
215 backwards selection with LLRT to select the final fixed effects, and refitted the final model
216 using REML. We tested whether the average slope for all plots was significantly different
217 from one and whether the average intercept for all plots was different from zero using one
218 sample t-tests. As per the methods in Greenwood & Elton [28], a slope different from one
219 indicates frequency dependent host preference and a intercept different from zero indicates
220 preference for a specific host type (budworm or other caterpillars).

221 To unpack any parasitoid community host preference response found in the analysis
222 above, we examined how the per capita emergences of parasitoids from budworm and other
223 caterpillars changed over time. For every combination of relative year and plot, we
224 calculated the average per capita parasitoid emergences from budworm and other
225 caterpillars for all parasitoid taxa (per capita emergences being the number of emergences
226 from budworm or other caterpillars divided by the total number of budworm or other
227 caterpillars reared). We ran a GLS regression to test the effects of relative year, caterpillar
228 type (budworm or other caterpillars), plot, and their interactions on per capita parasitoid
229 emergence. We added a `corAR1` autocorrelation structure to account for temporal
230 autocorrelation. We fitted the full model using ML, used backwards selection with LLRT to
231 select the final fixed effects, and refitted the final model using REML.

232 **Aggregate response**

233 To identify whether the response to the changing relative abundances of budworm to other
234 caterpillar species was driven by a single parasitoid taxon or by the whole community, we
235 found the three most frequently emerging parasitoid taxa. We then removed in turn the top
236 parasitoid taxon, the top two parasitoid taxa, and the top three parasitoid taxa from the
237 data and ran GLS regressions with the same final model as for the first analysis in the
238 parasitoid community host preference analysis. Using one-sample t-tests, we compared the
239 average slopes and intercepts for all plots of each of these models with the average slope
240 and intercepts for all plots produced in the model with all parasitoid taxa included. To
241 examine turnover in parasitoid taxa over time, we ran an nMDS analysis using the
242 Bray-Curtis dissimilarity measure where the abundances of individual taxa were divided by
243 the total number of parasitoid emergences (all taxa) for each relative year and plot
244 (function metaMDS, R package vegan, version 2.5.2, [23]). We ran a perMANOVA between
245 four groups (function adonis, R package vegan): three and two relative years before the
246 peak; one relative year before and after the peak, and the peak; two and three relative years
247 after the peak; and four to ten relative years after the peak. In this perMANOVA, we used
248 the Bray-Curtis dissimilarity measure, constrained permutations within each plot, and
249 maintained the temporal order of permutations.

250 **Food web topology and interaction strengths**

251 Given the potential for changes in total diversity, parasitism rates, and species turnover to
252 change food web structure, we examined how topology and interaction strengths changed in
253 the budworm food web on balsam fir. We calculated the number of emergences of each
254 parasitoid taxon from either budworm or other caterpillars for every relative year. To
255 examine changes in topology, we produced visual bipartite food webs from these numbers of
256 emergences (R package bipartite, version 2.11, [29]). To examine changes in interactions
257 strengths, we calculated the ratio of the median to maximum interaction strengths for every
258 relative year, where the number of emergences was used for interaction strengths. Note,
259 using the number of emergences or the per capita emergences for calculating the ratio of
260 median to maximum interaction strengths yields the same answer. Calculating the ratio
261 from per capita emergences cancels out the division by the number of sampled caterpillars
262 which is the same for the median and maximum, returning the ratio of median to maximum
263 number of emergences. We used the change in ratio of median to maximum interaction
264 strengths to qualitatively assess how the distributions of weak to strong interactions
265 strengths changed over time.

266 Results

267 Parasitoid taxa diversity

268 The final model explaining the number of parasitoid taxa emerging from budworm and
269 other caterpillars included the explanatory variables of relative year, caterpillar type, plot,
270 the interactions of relative year and caterpillar type, and the interaction relative year and
271 plot (Fig. 1). Graphically, we see that the number of parasitoid taxa that emerged from
272 budworm decreased at a faster rate than the number of parasitoid taxa that emerged from
273 other caterpillars (relative year:caterpillar type interaction, $L = 7.988$, $P = 0.0047$, $df = 1$,
274 log likelihood ratio test, Fig. 1).

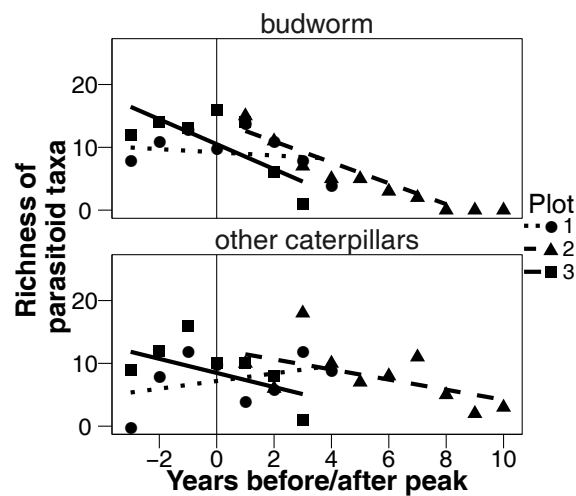


Fig. 1. Number of parasitoid taxa that emerged from budworm and other caterpillars over time. Each point is for a single relative year and a single plot. Year zero is the peak of the budworm populations in each plot.

275 Parasitoid community host preference

276 The final model explaining the log₁₀ ratio of parasitoid emergence from budworm to other
277 caterpillars included the explanatory variables of the log₁₀ ratio of abundances of budworm
278 to other caterpillars, plot, and their interaction (Fig. 2 A). The average slope for all plots,
279 signifying whether the parasitoid community had a statistical frequency preference for
280 either budworm or other caterpillars, was not significantly different from 1 (0.939 ± 0.282 ,
281 $df=15$, $P = 0.675$, one-sample t-test). The average intercept for all plots, indicating
282 whether the parasitoid community had density independent preference for budworm or
283 other caterpillars, was not significantly different from 0 (0.136 ± 0.399 , $df=15$, $P = 0.514$,
284 one-sample t-test).

285 The final model explaining the per capita parasitoid emergences from budworm and other
286 caterpillars included the variables of relative year, caterpillar type, plot, and all their

287 interactions (relative year:caterpillar:plot interaction, $L = 13.494$, $P = 0.0012$, $df = 1$, log
288 likelihood ratio test, Fig. 2 B).

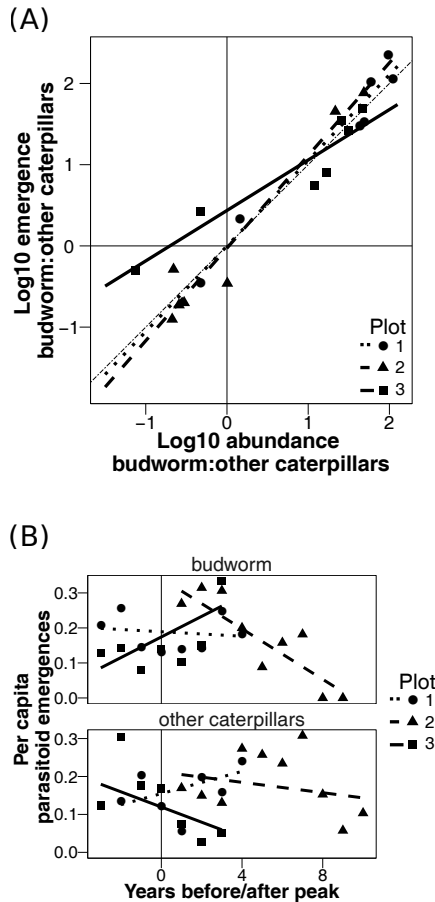


Fig. 2. (A) Log10 ratio of parasitoid emergences from budworm to other caterpillars for all parasitoid taxa used in our analysis as a function of the log10 ratio of all sampled budworm and other caterpillars. Each point is a single relative year and a single plot. The thin dashed line is the $y = x$ line. (B) Per capita emergences of parasitoids from budworm and other caterpillars over time. Each point is a single relative year and a single plot. Year zero is the peak of the budworm population in each plot.

289 Aggregate response

290 Neither dropping the most abundant parasitoid taxon with the most emergences from all
291 caterpillars (*Apanteles fumiferanae*), nor dropping the two most abundant parasitoid taxa
292 (*A. fumiferanae* and *Glypta fumiferanae*), nor dropping the three most abundant taxa (*A.*
293 *fumiferanae*, *G. fumiferanae*, and *Meteorus trachynotus*) caused the average slopes and
294 intercepts for all plots to be significantly different from when all parasitoid taxa were
295 included (original average slope was 0.939 and original average intercept was 0.136, Table
296 1). However, as each most abundant parasitoid taxon was dropped, there was a trend for
297 decreasing slopes and intercepts. The community of parasitoid taxa did not differ between
298 before and during the peak, but the parasitoid community in these two periods did differ
299 from after the peak and during the endemic periods ($F = 6.198$, $P = 0.003$, 999
300 permutations, perMANOVA, Fig. 3).

Table 1: Slopes and intercepts with corresponding standard errors, 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 Log10 ratio of abundance of budworm to other caterpillars, plot, and their interaction. The response variable was Log10 ratio of emergences from budworm to other caterpillars. Taxon 1 is *Apanteles fumiferanae*. Taxon 7 is *Glypta fumiferanae*. Taxon 6 is *Meteorus trachynotus*.

Dropped taxa	slope	slope SE	slope t	slope P	intercept	intercept SE	intercept t	intercept P	df
1	0.829	0.298	-0.723	0.481	-0.008	0.421	-0.670	0.513	15
1 & 7	0.731	0.386	-1.055	0.308	-0.056	0.546	-0.690	0.501	15
1 & 7 & 6	0.662	0.431	-1.258	0.228	-0.108	0.610	-0.783	0.446	15

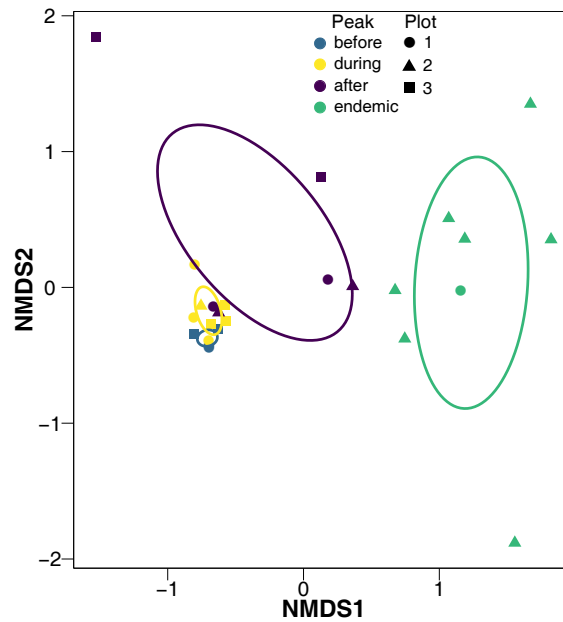


Fig. 3. nMDS of parasitoid community over time. The colour of each point and ellipse corresponds to the four temporal groups: three and two relative years before the peak (before); one relative year before and after the peak, and the peak (during); two and three relative years after the peak (after); and four to ten relative years after the peak (endemic). Each point is a single relative year and a single plot. Each ellipse is a covariance ellipse. 26 iterations. Final stress of 0.0798. Instability for preceding 10 iterations was 0.0196.

301 Food web topology and interaction strengths

302 There were some parasitoid taxa (e.g. *Diadegma pulicalvariae*) that were ephemerally found
303 in the food web (Figs 4, S4, & S5). Those parasitoid taxa (e.g. *Apanteles fumiferanae*) that
304 were found in the food web consistently through time, often were found to change as to
305 whether they emerged from both budworm and other caterpillars or just one caterpillar
306 type. The distribution of interactions strengths for budworm and other caterpillars changed
307 from a skewed distribution dominated by weak interactions towards a uniform distribution,
308 though the variation in the median:maximum interaction strengths between sequential
309 years is greater for other caterpillars than for budworm (Fig. 5).

310 Discussion

311 In our study, we have shown that this boreal insect food web is highly responsive and
312 flexible in time to changing budworm densities. We used long-term data of host/parasitoid
313 abundance and diversity to assess how parasitism rates and trophic interactions changed
314 over the course of a budworm cycle. We found a dramatic aggregated whole community
315 correspondence of parasitism rates with caterpillar relative abundance (budworm:other
316 caterpillar species abundance) and a sharp change in topology and interaction strength
317 distributions on balsam fir as budworm densities fluctuated.

318 A strong increase in parasitoid diversity was found when budworm densities increased [10].
319 In this study, as budworm densities decreased, we found a precipitous decline in parasitoid
320 diversity emerging from budworm in comparison to other caterpillars. This pattern is not
321 due simply to a drop in effective sampling effort when budworm densities decline because
322 Eveleigh et al. [10] mass implanted budworm on balsam fir at a time when budworm was
323 rare and found similar low parasitoid diversity. Instead, declining parasitoid populations
324 likely goes part way to explain this drop in diversity. A complementary explanation is
325 implicitly suggested by the birdfeeder analogy. Birds leave a birdfeeder when the feed
326 depletes. Similarly, parasitoids likely leave balsam firs when budworm densities decrease.
327 Therefore, combined with Eveleigh et al.'s [10] study, the full extent of the birdfeeder effect
328 can be seen: parasitoid diversity tracks budworm density. Implicit in this birdfeeder effect
329 is a source of parasitoids when budworm densities increase and a destination for the
330 parasitoids when budworm densities decrease. We suggest that hardwood stands are the
331 source and destination, where balsam fir is a softwood tree, and white birch (*Betula*
332 *papyrifera* Marshall) and red maple (*Acer rubrum* Linnaeus) are hardwood trees. Our
333 suggestion stems from two observations. First, we already know that some parasitoid
334 species including *Meteorus trachynotus* alternate between budworm and other caterpillars
335 on hardwoods every year [31]. We suggest that hardwood stands play a major role not just
336 for these parasitoid species that require alternate hosts but also for the larger parasitoid
337 community. Second, there have been several observations that budworm densities in stands
338 that contained a mixture of softwoods and hardwoods, otherwise known as mixed forest
339 stands, were lower than budworm densities in balsam fir dominated stands during an
340 outbreak, even after accounting for tree densities [10, 32]. Consequently, these researchers

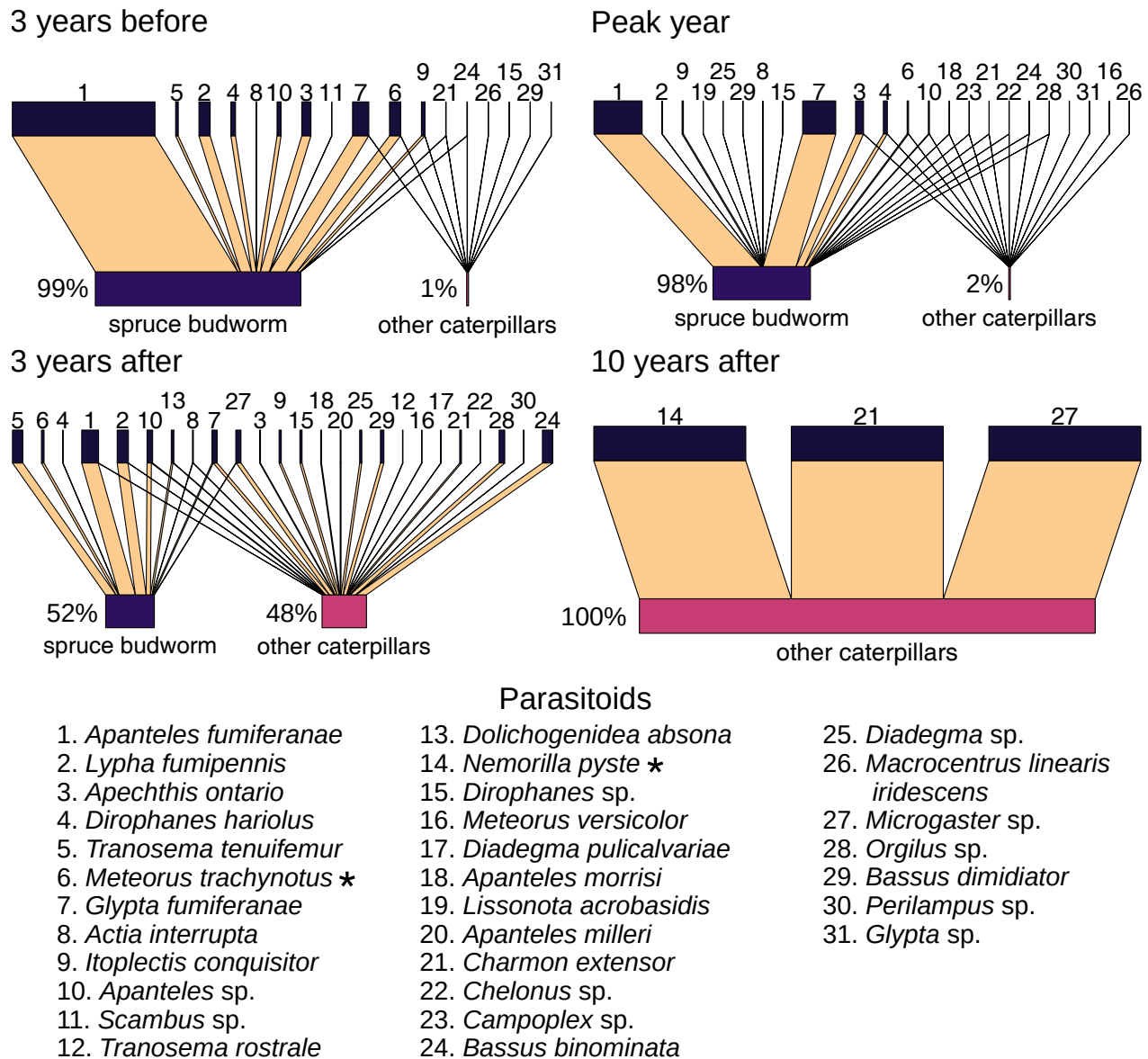


Fig. 4. Graphical representations of the number of emergences of each parasitoid taxon (top boxes) from budworm and other caterpillars (bottom boxes) over time. The width of links is proportional to the fraction of emergences of each parasitoid taxon from either budworm or other caterpillars. The width of the bottom boxes are 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) ten relative years after the peak. All other relative years can be found in Figs S4 & S5. A star denotes a taxon that requires an alternate caterpillar host to overwinter in. To find the corresponding taxon in Eveleigh et al. [10], see Table S1.

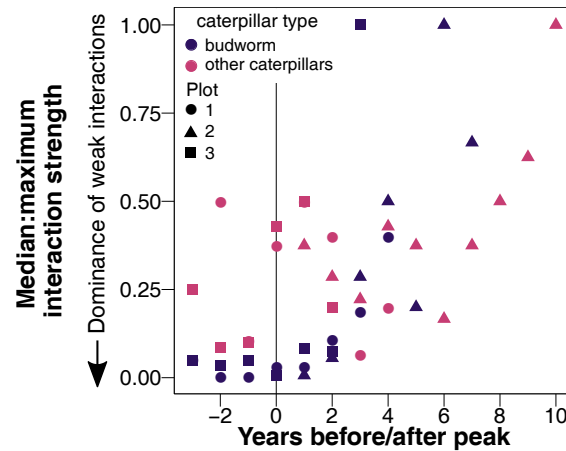


Fig. 5. Median:maximum interaction strength over time, for each plot and for each caterpillar type, where the number of emergences was used for interaction strengths. Figure inspired by the median:maximum interaction strength figure in Ushio et al. [30].

341 hypothesized that there must be greater diversity and abundances of parasitoids in mixed
342 forest stands, maintained by the greater diversity and abundances of caterpillar hosts in
343 mixed forest stands over the full duration of a budworm population cycle. We hypothesize
344 that hardwood trees are an important part of the budworm system by providing alternative
345 caterpillar hosts for the parasitoids that attack budworm.

346 Interestingly, we found that the parasitoid community overall did not show a preference for
347 budworm or other caterpillars by either frequency or type. This pattern suggests that the
348 parasitoid community indiscriminately attacks budworm and other caterpillars on balsam
349 fir. One implication of this parasitoid community indiscriminate response is for modeling of
350 the spruce budworm system, where we could model the parasitoids as a single entity with a
351 simple linear response to densities of budworm and other caterpillars on balsam fir. Clearly,
352 the addition of hardwood trees would be integral to any future modeling and further work
353 is required to ascertain the parasitoid community's response to other caterpillars on
354 hardwoods as well. Comparing between plots, plot 3 had a shallower slope and a intercept
355 greater than 0 indicating that the parasitoid community preferred the least abundant host
356 but still had a slight frequency independent preference for budworm. Similarly, Eveleigh
357 et al. [10] and Smith et al. [18] found different responses of parasitoids in plot 3 compared
358 to plots 1 and 2. Eveleigh et al. [10], using morphological methods, and Smith et al. [18],
359 using DNA barcoding methods, found greater parasitoid diversity in plot 3 compared to
360 plots 1 and 2. Plot 3 had a lower dominance of balsam fir compared to plots 1 and 2, but
361 plots 2 and 3 had equal proportions of hardwood trees (Eveleigh et al. 2007 SI Table 1).
362 The similar observations in host preference and parasitoid diversity between plots combined
363 with the observation of lower budworm density and balsam fir mortality in plots 2 and 3
364 from Eveleigh et al. [10] lead us to speculate that tree composition and likely hardwood
365 trees impacts the parasitoid community. Further support from our data is the increasing
366 and decreasing of per capita emergences of parasitoids on budworm (Fig. 2B). We again
367 acknowledge that population sizes of parasitoids increase and decrease in response to

368 budworm populations. However, we argue that changing parasitoid population densities
369 could not solely produce the increase and decrease in per capita emergence from budworm.
370 Instead, we suggest that immigration of parasitoids from other stands and changes in
371 searching efficiency both could produce this pattern. In support of immigration, Murakami,
372 Hirao & Kasei [33] found greater parasitism rates in a high-patch connectivity oak plot
373 compared to a low-patch connectivity oak plot. Although this study examined dispersal
374 between trees instead of between stands as in our case, the study still highlights the
375 importance of dispersal in host-parasitoid systems. In support of searching efficiency,
376 increasing host density plus increasing concentration of released host tree volatiles due to
377 herbivory likely reduce searching time for the parasitoids, increase oviposition rates and
378 lead to higher per capita emergences of parasitoids [34–36]. Whether on hardwood trees or
379 balsam fir trees, other caterpillars are important to the parasitoid community that attacks
380 spruce budworm. Even our study undersamples the interactions between other caterpillars
381 on balsam fir and parasitoids (63% of the potential interactions between parasitoids and
382 other caterpillars were sampled in this study), and yet the interactions of other caterpillars
383 on hardwoods with parasitoids are sampled even less. Consequently, to fully understand
384 budworm dynamics, it is imperative to sample the interactions of parasitoids with other
385 caterpillars on balsam fir and hardwoods.

386 The indiscriminate response by the whole parasitoid community could be caused either by a
387 few dominant parasitoid taxa or be a summation of all parasitoid taxa responses. When we
388 excluded the three most abundant parasitoid taxa from our dataset, the resultant
389 parasitoid communities still largely exhibited no host preference by type or by frequency.
390 When we examined when and what caterpillar type these three most abundant parasitoid
391 taxa were attacking (see Figs S1, S2, & S3), we see that a trend for decreasing slopes and
392 intercepts is unsurprising. These three parasitoid taxa either were found emerging from
393 caterpillars when budworm were abundant or were found to emerge more from budworm
394 than other caterpillars, thus dropping the slope and intercept. This indicates that
395 parasitoid taxa have differing preferences for budworm and other caterpillars, but
396 collectively, the community exhibits no preference. Corroborating this suggestion, we also
397 found species turnover over time. Parasitoid species turnover on balsam fir is likely
398 produced from the differing preferences of each parasitoid taxon. In support of differing
399 preferences leading to species turnover, Royama et al. [13] also found that no single
400 parasitoid functional group determined the yearly budworm cycle. Instead, as budworm
401 densities changed, there was turnover in the parasitoid functional group that attacked
402 budworm the most, which produced a relatively constant overall parasitism rate of
403 budworm. As a possible mechanism, Royama et al. [13] posited that the profitability of
404 budworm and other caterpillar species changes in time differently for each parasitoid
405 species. Consequently, different parasitoid species would attack budworm at different time
406 periods during the budworm cycle. Theoretical work supports this supposition where two
407 consumers attack a common resource at different rates during the cycling of the resource
408 [37, 38]. Overall, our results suggest that the parasitoid community act coherently in
409 response to fluctuating budworm densities.

410 The observed large coherent changes in total diversity, parasitism rates, and species
411 turnover should alter the topology and interactions strengths of the food web. Indeed from

412 our study, we can see large changes in topology with many parasitoid taxa emerging from
413 budworm and/or other caterpillars in some years and not others. We also found dramatic
414 shifts in the distribution of interaction strengths over the budworm cycle. When budworm
415 were at high densities, the distribution of interaction strengths showed a dichotomy of
416 strong-weak interaction strengths but skewed with a preponderance of weak interactions.
417 As budworm densities declined, the distribution of interaction strengths became uniform.
418 We acknowledge that spatial sampling effort (in terms of number of plots) differs between
419 years and because different plots were sampled at different times along the budworm cycle,
420 plot identity may impact the interactions found. However, there were several relative years
421 when multiple plots were sampled in the same relative year (-3 to 4). In these subset of
422 relative years, we see still see a trend of increasing median:maximum interaction strength.
423 Therefore, we predict that even if we had sampled balsam fir in all three plots from
424 budworm population peak to trough, then we would still find a change from skewed
425 interaction strengths distributions to uniform. Similarly, Ushio et al. [30] found that
426 interaction strengths distributions in a marine fish community were dominated by weak
427 interactions in the summer and were more uniform in the winter. A skewed distribution
428 dominated by weak interaction strengths is thought to stabilize foods webs [30, 39, 40].
429 However, apart from Ushio et al.'s [30] study, the pattern of fluctuating interaction strength
430 distributions has not been well explored. Ushio et al. [30] posited a few drivers for these
431 fluctuations including higher productivity in the summer months leading to higher fish
432 abundance [41] and behavioral or physiological responses that vary over time [42–44]. We
433 agree with Ushio et al.'s [30] assessment. Greater budworm densities could be thought of as
434 the same as high fish abundance in the summer. We suggest too that the behavioral
435 responses by the individual parasitoids are integral to the fluctuations in interaction
436 strength distributions.

437 Theory may help to further explain this coherent community response. One theoretical
438 model proposes that higher trophic level generalist apex consumers react to variation in
439 their resources by either starting consumer interactions with a species in one separated
440 subgroup of an entire food web (coupling to a resource compartment) or stopping consumer
441 interactions with a different species in another separate subgroup of the entire food web
442 (decoupling from a resource compartment) [45, 46]. This coupling and decoupling of
443 different resource compartments can mute large population variation in lower trophic level
444 organisms and so can stabilize food webs. In the budworm – parasitoid food web, although
445 individual parasitoid species may be specialists or generalists, the collective parasitoid
446 community acts as a generalist consumer and can couple or decouple the resource
447 compartment with balsam fir as the basal resource (hereafter referred to as balsam fir
448 resource compartment). This theoretical model suggests multiple resource compartments,
449 more than the single balsam fir resource compartment that we have examined in this study.
450 We suggest that the separate resource compartment has hardwood trees as the basal
451 resource. Another framework for understanding the dynamics of the parasitoid community
452 is rewiring of the food web, where rewiring is defined as large changes in food web structure
453 that alter nutrient and energy channels in an ecosystem [47]. The rewiring framework has
454 been applied to changes in food web topology and interaction strengths spatially due to
455 climate change. Here, there is likely a periodic rewiring of the interactions of parasitoids

456 with budworm on balsam fir and other caterpillars on hardwoods, due to the cyclical
457 fluctuations in budworm densities.

458 The parasitoid community response to changing budworm populations illustrates the
459 fantastic flexibility of food webs. Previous research found that as budworm densities
460 increase on balsam fir, the diversity of parasitoid species found on balsam fir increase at all
461 trophic levels [10]. In times of budworm rarity, parasitoid species diversity on balsam fir
462 drops and yet the parasitoid community must be maintained by some mechanism otherwise
463 the swift parasitoid community response to increased budworm abundance could not occur.
464 Our study revealed that the parasitoid community responded to changing densities of
465 budworm by linearly and indiscriminately following the relative densities of budworm and
466 other caterpillars on balsam fir. Large changes in topology and interaction strengths in the
467 budworm food web on balsam fir resulted from the changes in total diversity, parasitism
468 rates and species turnover. The other caterpillar species that these parasitoids attack are
469 not solely found on balsam fir, and in fact, many researchers have suggested that
470 caterpillars on hardwoods should be the dominant resource while budworm are rare. We
471 have corroborated this suggestion by observing that there must be net immigration of
472 parasitoids into balsam fir as budworm densities are increasing. Consequently, further
473 research should include caterpillars on hardwoods and could identify whether the
474 parasitism rates of budworm on balsam fir compared to the parasitism rates of caterpillars
475 on hardwoods change as budworm densities peak and ebb away. Such a response, which
476 appears to be created by the combined actions of all parasitoid species, is an excellent
477 example of community ecology driving the population ecology of a dominant species. For
478 budworm management, we have highlighted the importance of the potential use of other
479 caterpillars by parasitoids to the population dynamics of budworm. Therefore, increasing
480 the abundance and diversity of these other caterpillar species has the potential to mute the
481 amplitude of budworm outbreaks, thus helping to reduce the defoliation and destruction of
482 balsam fir forests in eastern North America.

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489 **Author's Contributions**

490 ESE designed the initial study. ESE and CJL performed the field and laboratory work.
491 CJGG and JF did the statistical analysis with assistance from ESE, MAS, and KSM. CJGG
492 wrote the first draft of the manuscript. All authors contributed to editing the manuscript.

493 Data accessibility

494 The data is currently privately archived in Dryad for journal editors and reviewers. If/when
495 the manuscript is accepted, the data will be publically available.

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