Parasitoid community responds indiscriminately to fluctuating spruce budworm and other caterpillars on balsam fir

Christopher J. Greyson-Gaito*[1], Kevin S. McCann[1], Jochen Fründ[2], Christopher J. Lucarotti[3,4], M. Alex Smith[1], Eldon S. Eveleigh[3,4]

Affiliations:

1. Department of Integrative Biology, University of Guelph, Guelph, Ontario, Canada

2. Department of Biometry and Environmental System Analysis, Albert-Ludwigs-Universität Freiburg, Freiburg, Germany

3. Natural Resources Canada, Canadian Forest Service, Atlantic Forestry Centre, Fredericton, New Brunswick, Canada

4. Population Ecology Group, Faculty of Forestry and Environmental Management, University of New Brunswick, Fredericton, New Brunswick, Canada

* Corresponding Author: Email: christopher@greyson-gaito.com (CJGG)

ORCID:

CJGG – 0000-0001-8716-0290

KSM – 0000-0001-6031-7913

JF – 0000-0002-7079-3478

CJL – 0000-0002-3490-568X

MAS – 0000-0002-8650-2575

ESE – 0000-0001-5060-8565

1

1 **Abstract**

2   The world is astoundingly variable, and individuals to whole communities must respond

3 to variability to survive. One example of nature's variability is the fluctuations in populations of

4 spruce budworm (*Choristoneura fumiferana* Clemens, Lepidoptera: Tortricidae), which cycle

5 every 35 years. We examined how a parasitoid community altered its parasitism of budworm

6 and other caterpillar species in response to these fluctuations. Budworm and other caterpillar

7 species were sampled from balsam fir in three plots for 14 years in Atlantic Canada, and then

8 reared to identify any emerging parasitoids. We found that the parasitoid community generally

9 showed an indiscriminate response (i.e., no preference, where frequencies dictated

10 parasitism rates) to changes in budworm frequencies relative to other caterpillar species on

11 balsam fir. We also observed changes in topology and distributions of interaction strengths

12 between the parasitoids, budworm and other caterpillar species as budworm frequencies

13 fluctuated. Our study contributes to the hypothesis that hardwood trees are a critical part of

14 the budworm-parasitoid food web, where parasitoids attack other caterpillar species on

15 hardwood trees when budworm populations are low. Taken together, our study shows that a

16 parasitoid community collectively alters species interactions in response to variable budworm

17 frequencies, fundamentally shifting food web pathways.

18

2

<u>Introduction</u>

19

20   Ecologists have long used equilibrium or steady state assumptions to examine

21 ecological patterns (Guichard & Gouhier, 2014). Furthermore, food web ecologists have

22 routinely assumed fixed interaction strengths (May, 1972; Allesina & Tang, 2012). Although

23 reasonable first approaches, nature is highly variable with many examples of non-equilibrium

24 ecological patterns and flexible interactions (Levin, 1998; Guichard & Gouhier, 2014). Yet,

25 human-driven impacts promise to significantly alter natural variation, and our understanding of

26 how organisms and communities respond to natural variation still remains limited (Cotton,

27 2003; Ims, Henden, & Killengreen, 2008). Therefore, examining how individuals to whole

28 communities respond to both natural variation and changes in this natural variation caused by

29 human modifications is integral to the future management and conservation of our natural

30 world.

31

32   Individual and species-level responses to variability, including behavioural and

33 population changes (Armstrong et al., 2016), can add together to produce community-level

34 responses, which include richness, evenness, and total biomass changes (Keitt, 2008; Supp

35 & Ernest, 2014). These individual and species-level responses can add together in a

36 compensatory manner, maintaining constant community metrics, or can add together in a

37 synchronous manner, causing synchronous changes in community metrics (Keitt, 2008). For

38 example, Supp and Ernest (2014) found compensatory dynamics ensured the maintenance of

39 constant community richness and evenness in terrestrial animal communities exposed to a

40 disturbance. In contrast, Stephens et al. (2017) found that although several sympatric small

3

41 mammal species exhibited varying abundance responses to forest type, the whole community

42 exhibited synchronous abundance and diversity changes over time. Regardless of the

43 mechanisms, these community-level responses can have large implications on food web

44 dynamics and on ecosystem function (Kent et al., 2007; Gouhier, Guichard, & Gonzalez,

45 2010).

46

47   One example of a community-level response to variability, with implications for the

48 management of a major forest pest, is the convergence of parasitoids on the periodic spruce

49 budworm (*Choristoneura fumiferana* Clemens, Lepidoptera: Tortricidae) outbreaks on balsam

50 fir (*Abies balsamea* Miller, Pinaceae) (Eveleigh et al., 2007). Budworm have massive and

51 relatively predictable outbreaks every thirty five years, followed by periods of budworm rarity

52 (Royama et al., 2005). This cycle is considered to be a predator – prey cycle, where the

53 predator is a complex of natural enemies including insects that parasitize and then kill a

54 caterpillar host (parasitoids) (Pureswaran et al., 2016; Royama et al., 2017). These

55 parasitoids collectively cause between 30-90% mortality depending on the surrounding forest

56 composition and the point in the budworm cycle (Dowden, Carolin, & Dirks, 1950; Cappuccino

57 et al., 1998; Seehausen et al., 2014; Royama et al., 2017). When budworm densities

58 increase, the parasitoid species collectively converge on high densities as measured by

59 increasing parasitoid diversity on balsam fir (the birdfeeder effect) (Eveleigh et al., 2007).

60 Because the parasitoid community has such a strong response to changing budworm

61 populations, the budworm-parasitoid food web provides an excellent system to examine

62 community responses to variability in host densities. Furthermore, a greater understanding of

63   the parasitoid community response to budworm density fluctuations could help to moderate

64   the severity of budworm outbreaks.

65

66   What is largely unknown about this budworm-parasitoid food web is how the parasitoid

67   community interacts with other caterpillar species in relation to the fluctuations of budworm.

68   We know that some budworm parasitoids are generalists that attack multiple species, and

69   other parasitoid species are either exclusively or largely specialist on budworm (Krombein et

70   al., 1979; Eveleigh et al., 2007; Smith et al., 2011). The question remains, how are the

71   parasitoid populations maintained when budworm are rare. Undoubtedly, parasitoid

72   populations decrease when budworm densities decline, but depending on the parasitoid

73   species a reserve population of parasitoids could be maintained by attacking other caterpillar

74   species. As with finding the community-level response of parasitoids converging on high

75   budworm densities, we could expect to find a community-level response of parasitoids

76   attacking other caterpillars when budworm densities decline. Specifically, there is limited

77   research on the relative attack rates of the parasitoid community on budworm and other

78   caterpillar species as budworm densities change.

79

80   Whereas Eveleigh et al. (2007) provided a qualitative examination of the entire

81   budworm food web on balsam fir, and Royama et al. (2017) examined the impact of

82   parasitoids on budworm only, in this exploratory study, we aimed to quantify the changing

83   trophic interactions of parasitoids with both budworm and other caterpillar species on balsam

84   fir as budworm densities changed from high to low. We analyzed rearing data of budworm

5

85 and other caterpillar species collected from balsam fir branches sampled from 1982 to 1995.

86 During this time period, balsam fir branches were collected from three plots and a

87 representative sample of budworm and all other caterpillar species were placed into feeding

88 vials to identify mortality causes including parasitoids. Using this dataset, we examined the

89 parasitoid community's response to changing relative frequencies of budworm and other

90 caterpillar species on balsam fir. First, we examined patterns of host preference at the

91 parasitoid community scale. Host preference was established by testing the relationship

92 between the relative abundances of caterpillars and the relative abundances of parasitoid

93 emergences from each caterpillar type. The underlying causes of the parasitoid community

94 host preference response were tested in two ways: by excluding the most abundant species

95 and reevaluating community host preference, and by testing for temporal species diversity

96 turnover. Second, because parasitism rates and species turnover impact the structure and

97 dynamics of food webs, we examined how the topology and interaction strengths of the

98 budworm food web on balsam fir changed with fluctuating budworm frequencies. Overall, we

99 found that the parasitoid community indiscriminately tracked changes in relative densities of

100 budworm and other caterpillar species on balsam fir, exhibiting a collective response akin to a

101 generalist consumer.

102

103 **Materials and methods**

104 *Study sites*

105   Three plots of approximately 1 hectare each were established in balsam fir forests in

106 New Brunswick, Canada. Plot 1 was in the Acadia Research Forest near Fredericton

6

107 (46°00'N, 66°25'W). Balsam fir branches were sampled in this plot from 1982 to 1989.

108 Because budworm caused 60% tree mortality in Plot 1 by the mid-1980s, Plot 2 was added,

109 which was also in the Acadia Research Forest. Balsam fir branches were sampled in this plot

110 from 1986 to 1995. In the late 1980s, the budworm populations in Plot 1 and 2 were so low

111 that Plot 3 was added, approximately 170km farther north near Saint-Quentin (47°29'N,

112 67°15'W). Balsam fir branches were sampled in Plot 3 from 1988 until 1994 when budworm

113 populations also declined to a low level. All plots had mostly balsam fir but also contained

114 spruces and a variety of hardwood trees (Eveleigh et al., 2007). All plots were outside areas

115 of biopesticide application. Full details of the three plots and all sampling and rearing

116 procedures can be found in Lucarotti et al. (2004), Eveleigh et al. (2007) (SI Materials and

117 Methods) and Royama et al. (2017). Here, we present only a brief synopsis.

118

119 *Branch sampling*

120   At the beginning of each season, a group of co-dominant balsam fir trees were

121 selected in 20 random locations within each plot. Co-dominant trees were selected because

122 the majority of balsam fir trees in the plots were co-dominant trees (Royama et al., 2017).

123 Every year and for each plot, before larval emergence from winter diapause, one balsam fir

124 branch from each of the 20 locations was collected. As soon as second instar larvae in the

125 field began emerging from diapause, balsam fir branches were sampled approximately every

126 day until the end of budworm adult eclosion (~50 days). On each sampling day during the

127 earlier years when budworm populations were high, one foliated mid-crown balsam fir branch

128 from one of the trees in each of the 20 locations was collected. During the later years when

7

129 budworm populations were low, two or more branches were collected from each location to

130 increase the number of collected budworm larvae at each sample date and location

131

132 *Caterpillar and parasitoid sampling*

133 Overall, all caterpillars (budworm and other caterpillar species) were sampled from a

134 subset of the collected branches with the goal of sampling a minimum of 100 budworm

135 individuals. For branches sampled before budworm emergence from winter diapause, all

136 caterpillars were collected for rearing from all 20 branches sampled. For branches sampled

137 after budworm emergence from winter diapause, all caterpillars from one of the 20 sampled

138 branches were reared. If a minimum of 100 budworm were obtained for rearing from this

139 branch, no more branches were selected for collection of caterpillars for rearing. If less than

140 100 budworm were obtained from the first branch selected, then another branch was selected

141 and all caterpillars from that branch were collected and reared, even if the final total number

142 of budworm exceeded 100. When budworm populations were low, obtaining more than 100

143 budworm individuals became difficult. As a result, all caterpillars that were found on all the

144 sampled branches were collected for rearing. All collected caterpillars were individually reared

145 on artificial diet (McMorran, 1965) and inspected every weekday for mortality. There was high

146 rearing success of both budworm and other caterpillar species because all of these hosts

147 feed on balsam fir and therefore readily feed on the artificial diet (see Table S1 for the total

148 number of budworm and other caterpillars reared in each relative year and plot). All

149 parasitoids that emerged from any reared caterpillars were morphologically identified to genus

150 and where possible to species. Any parasitoids unidentifiable to at least genus were excluded

8

151 from our analysis (11% of the total number of emergences from budworm or other

152 caterpillars). Note, budworm were implanted in Plot 2 between 1990-1995 for separate

153 manipulative experiments (see Eveleigh et al. (2007) SI Methods). These implanted budworm

154 were not collected in the budworm/other caterpillar sampling mentioned above.

155

156 *Dataset preparation*

157 Because we were interested in quantifying the trophic interactions of parasitoids that

158 attack budworm, we excluded all parasitoid taxa that attacked only other caterpillar species.

159 The 48 parasitoid taxa (listed in Fig. 3) found to attack budworm formed 81% of all recorded

160 trophic interactions with other caterpillar species. Using Chao2 (function specpool, R package

161 vegan, version 2.5.2, (Oksanen et al., 2018)), we checked how excluding parasitoid taxa that

162 attacked only other caterpillar species impacted our sampling of the total potential number of

163 interactions between parasitoids and budworm or other caterpillar species. This subsetted

164 dataset captured 74% of the potential interactions between parasitoids and budworm and

165 63% of the potential interactions between parasitoids and other caterpillar species.

166 Furthermore, using the full, original dataset, Eveleigh et al. (2007) established through

167 rarefaction that changes in diversity of parasitoid species were not due to sampling artifacts.

168 Consequently, we are confident that any patterns found by the analyses below are not due to

169 changes in branch sampling intensity but due to underlying ecological mechanisms.

170

171   *Parasitoid community host preference*

172   To examine how the parasitoid community utilizes budworm or other caterpillar species

173   on balsam fir, we calculated two values for every combination of relative year and plot: the

174   ratio of parasitoid emergence from budworm to other caterpillar species for all parasitoid taxa

175   combined, and the ratio of abundances of budworm to other caterpillar species. For this

176   relationship, we use the term preference. Here, preference is applied to the community-level,

177   similar to how preference is applied to the population-level in Krebs (2014). Also note, relative

178   year (and years before/after peak, see Fig. 4) refers to a created variable where zero was set

179   as the relative year at which budworm populations peaked in each plot (budworm peaked in

180   1985, 1985, and 1991 for Plots 1, 2 and 3 respectively). We ran a generalized least squares

181   (GLS) regression with the log10 of the ratio of emergence (hereafter referred to as relative

182   budworm utilization) as the response variable and the log10 of the ratio of the abundances of

183   budworm to other caterpillar species (hereafter referred to as relative budworm frequency),

184   plot, and their interaction as the explanatory variables (function gls, R package nlme, version

185   3.1-145, (Pinheiro et al., 2018)). We fitted the full model using maximum likelihood estimation

186   (MLE), and then used backwards selection with likelihood ratio tests (LLRT) to select the final

187   fixed effects. We refitted the final model using restricted maximum likelihood estimation

188   (REML) to give unbiased MLE predictors (Zuur et al., 2009). Following the methods in

189   Greenwood and Elton (1979), we assessed whether the parasitoid community host

190   preference was frequency dependent, where a slope different from one indicates frequency

191   dependent host preference and an intercept different from zero indicates frequency

192   independent preference. The interaction of relative budworm frequency and plot was

10

193 significant (see Results), thus we performed linear regressions for each plot separately with

194 relative budworm frequency as the explanatory variable and relative budworm utilization as

195 the response variable. From these linear regressions, we tested, using one sample t-tests,

196 whether the slopes were different from one and the intercepts different from zero.

197

198   We wanted to test two underlying causes of the parasitoid community host preference:

199 whether driven by a single parasitoid taxon or by the whole community, and whether

200 community composition changes over time. To test whether driven by a single parasitoid

201 taxon or by the whole community, first we found the three most frequently emerging parasitoid

202 taxa. We stopped at three parasitoid taxa because these three parasitoid taxa comprised 73%

203 of the total number of emergences from budworm and other caterpillars. Second, we then

204 removed in turn the top parasitoid taxon, the top two parasitoid taxa, and the top three

205 parasitoid taxa from the data. Third, using these three datasets, we ran linear regressions for

206 each plot with relative budworm frequency as the explanatory variable and relative budworm

207 utilization as the response variable. Using one-sample t-tests, we compared the slopes and

208 intercepts for each plot when the one, two, and three most abundant parasitoid taxa were

209 excluded with the corresponding plot's slope and intercepts produced in the linear regression

210 with all parasitoid taxa included. To examine community composition in parasitoid taxa over

211 time, we ran an nMDS analysis using the Bray-Curtis dissimilarity measure (function

212 metaMDS, R package vegan, version 2.5.2, (Oksanen et al., 2018)). The community matrix

213 for calculating the Bray-Curtis dissimilarities consisted of the abundances of individual taxa

214 divided by the total number of parasitoid emergences (all taxa) for each relative year and plot.

11

215 We ran a perMANOVA between four groups describing the phase of the budworm population

216 cycle that each year was in (function adonis, R package vegan version 2.5-6). The four

217 groups were before the peak (three and two relative years before the peak), during the peak

218 (one relative year before and after the peak, and the peak), after the peak (two and three

219 relative years after the peak), and endemic (four to ten relative years after the peak). In this

220 perMANOVA, we used the Bray-Curtis dissimilarity measure, constrained permutations within

221 each plot, and maintained the temporal order of permutations.

222

223 *Food web topology and interaction strengths*

224   Because parasitism rates and species turnover impact the structure and dynamics of

225 food webs, we assessed how the topology and interaction strengths of the budworm food web

226 on balsam fir changed with fluctuating budworm densities. To examine changes in topology,

227 we produced visual bipartite food webs using the number of emergences of each parasitoid

228 taxon from either budworm or other caterpillar species for every relative year (R package

229 bipartite, version 2.15, (Dormann, Gruber, & Fruend, 2008)). To examine changes in

230 interactions strengths, we calculated the ratio of the median to maximum interaction strengths

231 for every relative year, where the number of emergences was used for interaction strengths.

232 Note, using the number of emergences or the per capita emergences for calculating the ratio

233 of median to maximum interaction strengths yields the same answer. To reduce the biasing of

234 the median to maximum interaction strength ratio by low caterpillar frequencies, we removed

235 any median:maximum value where less than 50 caterpillars were collected (budworm and

236 other caterpillars were counted separately). To assess how the distribution of weak to strong

12

237   interaction strengths changed over time, we ran separate linear models for budworm and

238   other caterpillars with the response variable of the ratio of median to maximum interaction

239   strengths and the explanatory variables of relative year, relative year^2, and Plot. To simplify

240   the model, four was added to each relative year to make negative relative years positive (-3

241   relative year became 1, and 10 relative year became 14).

242

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

244

245   **Results**

246   *Parasitoid community host preference*

247   The final model explaining relative budworm utilization included the explanatory

248   variables of relative budworm frequency, plot, and their interaction (Relative budworm

249   frequency:Plot interaction, L = 11.429, P = 0.0033, df = 1, log likelihood ratio test, Fig. 1).

250   Plots 1 & 2 did not have slopes significantly different from one nor intercepts significantly

251   different from zero (Table 1). Plot 3 had a slope significantly different from one and an

252   intercept significantly different from zero (Table 1).

253

254   Neither dropping the most abundant parasitoid taxon with the most emergences from

255   all caterpillars (*Apanteles fumiferanae* Vireck, Hymenoptera: Braconidae), nor dropping the

256   two most abundant parasitoid taxa (*Apanteles fumiferanae* and *Glypta fumiferanae* Viereck,

257   Hymenoptera: Ichneumonidae), nor dropping the three most abundant taxa (*Apanteles*

13

258 *fumiferanae*, *Glypta fumiferanae*, and *Smidtia fumiferanae* Tothill, Diptera: Tachinidae) caused

259 the slopes and intercepts for plots 1 & 2 to be significantly different from when all parasitoid

260 taxa were included (Table 2). Dropping the most abundant, two most abundant, and three

261 most abundant parasitoid taxa in Plot 3 caused the slopes and intercepts to be different from

262 when all parasitoid taxa were included (Table 2). The parasitoid community did not differ

263 between before and during the peak, but the parasitoid community in these two periods did

264 differ from after the peak and during the endemic periods (F = 5.918, *P* = 0.003, 999

265 permutations, perMANOVA, Fig. 2).

266

267 *Food web topology and interaction strengths*

268   Some parasitoid taxa (e.g. *Diadegma pulicalvariae* Walley, Hymenoptera:

269 Ichneumonidae) were found throughout the sampling period but not every year (Figs 3, S4, &

270 S5). Parasitoid taxa that were found in the food web consistently through time (e.g. *Apanteles*

271 *fumiferanae*), often changed between years from emerging from both budworm and other

272 caterpillar species to just one caterpillar type (Figs 3, S4, & S5). The distribution of

273 interactions strengths for budworm changed from a skewed distribution dominated by weak

274 interactions when budworm frequencies were high towards a uniform distribution when

275 budworm frequencies were low (Year: β = -0.040, t = -1.592, p = 0.132, Year^2: β = 0.008, t =

276 2.920, p = 0.011, Fig. 4). The distribution of interaction strengths for other caterpillar species

277 did not change over time (Year: β = -0.022, t = -0.526, p = 0.605, Year^2: β = 0.002, t = 0.951, p

278 = 0.353, Fig. 4)

279

14

Discussion

280

281   In our study, we have shown that this boreal insect food web is highly responsive and

282 flexible in time to changing budworm frequencies. We used a 14 year dataset of

283 host/parasitoid abundance to assess how parasitism rates and trophic interactions changed

284 over the course of a budworm cycle. We found an aggregated whole community

285 correspondence of parasitism rates with caterpillar relative frequency (budworm:other

286 caterpillar species frequency) and a change in topology and interaction strength distributions

287 on balsam fir as budworm frequencies fluctuated.

288

289   We found that the parasitoid community's preference for budworm or other caterpillar

290 species by either frequency or type was dependent on the plot (Fig. 1). The parasitoid

291 community in Plot 3 appeared to prefer budworm regardless of the relative densities of

292 budworm and other caterpillars. In contrast, the parasitoid communities in Plots 1 & 2 did not

293 prefer budworm or other caterpillars by either frequency or type. There are two possible

294 explanations behind this discrepancy. First, Plot 3 was not sampled during the budworm

295 endemic time period compared to Plots 1 & 2. Therefore, Plot 3's slope may be smaller

296 because Plot 3 did not have multiple years of very low budworm populations. Second, there

297 could be parasitoid community differences due to plot differences. Whereas Plots 1 & 2 were

298 within 10km of each other, Plot 3 was 170km away from Plots 1 & 2. Plot 3 also had the

299 lowest percent cover of balsam fir (Eveleigh et al., 2007). Although at smaller scales, we

300 found heterogeneity in parasitoid community responses to relative budworm and other

301 caterpillar frequencies, it could be argued that at larger scales, the parasitoid emergences

15

302 followed the relative frequencies of budworm and other caterpillar species. In other words, the

303 parasitoid community indiscriminately attacked budworm and other caterpillar species on

304 balsam fir. The major implication for biological control of budworm is showing that other

305 caterpillars are an important resource for the parasitoid community potentially maintaining

306 higher populations of parasitoids and increasing the parasitism of budworm.

307

308   The indiscriminate response by the whole parasitoid community could be caused either

309 by a few dominant parasitoid taxa or be a summation of all parasitoid taxa responses. When

310 we excluded the three most abundant parasitoid taxa from our dataset, the resulting

311 parasitoid communities in Plots 1 & 2 still largely exhibited no host preference by frequency or

312 by type (Table 2). When we dropped the three most abundant parasitoid taxa in Plot 3, the

313 resulting parasitoid community exhibited reduced preference for the most abundant caterpillar

314 (smaller positive slope) (Table 2). This change in slope was probably caused by dropping

315 *Apanteles fumiferanae* because the resulting slopes when dropping the two most and three

316 most abundant parasitoid taxa were similar to dropping just *Apanteles fumiferanae* (the most

317 abundant parasitoid taxa). Overall, the less common parasitoids exhibited a greater

318 preference for other caterpillar species than the common parasitoids which is corroborated by

319 examining the preferences of each of the three most common parasitoids; *Apanteles*

320 *fumiferanae* emerged from budworm more than other caterpillar species regardless of the

321 relative frequencies of budworm and other caterpillar species (Fig. S1), *Glypta fumiferanae*

322 emerged from caterpillars (both budworm and other caterpillars) when budworm were

323 abundant but were generally not found when budworm were rare (Fig. S2), and *Smidtia*

16

324 *fumiferanae* emerged from only budworm (Fig. S3). This indicates that parasitoid taxa have

325 differing preferences for budworm and other caterpillars, but collectively, the community

326 exhibited little to no preference depending on the plot. Differing preferences of each parasitoid

327 taxon could produce species turnover over time and indeed we did find species turnover (Fig.

328 2). Further support of differing preferences leading to species turnover comes from Royama

329 et al. (2017), who found that as budworm densities changed, there was turnover in the

330 parasitoid functional group that attacked budworm the most, which produced a relatively

331 constant overall parasitism rate of budworm. As a possible mechanism, Royama et al. (2017)

332 posited that the relative profitability of budworm and other caterpillar species changes in time

333 differently for each parasitoid species, where profitability is defined as the relative energy

334 content plus the number of caterpillars that can be attacked for a given amount of hunting

335 effort. Consequently, different parasitoid species would attack budworm at different time

336 periods during the budworm cycle. Overall, our results suggest that the parasitoids act

337 individually but produce a compensatory response to fluctuating budworm frequencies.

338

339   The observed large changes in parasitism rates and species turnover appeared to

340 translate into fluctuating topology and interaction strengths of the food web. We found large

341 changes in topology with many parasitoid taxa emerging from budworm and/or other

342 caterpillar species in some years and not others (Fig. 3). We also found shifts in the

343 distribution of interaction strengths over the budworm cycle (Fig. 4). When budworm were at

344 high frequencies, we found few strong interactions and many weak interactions. As budworm

345 frequencies declined, the distribution of interaction strengths became uniform. We

17

346 acknowledge that the likely cause behind this change in interaction strength distribution is

347 declining budworm frequencies. By random chance alone the parasitoids that rarely attack

348 budworm (the parasitoids that form the weak interactions) would rarely be found by our

349 sampling, leaving the parasitoids that often attack budworm (the parasitoids that form the

350 strong interactions) to be found in our sampling, thus biasing the median:maximum interaction

351 strength metric towards higher values (see Table S1 for total number of budworm and other

352 caterpillars sampled). Indeed, our observed pattern of increasing median:maximum

353 interaction strength metric was not different from 10,000 simulations of a parasitoid

354 community attacking declining budworm populations (see Figs. S6 & S7). In contrast, Ushio et

355 al. (2018) posited that behavioural and physiological responses or higher productivity in the

356 summer months drove interaction strengths distributions in a marine fish food web to be

357 skewed towards weak interactions in the summer and more uniform in the winter. Greater

358 budworm densities could be thought of as the same as high fish productivity in the summer.

359 Thus, finding weak interactions dominating during high productivity periods in both the

360 budworm and marine fish food webs is intriguing because these high productivity periods may

361 be a temporal period that most requires stabilization (Rosenzweig, 1971; Mougi & Nishimura,

362 2007) and weak interactions are thought to be a major stabilizing mechanism in food webs

363 (McCann, Hastings, & Huxel, 1998; Gellner & McCann, 2016). Regardless of the specific

364 mechanism behind the shifting distribution of interaction strengths, a major proportion of

365 budworm were parasitized by parasitoids that form weak interactions. All of these parasitoids

366 must have other sources of caterpillars.

367

18

368   Theory centred on responses to variable resources may help to explain the observed

369   aggregated indiscriminate community response and changes in interaction strength

370   distributions. One theoretical model proposes that higher trophic level generalist consumers

371   react to variation in their resources by either increasing consumption of a resource in one

372   separated subgroup of an entire food web (coupling to a resource compartment) or

373   decreasing consumption of a different resource in another separate subgroup of the entire

374   food web (decoupling from a resource compartment) (McCann, Rasmussen, & Umbanhowar,

375   2005; McMeans et al., 2016). This coupling and decoupling of different resource

376   compartments can mute large population variation in lower trophic level organisms, stabilizing

377   food webs. In the budworm-parasitoid food web, although individual parasitoid species may

378   be specialists or generalists, the aggregate response suggests that the collective parasitoid

379   community could be seen as a generalist consumer that couples and decouples the resource

380   compartment with balsam fir as the basal resource (hereafter referred to as balsam fir

381   resource compartment). However, this hypothesis for the parasitoid community response

382   requires another resource compartment separate from the balsam fir resource compartment.

383

384   We suggest that the other resource compartment in the budworm-parasitoid food web

385   has hardwood trees as the basal resource, where white birch (*Betula papyrifera* Marshall,

386   Betulaceae) and red maple (*Acer rubrum* Linnaeus, Sapindaceae) are hardwood trees. This

387   supposition come from observations that, during an outbreak, budworm densities were lower

388   and budworm parasitoid diversity was higher in stands that contained a mixture of softwoods

389   and hardwoods, otherwise known as mixed forest stands, compared to balsam fir dominated

19

390 stands (Su, Needham, & MacLean, 1996; Cappuccino et al., 1998; Eveleigh et al., 2007;

391 Smith et al., 2011). Consequently, these researchers hypothesized that there must be greater

392 diversity and abundances of parasitoids in mixed forest stands, maintained by the greater

393 diversity and abundances of caterpillar hosts in mixed forest stands. Both the hardwood

394 resource compartment hypothesis and this mixed stand hypothesis posit that hardwood trees

395 provide an important alternative source of caterpillar hosts for the budworm parasitoid

396 community. Indeed, our study shows that other caterpillar species are important to the

397 parasitoid community that attacks budworm suggesting that the mixed stand and hardwood

398 resource compartment hypotheses are mechanistically feasible. However, our study

399 undersamples the interactions between other caterpillar species on balsam fir and parasitoids

400 (using Chao2 with interactions, 63% of the potential interactions between parasitoids and

401 other caterpillar species were sampled in this study). In the wider budworm research, the

402 interactions of parasitoids with other caterpillar species on hardwoods are sampled even less,

403 thus preventing a clear test of these interrelated hypotheses. Consequently, because the

404 application of these hypotheses could reduce the severity of budworm outbreaks, further

405 research should sample the interactions of parasitoids with other caterpillar species on

406 balsam fir and hardwoods.

407

408   The parasitoid community response to changing budworm populations illustrates the

409 fantastic flexibility of food webs. Previous research found that as budworm densities increase

410 on balsam fir, the diversity of parasitoid species found on balsam fir increase at all trophic

411 levels (Eveleigh et al., 2007). In times of budworm rarity, parasitoid species diversity on

20

412 balsam fir drops and yet the parasitoid community must be maintained by some mechanism

413 otherwise the swift parasitoid community response to increased budworm abundance could

414 not occur (Eveleigh et al., 2007). Our study revealed that the parasitoid community responded

415 to changing densities of budworm by largely indiscriminately following the relative frequencies

416 of budworm and other caterpillar species on balsam fir. Changes in topology and interaction

417 strengths in the budworm food web on balsam fir resulted from the changes in parasitism

418 rates and species turnover. The other caterpillar species that these parasitoids attack are not

419 solely found on balsam fir, and in fact, many researchers have suggested that caterpillars on

420 hardwoods should be the dominant resource while budworm are rare (Su, Needham, &

421 MacLean, 1996; Cappuccino et al., 1998; Eveleigh et al., 2007). Consequently, including

422 caterpillars on hardwoods is imperative in further budworm research. Specifically, further

423 research could identify whether the parasitism rates of budworm on balsam fir compared to

424 the parasitism rates of caterpillars on hardwoods change as budworm densities peak and

425 ebb. Such a response, which appears to be created by the combined actions of all parasitoid

426 species, would be an excellent example of community ecology driving the population ecology

427 of a dominant species. For budworm management, if other caterpillars on hardwoods are

428 found to maintain budworm parasitoid populations, bolstering this mechanism could mute the

429 amplitude of budworm outbreaks, helping to reduce the defoliation and destruction of balsam

430 fir forests in eastern North America.

431

Acknowledgements

Author's Contributions

ESE designed the initial study. ESE and CJL performed the field and laboratory work. CJGG

and JF did the statistical analysis with assistance from ESE, MAS, and KSM. CJGG wrote the

first draft of the manuscript. All authors contributed to editing the manuscript.

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).

22

454 **References**

Allesina, S., & Tang, S. 2012. Stability criteria for complex ecosystems. Nature, **483**: 205–208.

Armstrong, J. B., Takimoto, G., Schindler, D. E., Hayes, M. M., & Kauffman, M. J. 2016. Resource waves: phenological diversity enhances foraging opportunities for mobile consumers. Ecology, **97**: 1099–1112.

Cappuccino, N., Lavertu, D., Bergeron, Y., & Régnière, J. 1998. Spruce budworm impact, abundance and parasitism rate in a patchy landscape. Oecologia, **114**: 236–242.

Cotton, P. A. 2003. Avian migration phenology and global climate change. Proceedings of the National Academy of Sciences, **100**: 12219–12222.

Dormann, C. F., Gruber, B., & Fruend, J. 2008. Introducing the bipartite package: Analysing ecological networks. R News, **8**: 8–11.

Dowden, P. B., Carolin, V. M., & Dirks, C. O. 1950. Natural control factors affecting the spruce budworm in the Adirondacks during 1946–19481. Journal of Economic Entomology, **43**: 774–783.

Eveleigh, E. S., McCann, K. S., McCarthy, P. C., Pollock, S. J., Lucarotti, C. J., Morin, B., McDougall, G. A., Strongman, D. B., Huber, J. T., Umbanhowar, J., & Faria, L. D. 2007. Fluctuations in density of an outbreak species drive diversity cascades in food webs. Proceedings of the National Academy of Sciences, **104**: 16976–16981.

Gellner, G., & McCann, K. S. 2016. Consistent role of weak and strong interactions in high- and low-diversity trophic food webs. Nature Communications, **7**: 11180.

Gouhier, T. C., Guichard, F., & Gonzalez, A. 2010. Synchrony and stability of food webs in metacommunities.. The American Naturalist, **175**: E16–E34.

23

Greenwood, J. J. D., & Elton, R. A. 1979. Analysing experiments on frequency-dependent selection by predators. Journal of Animal Ecology, **48**: 721–737.

Greyson-Gaito, C. J., McCann, K. S., Fruend, J., Lucarotti, C. J., Smith, M. A., & Eveleigh, E. S. 2020. Data and R Script for: Parasitoid community responds indiscriminately to fluctuating spruce budworm and other caterpillars on balsam fir (Version v4.2). Zenodo. https://doi.org/10.5281/zenodo.1305399.

Guichard, F., & Gouhier, T. C. 2014. Non-equilibrium spatial dynamics of ecosystems. Mathematical Biosciences, **255**: 1–10.

Ims, R., Henden, J., & Killengreen, S. 2008. Collapsing population cycles. Trends in Ecology & Evolution, **23**: 79–86.

Keitt, T. H. 2008. Coherent ecological dynamics induced by large-scale disturbance. Nature, **454**: 331–334.

Kent, A. D., Yannarell, A. C., Rusak, J. A., Triplett, E. W., & McMahon, K. D. 2007. Synchrony in aquatic microbial community dynamics. The ISME Journal, **1**: 38–47.

Krebs, C. J. 2014. Chapter 14 Niche Measures and Resource Preferences. In: Ecological Methodology (3rd ed.). Pearson Education: United States of America, pp. 596–653.

Krombein, K. V., Hurd, Jr., P. D., Smith, D. R., & Burks, B. D. 1979. Catalog of Hymenoptera in America North of Mexico (Vol. 1). Washington D.C., U.S.A.: Smithsonian Institution Press.

Levin, S. A. 1998. Ecosystems and the biosphere as complex adaptive systems. Ecosystems, **1**: 431–436.

Lucarotti, C. J., Eveleigh, E. S., Royama, T., Morin, B., McCarthy, P., Ebling, P. M., Kaupp, W. J., Guertin, C., & Arella, M. 2004. Prevalence of baculoviruses in spruce budworm

(Lepidoptera: Tortricidae) populations in New Brunswick. Canadian Entomologist, **136**: 255–264.

May, R. M. 1972. Will a large complex system be stable? Nature, **238**: 413–414.

McCann, K. S., Hastings, A., & Huxel, G. R. 1998. Weak trophic interactions and the balance of nature. Nature, **395**: 794–798.

McCann, K. S., Rasmussen, J. B., & Umbanhowar, J. 2005. The dynamics of spatially coupled food webs. Ecology Letters, **8**: 513–523.

McMeans, B. C., McCann, K. S., Tunney, T. D., Fisk, A. T., Muir, A. M., Lester, N., Shuter, B., & Rooney, N. 2016. The adaptive capacity of lake food webs: from individuals to ecosystems. Ecological Monographs, **86**: 4–19.

McMorran, A. 1965. A synthetic diet for the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). The Canadian Entomologist, **97**: 58–62.

Mougi, A., & Nishimura, K. 2007. A resolution of the paradox of enrichment. Journal of Theoretical Biology, **248**: 194–201.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. 2018. vegan: Community Ecology Package.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. 2018. nlme: Linear and Nonlinear Mixed Effects Models.

Pureswaran, D. S., Johns, R., Heard, S. B., & Quiring, D. 2016. Paradigms in eastern spruce budworm (Lepidoptera: Tortricidae) population ecology: a century of debate. Environmental Entomology, **45**: 1333–1342.

R Core Team. 2012. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.

Rosenzweig, M. L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. Science, **171**: 385–387.

Royama, T., Eveleigh, E. S., Morin, J. R. B., Pollock, S. J., McCarthy, P. C., McDougall, G. A., & Lucarotti, C. J. 2017. Mechanisms underlying spruce budworm outbreak processes as elucidated by a 14-year study in New Brunswick, Canada. Ecological Monographs, **87**: 600–631.

Royama, T., MacKinnon, W. E., Kettela, E. G., Carter, N. E., & Hartling, L. K. 2005. Analysis of spruce budworm outbreak cycles in New Brunswick, Canada, since 1952. Ecology, **86**: 1212–1224.

Seehausen, M. L., Bauce, É., Régnière, J., & Berthiaume, R. 2014. Influence of partial cutting on parasitism of endemic spruce budworm (Lepidoptera: Tortricidae) populations. Environmental Entomology, **43**: 626–631.

Smith, M. A., Eveleigh, E. S., McCann, K. S., Merilo, M. T., McCarthy, P. C., & Van Rooyen, K. I. 2011. Barcoding a quantified food web: crypsis, concepts, ecology and hypotheses. PLoS ONE, **6**: e14424.

Stephens, R. B., Hocking, D. J., Yamasaki, M., & Rowe, R. J. 2017. Synchrony in small mammal community dynamics across a forested landscape. Ecography, **40**: 1198–1209.

Su, Q., Needham, T. D., & MacLean, D. A. 1996. The influence of hardwood content on balsam fir defoliation by spruce budworm. Canadian Journal of Forest Research, **26**: 1620–1628.

Supp, S. R., & Ernest, S. K. M. 2014. Species-level and community-level responses to disturbance: a cross-community analysis. Ecology, **95**: 1717–1723.

Ushio, M., Hsieh, C., Masuda, R., Deyle, E. R., Ye, H., Chang, C.-W., Sugihara, G., & Kondoh, M. 2018. Fluctuating interaction network and time-varying stability of a natural fish community. Nature, **554**: 360–363.

Zuur, A., Leno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. 2009. Mixed effects models and extensions in ecology with R (1st ed.). New York, New York, United States of America: Springer-Verlag New York.

455

456 Table 1 Slopes and intercepts with corresponding t statistics, p values, and degrees of

457 freedom for each plot. The explanatory variable in the linear models for each plot was relative

458 budworm frequency. The response variable was relative budworm utilization.

459

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

460

461

462

463

28

464 Table 2 Slopes and intercepts with corresponding t statistics, p values, and degrees of

465 freedom when the three most abundant parasitoid taxa were dropped consecutively. The

466 explanatory variables in this model were relative budworm frequency, plot, and their

467 interaction. The response variable was relative budworm utilization.

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 & 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 & G. fumiferanae & 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

468

469

470

471

29

472 **<u>Figures</u>**
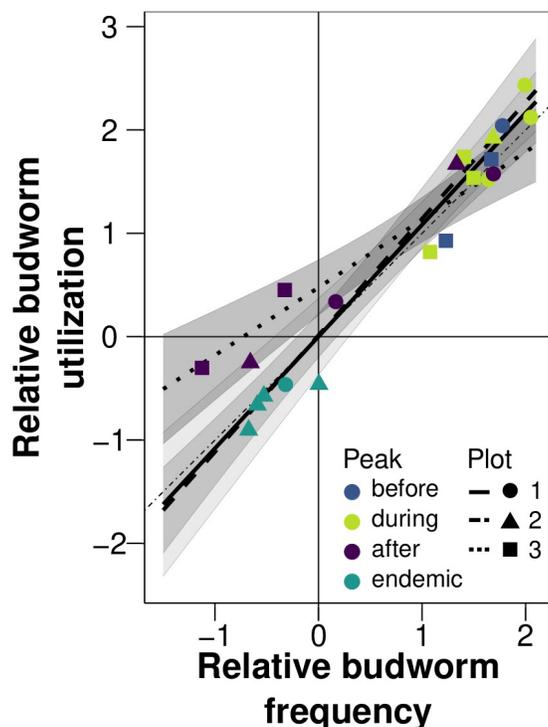
473 Figure 1 With some differences between plots, generally the parasitoid community did not

474 show a preference for budworm or other caterpillar species by either frequency or type.

475 Relative budworm utilization (Log10 ratio of parasitoid emergences from budworm to other

476 caterpillar species) for all parasitoid taxa used in our analysis as a function of the relative

477 budworm frequency (log10 ratio of all sampled budworm and other caterpillars). Each point is

478 a single relative year and a single plot. Shaded areas are 95% confidence intervals. The thin

479 dashed line is the y=x line.

480

481

482

30
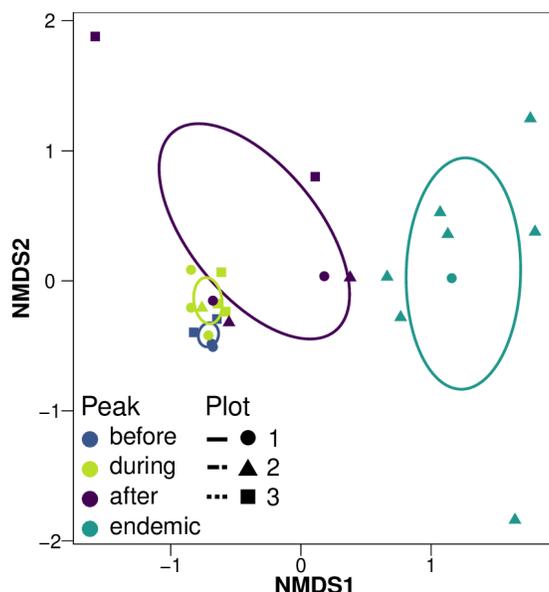
483 Figure 2 The parasitoid communities before and during the peak were significantly different

484 from after the peak. nMDS of parasitoid community emerging from budworm and other

485 caterpillar species on balsam fir over time. The colour of each point and ellipse corresponds

486 to the four temporal groups: three and two relative years before the peak (before – average

487 budworm abundance 7296); one relative year before and after the peak, and the peak (during

488 – average budworm abundance 8067); two and three relative years after the peak (after –

489 average budworm abundance 1128); and four to ten relative years after the peak (endemic –

490 average budworm abundance 29). Each point is a single relative year and a single plot. Each

491 ellipse is a covariance ellipse. 20 iterations were run with a final stress of 0.087 and instability

492 for the preceding 10 iterations of 0.0196.

493

494

495

31

Parasitoids

1. *Apanteles fumiferanae*
2. *Glypta fumiferanae*
3. *Smidtia fumiferanae*
4. *Meteorus trachynotus* ✶
5. *Dirophanes hariolus*
6. *Apechthis ontario*
7. *Lypha fumipennis*
8. *Phyxe pecosensis*
9. *Apanteles* sp.
10. *Eumea caesar*
11. *Mesopolobus tortricus*
12. *Itoplectis conquisitor*
13. *Tranosema tenuifemur*
14. *Agria affinis*
15. *Actia interrupta*
16. *Apanteles morrisi*
17. *Bassus binominata*
18. *Dolichogenidea absona*
19. *Dirophanes* sp.
20. *Madremyia saundersii*
21. *Scambus* sp.
22. *Macrocentrus linearis iridescens*
23. *Enytus montanus*
24. *Charmon extensor*
25. *Apanteles petrovae*
26. *Tranosema rostrale*
27. *Chelonus* sp.
28. *Diadegma pulicalvariae*
29. *Orgilus* sp.
30. *Apanteles milleri*
31. *Sympiesis* sp.
32. *Stictophisthus flaviceps*
33. *Pimpla pedalis*
34. *Meteorus versicolor*
35. *Elachertus cacoeciae*
36. *Aprostocetus esurus*
37. *Sarcophaga aldrichi*
38. *Pristomerus* sp.
39. *Perilampus* sp.
40. *Nemorilla pyste* ✶
41. *Microgaster* sp.
42. *Lissonota acrobasidis*
43. *Glypta* sp.
44. *Exochus nigripalpis*
45. *Diadegma* sp.
46. *Ceromasia auricaudata*
47. *Campoplex* sp.
48. *Bassus dimidiator*

Figure 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

501 quantitatively. Four different relative years are shown, where all plots were combined within a

502 relative year: (A) three relative years before the peak, (B) peak relative year, (C) three relative

503 years after the peak, and (D) ten relative years after the peak. All other relative years can be

504 found in Figs. S4 & S5. A star denotes a taxon that requires an alternate caterpillar host to

505 overwinter in. To find the corresponding taxon in Eveleigh et al. (2007), see Table S2.

506
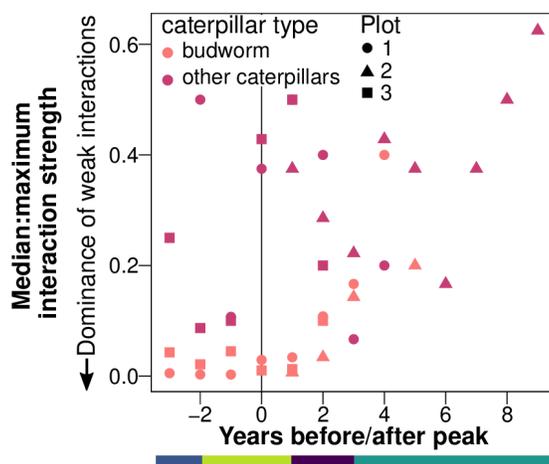
507 Figure 4 As budworm frequencies decreased, the distribution of interaction strengths shifted

508 from a dichotomy of strong and weak interaction strengths but skewed with a preponderance

509 of weak interactions to a uniform distribution of interaction strengths. Median:maximum

510 interaction strength over time, for each plot and for each caterpillar type, where the number of

511 emergences was used for interaction strengths. Bar at bottom depicts the Peak variable level

512 each year is in: (going from left to right) before, during, after, endemic.

513

514

Supporting Information

515 **For Greyson-Gaito, CJ*, McCann KS, Fründ, J, Lucarotti, CJ, Smith, MA, Eveleigh, ES.**

516 **Parasitoid community responds indiscriminately to fluctuating spruce budworm and**

517 **other caterpillars on balsam fir.**

* Corresponding Author: Email: christopher@greyson-gaito.com (CJGG)

ORCID:
CJGG – 0000-0001-8716-0290
KSM – 0000-0001-6031-7913
JF – 0000-0002-7079-3478
CJL – 0000-0002-3490-568X
MAS – 0000-0002-8650-2575
ESE – 0000-0001-5060-8565

518

519

520

521

522

523

524

525

526
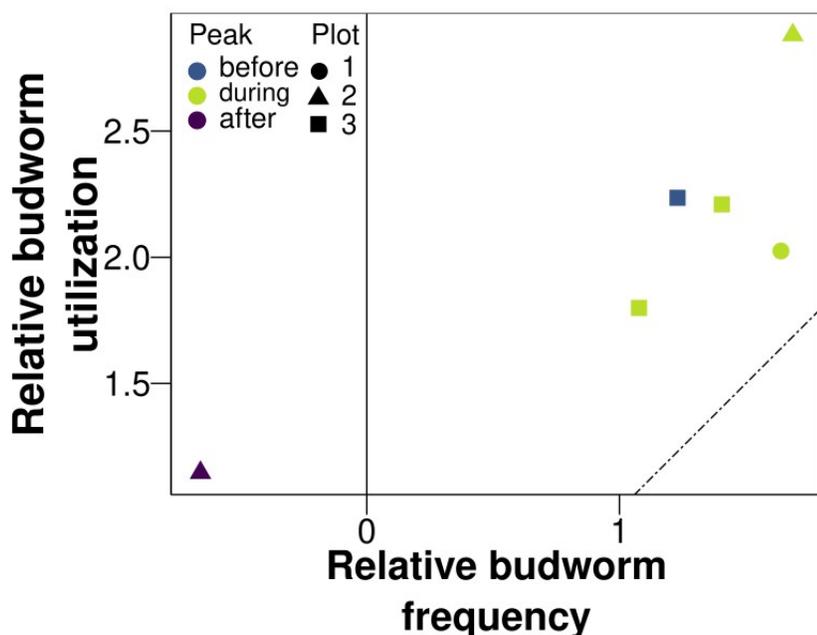
527 Figure S1 Relative budworm utilization by *Apanteles fumiferanae* (log10 ratio of *Apanteles*

528 *fumiferanae* emergences from budworm to other caterpillar species) as a function of the

529 relative budworm frequency (log10 ratio of all sampled budworm and other caterpillars). Each

530 point is a single relative year and a single plot. The thin dashed line is the y = x line.

34

531

532

533

534

535

536

537

538

539

540

541

542

543

544
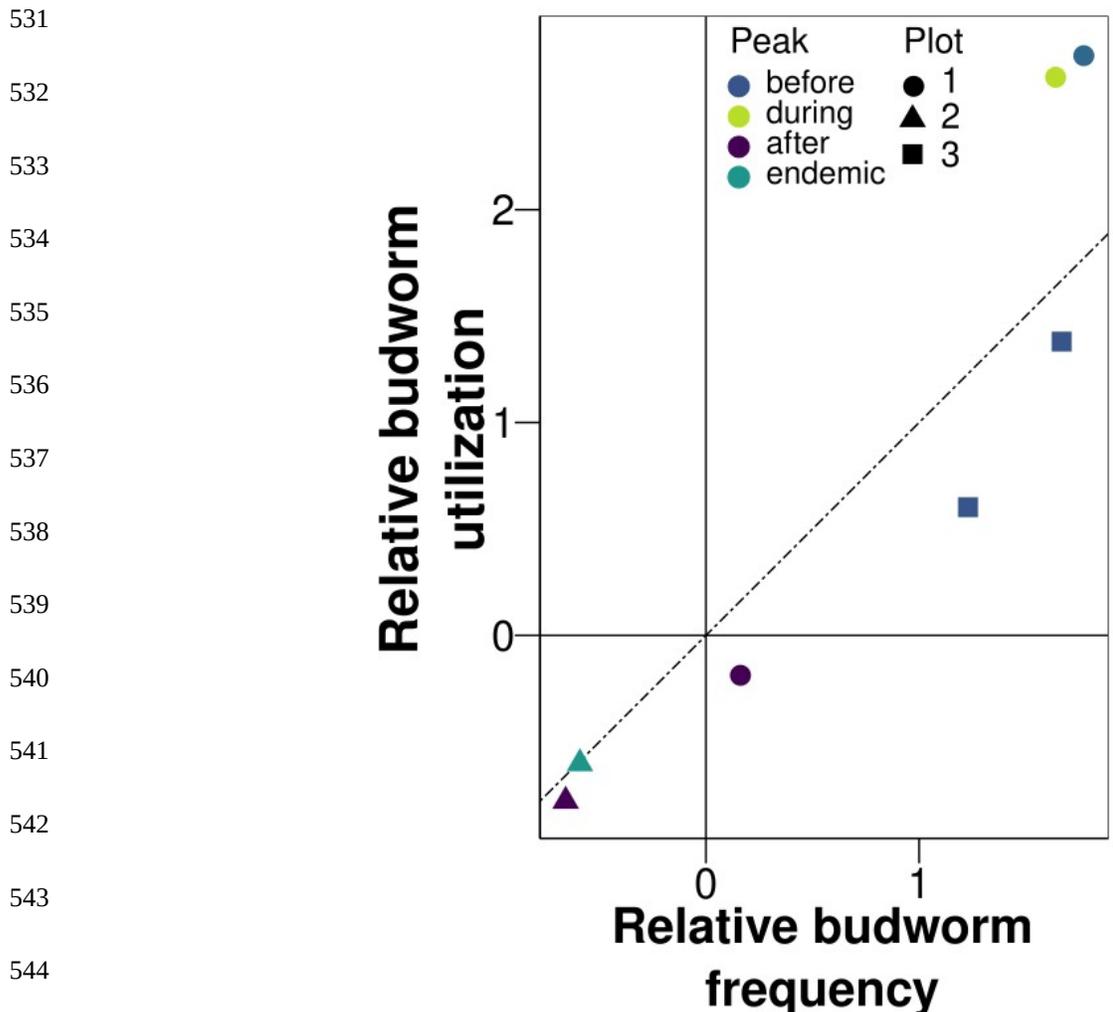
545 Figure S2 Relative budworm utilization by *Glypta fumiferanae* (log10 ratio of *Glypta*

546 *fumiferanae* emergences from budworm to other caterpillar species) as a function of the

547 relative budworm frequency (log10 ratio of all sampled budworm and other caterpillars). Each

548 point is a single relative year and a single plot. The thin dashed line is the y = x line.

549

550

551

35

552
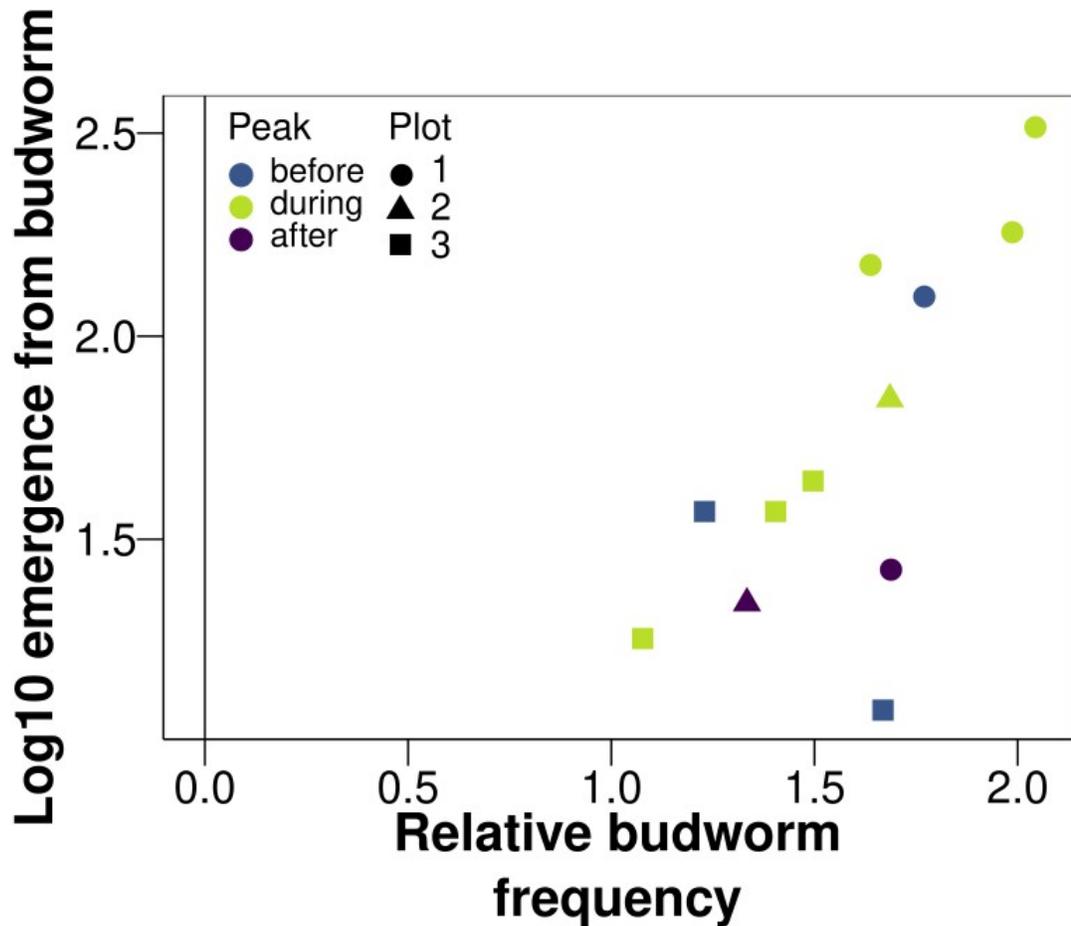
553 Figure S3 Log10 of *Smidtia fumiferanae* emergences from budworm as a function of the

554 relative budworm frequency (log10 ratio of all sampled budworm and other caterpillars). Each

555 point is a single relative year and a single plot. Note in this dataset, *Smidtia fumiferanae* did

556 not emerge from other caterpillar species and so a ratio of emergences from budworm to

557 other caterpillar species can not be calculated.

558

36

Parasitoids

|		
1. *Apanteles fumiferanae*	17. *Bassus binominata*	33. *Pimpla pedalis*
2. *Glypta fumiferanae*	18. *Dolichogenidea absona*	34. *Meteorus versicolor*
3. *Smidtia fumiferanae*	19. *Dirophanes* sp.	35. *Elachertus cacoeciae*
4. *Meteorus trachynotus* ✶	20. *Madremyia saundersii*	36. *Aprostocetus esurus*
5. *Dirophanes hariolus*	21. *Scambus* sp.	37. *Sarcophaga aldrichi*
6. *Apechthis ontario*	22. *Macrocentrus linearis*	38. *Pristomerus* sp.
7. *Lypha fumipennis*	*iridescens*	39. *Perilampus* sp.
8. *Phyxe pecosensis*	23. *Enytus montanus*	40. *Nemorilla pyste* ✶
9. *Apanteles* sp.	24. *Charmon extensor*	41. *Microgaster* sp.
10. *Eumea caesar*	25. *Apanteles petrovae*	42. *Lissonota acrobasidis*
11. *Mesopolobus tortricus*	26. *Tranosema rostrale*	43. *Glypta* sp.
12. *Itoplectis conquisitor*	27. *Chelonus* sp.	44. *Exochus nigripalpis*
13. *Tranosema tenuifemur*	28. *Diadegma pulicalvariae*	45. *Diadegma* sp.
14. *Agria affinis*	29. *Orgilus* sp.	46. *Ceromasia auricaudata*
15. *Actia interrupta*	30. *Apanteles milleri*	47. *Campoplex* sp.
16. *Apanteles morrisi*	31. *Sympiesis* sp.	48. *Bassus dimidiator*
	32. *Stictophisthus flaviceps*	

Figure S4 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: two relative years before the peak, one relative year before the peak, one relative year after the peak, and two relative years after the peak. 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 S2.

37
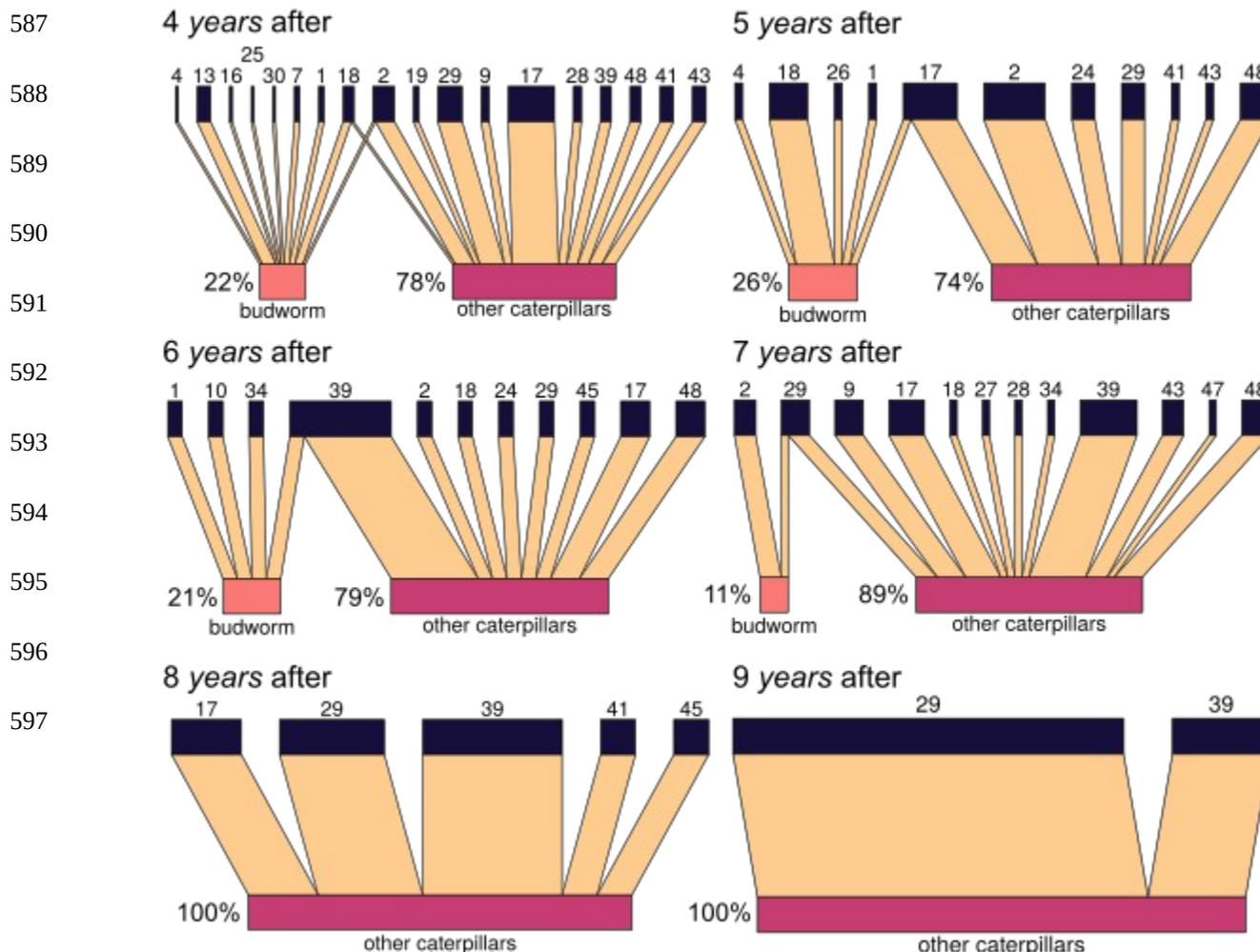
Figure S5 Graphical representations of the number of emergences of each parasitoid taxon (top boxes) from budworm and other caterpillar species (bottom boxes) over time. Six different relative years are shown: four relative years after the peak, five relative years after the peak, six relative years after the peak, seven relative years after the peak, eight relative years after the peak, and nine relative years after the peak.
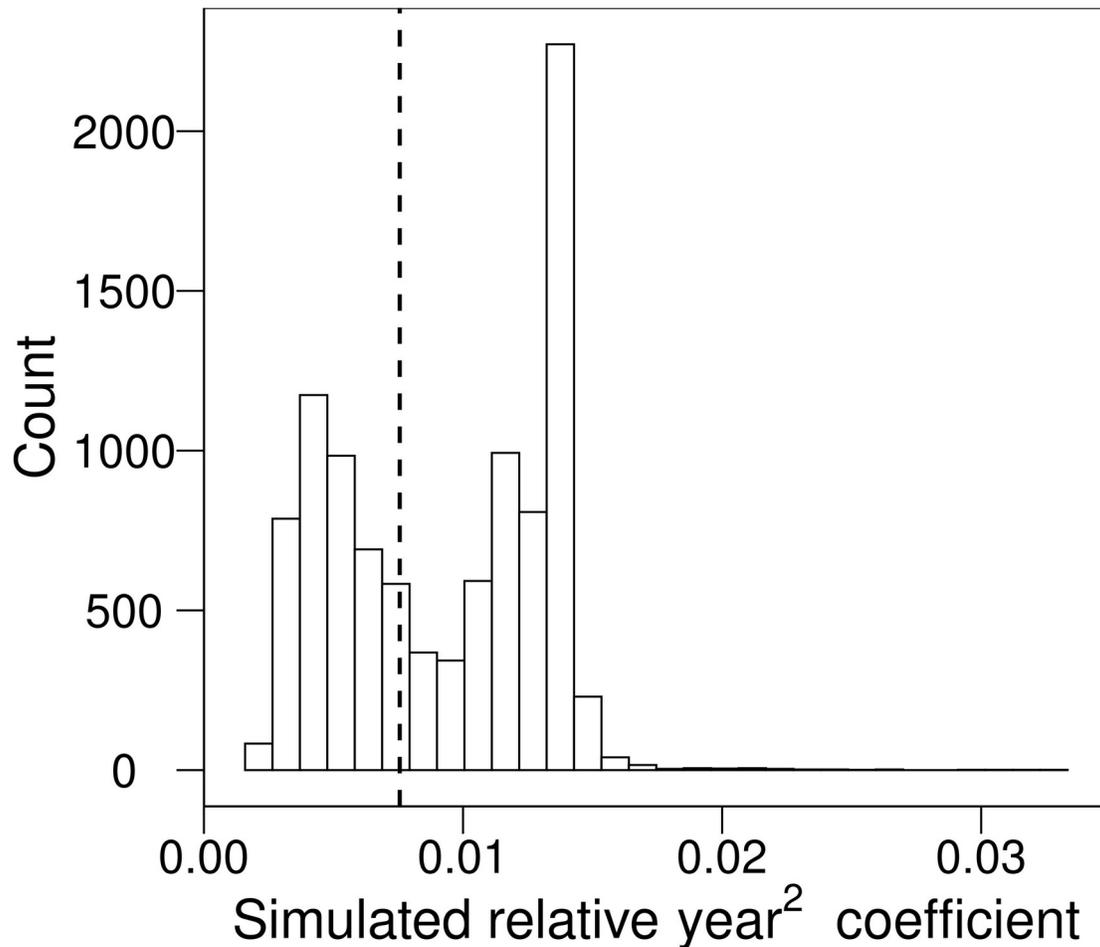
606   Figure S6 Histogram of 10,000 simulations to calculate the relative year^2 coefficient of a linear

607   model with median:maximum interaction strengths as the response variable and relative year,

608   relative year^2, and plot as the explanatory variables. The dashed line is our observed relative

609   year^2 coefficient. In these 10,000 simulations, a parasitoid community of 50 taxa attacked

610   budworm each year where budworm "populations" were taken from our observed sampling

611   frequency (Table S1). The parasitoid community attacked 17.85% of the budworm

612   "population" each year. Seven parasitoid taxa attacked 9.1%, 2.8%, 0.91%, 0.34%, 0.17%,

613   0.12%, 0.11% of the budworm population respectively. The rest of the parasitoid taxa attacked

614   0.1% of the budworm population each.

39

615
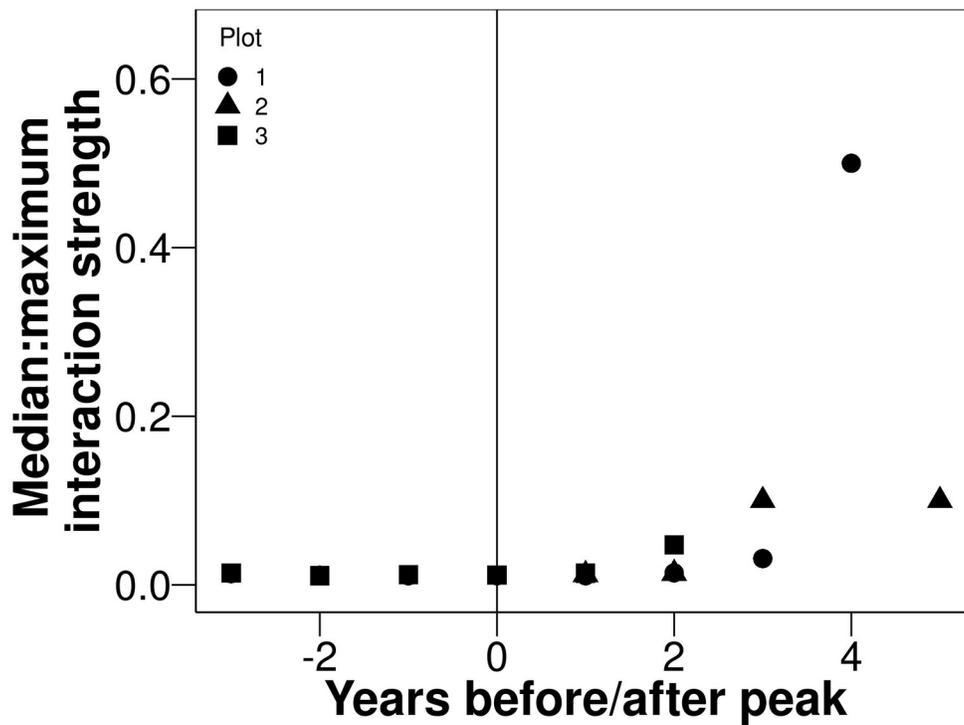
616 Figure S7 An example of one simulation of a parasitoid community attacking a declining

617 population of budworm. Similar to Fig. 4, median:maximum interaction strength increases

618 after 2 years after the peak.

619

620

621

622

623

624

625

626

627

40

628 Table S1 Total budworm and other caterpillar individuals sampled for each relative year and

629 plot. Total parasitoids that emerged from budworm or other caterpillars and parasitism rates of

630 budworm and other caterpillars.

Relative Year	Plot	Total budworm sampled	Total other caterpillars sampled	Total # parasitoids emerged from budworm	Total # parasitoids emerged from other caterpillars	Budworm parasitism rate	Other Caterpillars parasitism rate
-3	1	5095	0	1109	0	0.22	NA
-3	3	6481	139	886	17	0.14	0.12
-2	1	12230	209	3313	29	0.27	0.14
-2	3	5378	317	814	96	0.15	0.30
-1	1	10877	252	1783	52	0.16	0.21
-1	3	4708	394	456	69	0.10	0.18
0	1	16802	153	2623	19	0.16	0.12
0	3	6369	203	1170	34	0.18	0.17
1	1	8192	85	1417	5	0.17	0.06
1	2	5431	112	1588	19	0.29	0.17
1	3	4088	161	660	12	0.16	0.07
2	1	3392	70	548	14	0.16	0.20
2	2	2739	127	886	19	0.32	0.15
2	3	214	453	34	12	0.16	0.03
3	1	310	216	79	35	0.25	0.16
3	2	111	505	37	66	0.33	0.13
3	3	3	40	1	2	0.33	0.05
4	1	54	115	10	28	0.19	0.24
4	2	30	117	7	32	0.23	0.27
5	2	102	101	9	26	0.09	0.26
6	2	19	64	4	15	0.21	0.23
7	2	22	104	4	32	0.18	0.31
8	2	2	72	0	11	0.00	0.15
9	2	1	87	0	5	0.00	0.06
10	2	0	29	0	3	NA	0.10

631
632
633
634
635
636

41

637 Table S2 Parasitoid taxa found to attack budworm and other caterpillar species on balsam fir

638 from this study compared to the corresponding parasitoid taxon found to attack budworm in

639 Eveleigh et al. (2007)

Our parasitoids	**Eveleigh et al. (2007) PNAS parasitoids**
1. *Apanteles fumiferanae*	9. *Apanteles fumiferanae*
2. *Glypta fumiferanae*	10. *Glypta fumiferanae*
3. *Smidtia fumiferanae*	1. *Smidtia fumiferanae*
4. *Meteorus trachynotus*	11. *Meteorus trachynotus*
5. *Dirophanes hariolus*	14. *Dirophanes hariolus*
6. *Apechthis ontario*	15. *Apechthis ontario*
7. *Lypha fumipennis*	2. *Lypha fumipennis*
8. *Phyxe pecosensis*	3. *Phyxe pecosensis*
9. *Apanteles* sp.	67. *Apanteles* sp.
10. *Eumea caesar*	4. *Eumea caesar*
11. *Mesopolobus tortricus*	13. *Mesopolobus tortricus*
12. *Itoplectis conquisitor*	16. *Itoplectis conquisitor*
13. *Tranosema tenuifemur*	66. *Synetaeris* sp.
14. *Agria affinis*	8. *Agria affinis*
15. *Actia interrupta*	6. *Actia interrupta*
16. *Apanteles morrisi*	19. *Apanteles morrisi*
17. *Bassus binominata*	20. *Bassus binominata*
18. *Dolichogenidea absona*	18. *Dolichogenidea absona*
19. *Dirophanes* sp.	48. *Phaeogenes* sp.
20. *Madremyia saundersii*	7. *Madremyia saundersii*
21. *Scambus* sp.	80. *Scambus* sp.
22. *Macrocentrus linearis iridescens*	41. *Macrocentrus linearis iridescens*
23. *Enytus montanus*	27. *Enytus montanus*
24. *Charmon extensor*	22. *Charmon extensor*
25. *Apanteles petrovae*	17. *Apanteles petrovae*
26. *Tranosema rostrale*	45. *Tranosema rostrale*
27. *Chelonus* sp.	29. *Chelonus* sp.
28. *Diadegma pulicalvariae*	50. *Diadegma pulicalvariae*
29. *Orgilus* sp.	21. *Orgilus* sp.

42

30. *Apanteles milleri*	38. *Apanteles milleri*
31. *Sympiesis* sp.	36. *Sympiesis* sp.
32. *Stictophisthus flaviceps*	93. *Stictophisthus* sp.
33. *Pimpla pedalis*	44. *Pimpla pedalis*
34. *Meteorus versicolor*	60. *Meteorus* sp. (versicolor?)
35. *Elachertus cacoeciae*	98. *Elachertus*
36. *Aprostocetus esurus*	35. *Aprostocetus*
37. *Sarcophaga aldrichi*	47. *Sarcophaga aldrichi*
38. *Pristomerus* sp.	30. *Pristomerus* sp.
39. *Perilampus* sp.	54. *Perilampus* sp.
40. *Nemorilla pyste*	5. *Nemorilla pyste*
41. *Microgaster* sp.	49. *Microgaster* sp. & 74. *Microgasterinae*
42. *Lissonota acrobasidis*	62. *Lissonota acrobasidis*
43. *Glypta* sp.	56. *Glypta* sp.
44. *Exochus nigripalpis*	37. *Bathythrix nigripalpis*
45. *Diadegma* sp.	39. *Diadegma* sp.
46. *Ceromasia auricaudata*	Not in Eveleigh et al. (2007) PNAS parasitoids
47. *Campoplex* sp.	24. *Campoplex* sp.
48. *Bassus dimidiator*	40. *Bassus dimidiator*

640

43