

1 Quantifying the unquantifiable:

2 why Hymenoptera – not Coleoptera – is the most speciose animal order

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15 Abstract: We challenge the oft-repeated claim that the beetles (Coleoptera) are the most species-  
16 rich order of animals. Instead, we assert that another order of insects, the Hymenoptera, are more  
17 speciose, due in large part to the massively diverse but relatively poorly known parasitoid wasps.  
18 The idea that the beetles have more species than other orders is primarily based on their  
19 respective collection histories and the relative availability of taxonomic resources, both which  
20 disfavor parasitoid wasps. Since it is unreasonable to directly compare numbers of described  
21 species in each order, we present a simple logical model that shows how the specialization of  
22 many parasitic wasps on their hosts suggests few scenarios in which there would be more beetle  
23 species than parasitic wasp species. We couple this model with an accounting of what we call the  
24 “genus-specific parasitoid-host ratio” from four well-studied genera of insect hosts, a metric by  
25 which to generate extremely conservative estimates of the average number of parasitic wasp  
26 species attacking a given beetle or other insect host species. Synthesis of these two approaches  
27 suggests that the Hymenoptera may have 2.5 - 3.2x more species than the Coleoptera.

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35 “...if the micro-hymenopterists would get off their lazy asses  
36 and start describing species, there would be more micro-  
37 Hymenoptera than there are Coleoptera.”

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39 – Terry Erwin (in Rice 2015)

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41 The beetles (order Coleoptera), have historically (Kirby and Spence 1818; Westwood 1833;  
42 Hutchinson 1959) and contemporaneously (Farrell 1998; Hunt et al. 2007; McKenna et al. 2009;  
43 Zhang 2011; Wiens et al. 2015; Zhang et al. 2018) been described as the most speciose order of  
44 animals on Earth. The great diversity of beetles was sufficiently established by the middle of last  
45 century such that J.B.S. Haldane (possibly apocryphally<sup>1</sup>) quipped that an intelligent creator of  
46 life must have had “...an inordinate fondness for beetles” (Gould 1993). However, what  
47 evidence underlies the claim that the Coleoptera are more species-rich than the other insect  
48 orders? Certainly, more species of beetles (>350,000) have been *described* than any other order  
49 of animal, insect or otherwise (Bouchard et al. 2009), but does this reflect their actual diversity  
50 relative to other insects?

51 Why are beetles thought to be so diverse in the first place? In part, historical biases in beetle  
52 collecting and an associated accumulation of taxonomic resources for the Coleoptera may have  
53 had an outsized influence on our perception of diversity. In the mid-to-late 1800s, beetles were  
54 prized among insects for their collectability. Many landed gentlemen - including, notably,

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<sup>1</sup> Whether or not Haldane ever actually said it exactly in this way is unresolved (Gould 1995). This phrase does not occur in any of Haldane's writing, but he does write that “The Creator would appear as endowed with a passion for stars, on the one hand, and for beetles on the other.” (Haldane 1949)

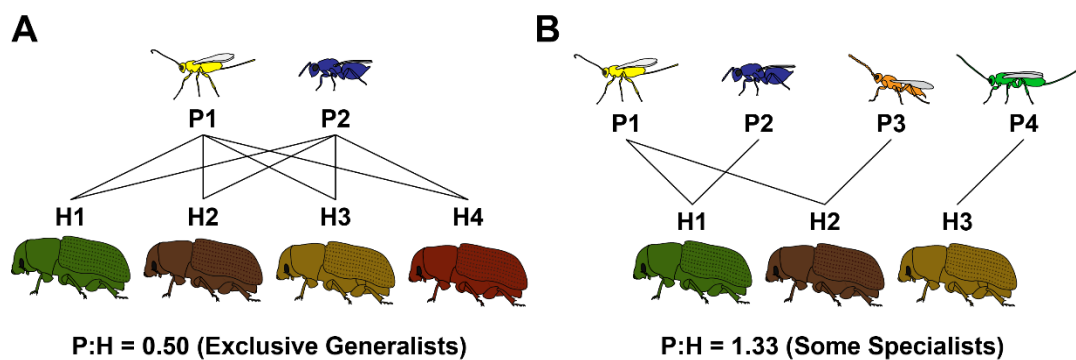
55 Charles Darwin - collected beetles for sport and would make a great show of comparing the sizes  
56 of their respective collections (Browne 1996; Sheppard 2004). This preconception was then  
57 reinforced by studies that extrapolated from specific, targeted collections of insect diversity that  
58 focused on beetles. Of these, perhaps the highest in profile was a study conducted by Terry  
59 Erwin. Erwin (1982) used an insecticide to fog the canopies of 19 individual *Luehea seemannii*  
60 trees in a Panamanian rainforest and then collected and identified the insect species that fell out  
61 of those trees. After having identified the proportion of the beetle species that were apparently  
62 host-specific to *L. seemannii* (163 of 955), he estimated that there might be as many as 12.2  
63 million beetle species in the tropics. Similar studies seeking to estimate global insect diversity  
64 have also tended to emphasize beetles (e.g., Ødegaard 2000; Stork et al. 2015).

65 Nevertheless, some previous work has challenged the canon, with various authors suggesting –  
66 though never quite insisting – that the Hymenoptera may be more speciose than the Coleoptera  
67 (LaSalle and Gauld 1993; LaSalle 1993; Gaston 1993; Austin and Downton 2000). The premise  
68 behind this suggestion is that most of the larvae of the Parasitica (one of the two infraorders of  
69 apocritan Hymenoptera; the other is the Aculeata, which includes ants, bees, and wasps), are  
70 obligate parasites of insect and other arthropod hosts that feed on the host's tissue until the host'  
71 dies ( $\approx$  "parasitoids"). Why is this parasitic life history relevant to the Hymenoptera's  
72 proportional contribution to insect diversity? Simply put, species of parasitoid Hymenoptera  
73 (including the Parasitica, as well as some other groups such as the Orussidae and some  
74 Chrysidoidea) attack all orders of insects as well as some non-insect arthropods (Gibson et al.  
75 1997; Wharton et al. 1997; Noyes 2017), and, reciprocally, most holometabolous insect species  
76 are attacked by at least one – and often many more than one – species of hymenopteran  
77 parasitoid (Schoenly 1990; Memmott and Godfray 1993). For instance, Hawkins and Lawton

78 (1987) examined parasitoid communities associated with 158 genera of British insects across  
79 five different orders, and found that parasitoid species richness ranged from 2.64 – 9.40 per host  
80 species across different host insect orders.

81 If parasitoid wasps are ubiquitous and most hosts are attacked by many different species, why is  
82 there any debate at all about the Hymenoptera being more diverse than other orders? One reason  
83 may be that estimates of the regional and global species-richness of parasitoid wasps remain  
84 elusive. Their small size and a relative paucity of taxonomic resources have left the parasitoid  
85 Hymenoptera relatively under-described compared to other insect orders (Gaston 1993; Huber  
86 2009). As a consequence, when collection-based estimates of regional insect diversity have been  
87 attempted, they have often excluded all but the largest and easiest-to identify families of parasitic  
88 Hymenoptera (e.g., Novotny et al. 2002; Pietsch et al. 2003; Bassett et al. 2012; though see  
89 Gaston 1991; Stork 1991).

90 A second reason for uncertainty regarding the species richness of the parasitoid Hymenoptera is  
91 that their host ranges are often unknown. While it may be true that most insects harbor many  
92 parasitoid species, the question remains whether these parasitoid communities are exclusively  
93 composed of oligophagous or polyphagous wasps that attack many hosts, or if instead the  
94 average insect host tends to have some number of specialist wasps among its many predators  
95 (**Figure 1**). Only in the latter case would one be able to confidently assert that the Hymenoptera  
96 is the largest of the insect orders.



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**Figure 1.** An illustration of how uncertainty about specialist vs. generalist

behaviors might lead to misleading conclusions about parasitoid species

richness. In panel A, each host species (differently colored beetles) is attacked

by two parasitoids. However, because all parasitoids attack all four beetles the

overall species richness of hosts exceeds that of the parasitoids (i.e.,  $P:H < 1$ ).

In panel B, while some hosts have only one parasitoid, overall parasitoid

richness exceeds host richness ( $P:H > 1$ ) because some parasitoids are more

specialized.

How then to approach this question without asking the micro-hymenopterists (and the

coleopterists, dipterists, lepidopterists, etc.) to hurry up and describe all of the world's insect

species? We suggest two complementary approaches: 1) mathematically describing the values of

parasitoid-to-host ("P:H") ratios that would support – or contradict – the notion that the

Hymenoptera is the most speciose insect order and 2) tabulating – wherever possible – actual

P:H ratios for various genera of host insects.

**What parasitoid-to-host ratios would suggest that the Hymenoptera are more species-rich**

**than other insect orders?**

114 For the Hymenoptera to be the largest order of insects, the global ratio of wasp parasitoids to  
115 hosts (P:H) need not – in fact – equal or exceed 1.0. Indeed, a global P:H of 1.0 (i.e., an average  
116 of one unique hymenopteran parasitoid species for each other insect species) would mean that  
117 parasitoids account for a full half of all insects. Instead, P:H ratios need only reach values such  
118 that the Hymenoptera are more species-rich than the next largest order (which, for the sake of  
119 argument, we will assume is the Coleoptera). Here, we work towards finding parameters that  
120 describe that space. First, it will be true that:

121 Equation 1: 
$$I = 1 - (P + C)$$

122 Where  $P$  is the proportion of all insect species that are parasitoid Hymenoptera,  $C$  is the  
123 proportion of insects that are Coleoptera, and  $I$  is the remaining proportion of insect species  
124 (**Figure 2 A**). Note that  $I$  includes the non-parasitoid Hymenoptera while both  $I$  and  $P$  exclude  
125 the many Hymenoptera that are parasitic on other parasitoids (“hyperparasitoids”).

126 Additionally, because of the intimate relationship between parasitoids and their hosts, we can  
127 describe the proportion of species that are parasitoid Hymenoptera using the following  
128 expression:

129 Equation 2: 
$$P = C(p_C) + I(p_I)$$

130 , where  $p_C$  and  $p_I$  represent the mean P:H ratios for all coleopterans and all non-coleopterans,  
131 respectively. The true values of  $p_C$  and  $p_I$  are unknowable, but can be estimated (see next  
132 section), and their use in this way allows for exploration of the ranges of P:H ratios that would  
133 result in different relative numbers of Hymenoptera and Coleoptera. Equation 2 again excludes  
134 hyperparasitoids, as well as parasitoids of non-insect arthropods, which makes  $P$  a conservative  
135 estimate of the proportion of insect species that are parasitoids.

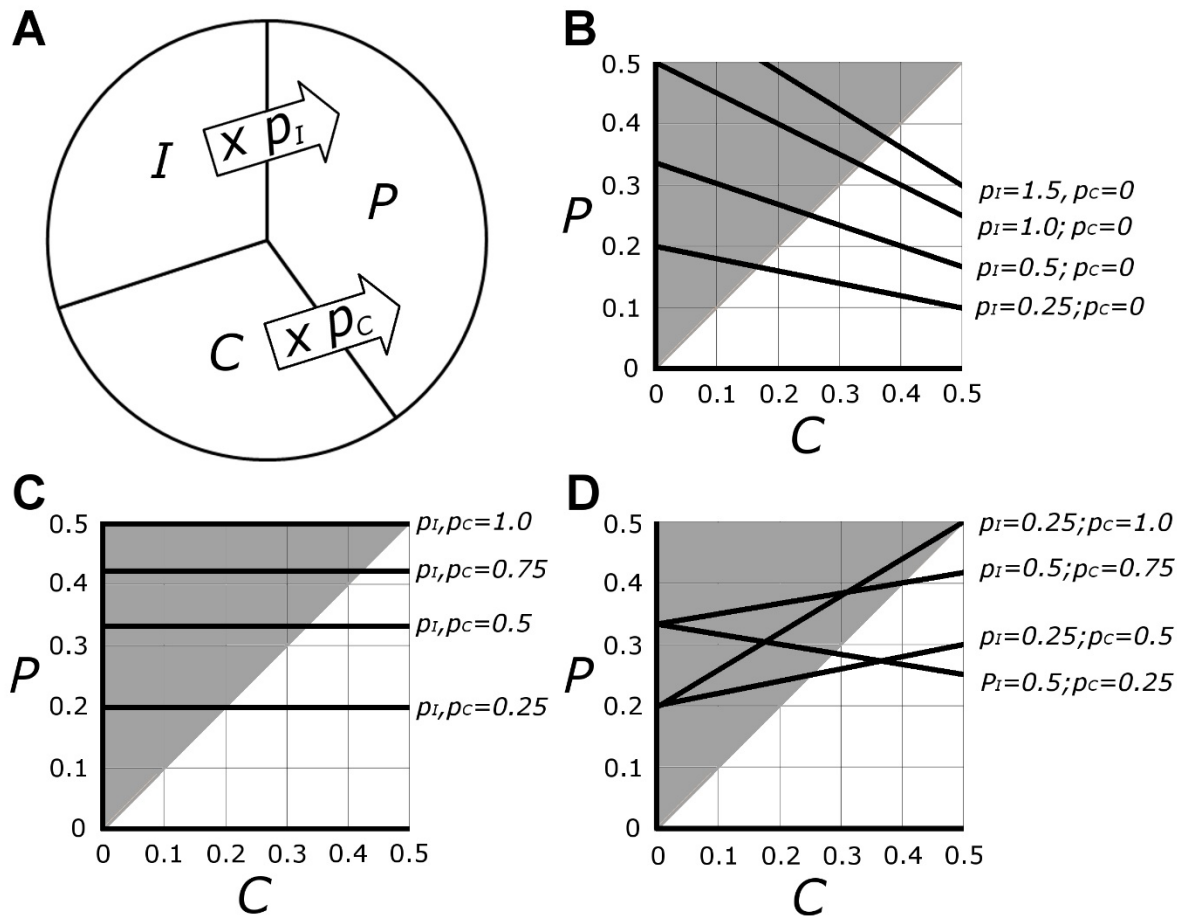
136 Given these two relationships, we can substitute Eq.1 into Eq. 2:

137 Equation 3: 
$$P = C(p_C) + p_I - p_I(P + C)$$

138 Equation 3 allows us to find the values of  $p_C$  and  $p_I$  that result in a  $P > C$  or vice versa. As  
139 shown in **Figure 2**, the space where  $P > C$  includes a substantial area where  $p_C$  or  $p_I$  (or both)  
140 can be  $< 1$ . For instance, if the Coleoptera make up 25% of all insects, as suggested by many  
141 contemporary authors (Hamilton et al. 2013; Stork et al. 2015), a  $p_C$  of only 0.25 (or one species-  
142 specialist parasitoid for every four beetle species), coupled with a  $p_I$  of 0.50, results in  $P = C$   
143 (and the many tens of thousands of non-parasitoid Hymenoptera will then tip the scale in their  
144 favor). Even if the Coleoptera amount to 40% of the insects, which reflects the percentage of  
145 currently-described insect species that are beetles, there will be more parasitoid Hymenoptera  
146 than beetles if  $p_C$  and  $p_I$  are equal to or in excess of 0.67 (two specialist parasitoid species for  
147 every three host species).

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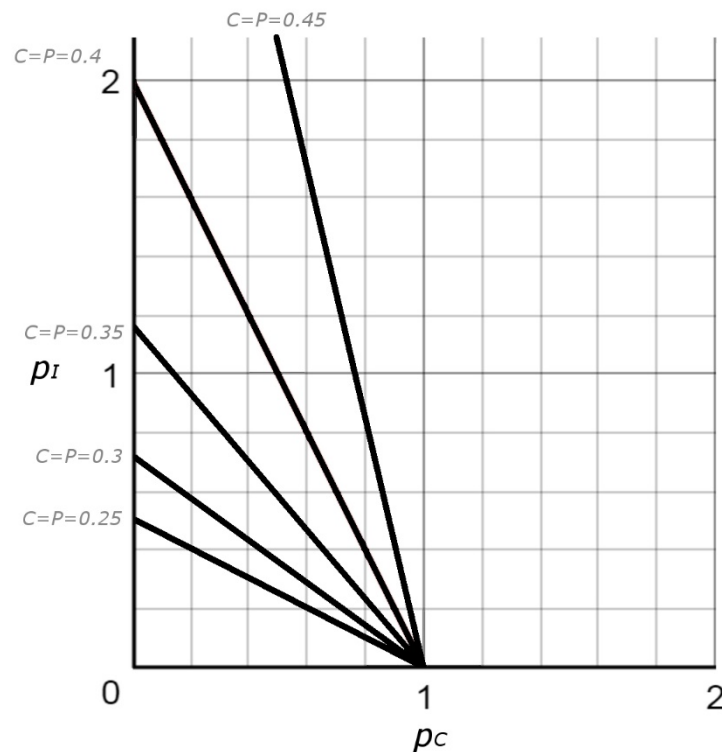
**Figure 2.** Representations of the space where the number of parasitoid wasp species would outnumber the Coleoptera, given different parasitoid-to-host ratios for coleopteran hosts and for other insect hosts. A) Pictorial representation of the model, wherein the total number of parasitoid species ( $P$ ) will be the sum of the number of species of Coleoptera ( $C$ ) and of other insects ( $I$ ), each first multiplied by their respective overall parasitoid-to-host ratio ( $p_C$  or  $p_I$ ); B) Black lines show results of the model for four different values of  $p_I$  and with  $p_C$  held at zero (i.e., when the average coleopteran has no specialist parasitoids). Where black lines overlap with gray shaded areas represents space where  $P > C$ ; C) Results of four different scenarios in which

160  $p_C$  and  $p_I$  are equal; D) Some additional combinations of  $p_C$  and  $p_I$ . Though  
161 both axes could continue to 1.0, some high values of  $P$  and  $C$  are not  
162 mathematically possible or biologically likely, and at  $P$  or  $C$  values above 0.5  
163 the question about relative species-richness becomes moot.

164 Another way to explore the values of  $p_C$  and  $p_I$  at which  $P$  will be greater than  $C$  is find the  
165 moments when the two will be equal. If we substitute  $C$  for  $P$  into Eq.3, we get:

166 Equation 4: 
$$p_C = 1 + 2p_I - \frac{p_I}{C}$$

167 We can then plot  $p_C$  vs  $p_I$  for values of  $C$  between 0 and 0.5 (**Figure 3**). Here, each line  
168 represents moments when  $P = C$ , such that the area above and to the right of each line represents  
169 values of  $p_C$  and  $p_I$  that result in a  $P > C$ . Here again,  $p_C$  and  $p_I$  need not be particularly large for  
170 the parasitoid Hymenoptera to exceed the species richness of the Coleoptera. For instance, if one  
171 quarter of all insects are beetles,  $p_C$  and  $p_I$  need only exceed 0.4 (the equivalent of two  
172 parasitoid species for every five host species).



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### 181 **What do actual P:H ratios look like in nature?**

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**Figure 3.** Plot based on Equation 4, with five representations of moments

when  $C$  and  $P$  are equal proportions (solid black lines).  $p_I$  = overall P:H ratio

for non-coleopteran insect hosts;  $p_C$  = overall P:H ratio for the Coleoptera.

Space above and to the right of each line represents values of  $p_C$  and  $p_I$  where

$P > C$ , while space below and to the left of each line represents values where

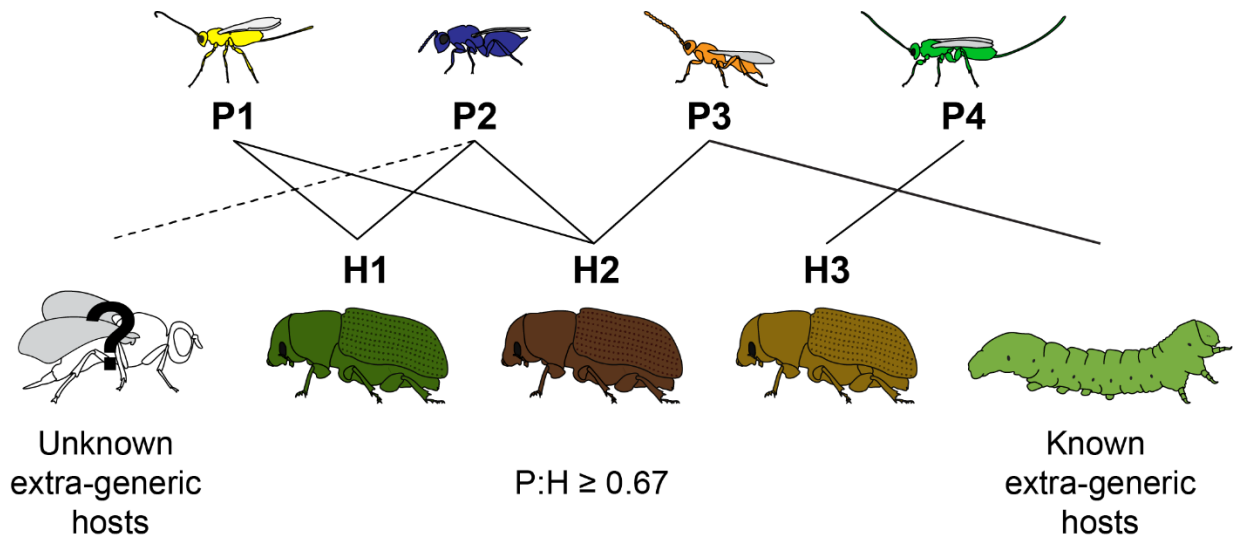
$C > P$ .

The next question becomes: can we estimate parasitoid: host ratios (e.g.,  $p_C$ ,  $p_I$ ) for different

host insects? Quantifying global P:H ratios for entire insect orders is as unapproachable as the

task of counting all of the living insect species: not only are most Hymenoptera undescribed, host

185 records for described species are often incomplete, such that multiplying each host species by its  
186 supposed number of specialist parasitoids may often inadvertently include parasitoids that share  
187 hosts (**Figure 4**). While this is problematic, recognition of the problem helps present paths  
188 forward. For indeed, *some* host-parasitoid systems are exceedingly well studied and well-  
189 understood, such that we can be reasonably confident about the completeness of the host records  
190 of at least some parasitoids. With this information, we can calculate a metric that we call the  
191 genus-specialist parasitoid:host ratio. This metric interrogates all members of a host insect genus  
192 in the same geographic region and identifies all of the parasitoids known to attack only members  
193 of that genus (the “genus-specialist” parasitoids). Because this P:H ratio ignores all parasitoids  
194 known to attack any extra-generic host – as well as those whose host range is unknown or has  
195 been incompletely studied – it is therefore an extremely conservative estimate of the overall P:H  
196 ratio for an insect genus.



198 **Figure 4.** Known genus-specialist parasitoids can be used to calculate a  
199 minimum P:H ratio for an insect host genus. The focal beetle genus H (three  
200 species) has four known parasitoids, P1-P4. P1 and P4 are relatively well-

201 studied, and known to be genus-specialists, attacking only hosts in this beetle  
202 genus. P3 has some known extra-generic hosts, while the host range of P2 is  
203 poorly studied and unknown extra-generic hosts may exist. For the purposes  
204 of estimating a genus-specialist P:H, one would therefore use only P1 and P4,  
205 such that a minimum P:H for this beetle genus would be  $2/3$ , or 0.67. Note  
206 that if the total number and identities of extra-generic hosts were known for  
207 P2 and P3, a “true” P:H for the genus could be calculated (see **Synthesis**,  
208 below).

209 Below, we present four case studies, representing host-parasitoid systems with records  
210 sufficiently complete to allow for calculation of genus-specialist parasitoid:host ratios. For each  
211 system, we focus on a single host genus in North America. We restricted geography so that  
212 parasitoid numbers would not be inflated by large biogeographic differences between hosts in  
213 their parasitoid assemblages. North America was chosen because sampling is relatively strong,  
214 and several robust resources exist for Nearctic parasitoids (e.g., Krombein et al. 1979; Peck  
215 1963; Noyes 2017).

216 For each system, we searched for all literature that mentioned the name of the host genus (or  
217 historical synonyms) and either “parasite” or “parasitoid” and compiled a database of records,  
218 performing reticulated searches on each parasitoid species name as it was added to the database  
219 in order to determine known parasitoids host ranges. From among all parasitoid records, we  
220 classified parasitoids as “genus-specialists” if they had only ever been reared from hosts in this  
221 same genus. We then split these “genus-specialists” into two groups: those for which an  
222 argument can be made that they do not have unknown extra-generic hosts, and those that were  
223 “possible genus-specialists” but for which records were less complete. Non-hymenopteran

224 parasitoids (e.g., Tachinidae) were excluded, but in any case were only present for two of the  
225 four hosts we examined (*Malacosoma* and *Neodiprion*), and generally do not have the  
226 taxonomically cosmopolitan host ranges of the hymenopteran parasitoids. For cases where host  
227 genera were found on multiple continents, only host species in North America were included in  
228 the study, and to be conservative, a parasitoid was still considered “generalist” if it occurred on  
229 an extra-generic host species outside of North America. Introduced host species were noted but  
230 not counted in host lists, as they do not represent long-term host-parasite relationships.  
231 Introduced parasitoid species were included in generalist lists, regardless of whether they were  
232 specialists on that genus in North America or elsewhere. We describe each system below and  
233 refer the reader to Supplemental Materials for species lists, specialist / generalist classifications,  
234 and citations. A summary of data across the four genera can be found in **Table 1**.

### 235 **System 1: *Rhagoletis* (Diptera: Tephritidae)**

236 Many North American *Rhagoletis* flies are pests of agriculturally-important fruits. Eggs are  
237 deposited in ripening fruits by the female fly, and larvae develop through several instars while  
238 feeding on fruit pulp (Bush 1966). For most species, larvae then exit the fruit and pupate in the  
239 soil. Parasitoids are known from egg, larval and pupal stages of many *Rhagoletis* species.  
240 Several studies have described the parasitoid communities associated with *Rhagoletis*  
241 agricultural pest species (e.g., Lathrop and Newton 1933; Bush 1966; Cameron and Morrison  
242 1974; Wharton and Marsh 1978; Feder 1995), though records of parasitoids of non-pest species  
243 also exist (e.g., Rull et al. 2009; Forbes et al. 2010, 2012). Moreover, many of the associated  
244 parasitoid species are well-studied in their own right, with robust records of their biology,  
245 ecology, and host-ranges (Wharton and Marsh 1978; Muesebeck 1980; Forbes et al. 2009;  
246 Wharton and Yoder 2017).

247 Of the 24 species of North American *Rhagoletis* flies, 16 have a published record of parasitoid  
248 associations. Across these 16 flies, we found records of 39 parasitoid species, among which 24  
249 “genus-specialists” have been described only from North American *Rhagoletis* and no other  
250 insect host (**Supplemental Table 1**). Of these, we set aside three “possible” genus-specialist  
251 species that did not have a strong collection record and for which host records may possibly be  
252 incomplete. The remaining set of genus-specialists included 14 braconids (genera *Diachasma*,  
253 *Diachasmimorpha*, *Utetes*, and *Opius*), six diapiroids (genus *Coptera*), and a pteromalid (genus  
254 *Halticoptera*). The genus-specialist P:H ratio for *Rhagoletis* is therefore either 1.31 (21/16), or  
255 1.50 (24/16), depending on whether “possible genus-specialists” are included. An extra-  
256 conservative P:H ratio might also include the eight *Rhagoletis* hosts that have no record of  
257 parasitoids ( $P:H = 21/24 = 0.88$ ), though this almost certainly ignores some number of unknown  
258 genus-specialist parasitoids.

259 Some of the 15 “generalist” parasitoids of *Rhagoletis* have been reared from a diverse set of  
260 extra-generic hosts, but in some cases only from one other fruit-infesting tephritid (e.g.,  
261 *Phygadeuon epochrae* and *Coptera evansi*, both of which have only been reared from *Rhagoletis*  
262 and from *Epochra canadensis* [Diptera: Tephritidae]). These 15 “generalists” are listed in  
263 **Supplemental Table 1**.

## 264 **System 2: *Malacosoma* (Lepidoptera: Lasiocampidae)**

265 The tent caterpillars (genus *Malacosoma*) are shelter building, cooperatively-foraging moths that  
266 damage both coniferous and deciduous trees across at least 10 families. Most species use >1 host  
267 tree genus, though some (e.g., *Malacosoma constrictum*; *Malacosoma tigris*) are more  
268 specialized (Fitzgerald 1995). There are six North American species of *Malacosoma*, some with  
269 overlapping geographic distributions (Fitzgerald 1995). Female moths lay eggs in a mass

270 wrapped around a branch of the host tree. Larvae of most species (*M. disstria* is an exception)  
271 live colonially inside “tents” made of spun silk and make regular excursions to feed on host  
272 leaves. The caterpillar stage is eaten by birds, mammals and several insect predators, but the  
273 most taxonomically diverse natural enemies are the parasitoids (Fitzgerald 1995). Of these,  
274 approximately one third are Dipteran (family Tachinidae), while the remaining two thirds are  
275 Hymenopteran parasitoids. Parasitoids attack all immature life stages, but most appear to emerge  
276 during the pre-pupal or pupal stage. Parasitoids of the North American tent caterpillars have been  
277 well documented, and often in the context of other available forest caterpillar hosts, such that it is  
278 reasonable to assert that some parasitoid species are *Malacosoma*-specific (e.g., Langston 1957;  
279 Stacey et al. 1975; Shaw 2006).

280 All six of the North American *Malacosoma* species have at least one known parasitoid  
281 association, and we compiled a total of 78 different parasitoid species across all hosts  
282 (**Supplemental Table 2**). Of these, eleven had only been reared from *Malacosoma*. Five of these  
283 eleven species we assigned to the “possible genus-specialists” category, on account of their not  
284 having been assigned a specific name (which makes it hard to determine whether other hosts  
285 exist), or because they had only been reared a single time from the host. The remaining six  
286 “genus-specialists,” were from four different hymenopteran families. The genus-specialist P:H  
287 ratio for *Malacosoma* is therefore between 1.00 and 1.83.

288 *Malacosoma* have many more “generalists” than *Rhagoletis*: 68 species have been reared from  
289 both *Malacosoma* and at least one other extra-genetic host (**Supplementary Table 2**). Many of  
290 these appear to be specific to Lepidopteran hosts.

291 **System 3: *Dendroctonus* (Coleoptera: Curculionidae).**



292 Approximately 14 species of *Dendroctonus* bark beetles are found in North America (Six and  
293 Bracewell 2015). *Dendroctonus* are specific to conifers in family Pinaceae, and can be highly  
294 destructive to their host trees. Female beetles construct nuptial chambers in trees where they  
295 mate with males and then deposit eggs in tunnels in the phloem. Larvae feed on phloem and  
296 outer bark and leave the tree only after pupation and adult emergence (Six and Bracewell 2015).  
297 Most species are tree genus- or species-specific.

298 Parasitoids have been described for eight of the 14 North American *Dendroctonus* species,  
299 though for two of these (*D. adjunctus* and *D. murryanae*) only one or two parasitoid species are  
300 known. The total list of *Dendroctonus*-associated parasitoids is long, but the records are also  
301 often problematic, as *Dendroctonus* share their habitat with several other genera of bark beetles,  
302 which may or may not be attacked by the same parasitoids. In many studies, parasitoids are listed  
303 as “associates” of either *Dendroctonus*, or of one of the other species, or of both, but this does  
304 not always necessarily mean that a parasitoid attacks that beetle (e.g., Overgaard 1968; Langor  
305 1991; Berisford 2011). We have here again tried to be conservative, though in one case  
306 (*Meterorus hypophloeii*) we have ignored a claim of “association” with *Ips* beetles (Kulhavy et al.  
307 1989) as it did not seem to be well justified and other authors describe *M. hypophloeii* as a  
308 *Dendroctonus frontalis* specialist (Coster and Stein 1977; Berisford 2011). In total, we found  
309 nine *Dendroctonus* genus-specialists, two possible genus-specialists, and 48 “generalists”  
310 (**Supplemental Table 3**). The genus-specific P:H ratio for *Dendroctonus* is therefore between  
311 1.13 and 1.38.

#### 312 **System 4: *Neodiprion* (Hymenoptera: Diprionidae)**

313 *Neodiprion* is a Holarctic genus of pine-feeding sawflies specializing on conifers in the family  
314 Pinaceae (Smith 1993). These sawflies have close, life-long associations with their tree hosts.

315 The short-lived, non-feeding adults mate on the host plant shortly after eclosion, after which the  
316 females deposit their eggs into pockets cut within the host needles. The larvae hatch and feed  
317 externally on the host needles throughout development, and then spin cocoons on or directly  
318 beneath the host (Coppel & Benjamin 1965; Knerer & Atwood 1973; Knerer 1993). Many  
319 species also have highly specialized feeding habits, and feed on a single or small handful of host-  
320 plant species in the genus *Pinus*. Since many of the ~33 *Neodiprion* species native to North  
321 America are considered economic pests (Arnett 1993), considerable effort has gone into  
322 describing their natural history and exploring potential methods to control *Neodiprion* outbreaks.  
323 Despite the wealth of natural history information, compiling a list of parasitoids attacking  
324 *Neodiprion* is complicated by a history of accidental and intentional introductions. In addition to  
325 the native species, the European pine sawfly, *Neodiprion sertifer*, and three species from the  
326 closely related genera *Diprion* and *Gilpinia* were introduced in the past ~150 years and have  
327 spread across the United States and Canada (Britton 1915; Gray 1938; Schaffner 1939; Balch  
328 1939). In an attempt to control these invasive pests, several parasitoids have been introduced,  
329 and now attack both native and invasive diprionids (Finlayson & Reeks 1936; Finlayson 1963;  
330 MacQuarrie et al. 2016).

331 We found 20 genus-specialist parasitoid species associated with the 21 species of North  
332 American *Neodiprion* for which parasitoid records exist. An additional seven parasitoids were  
333 classified as “possible” genus-specialists. The genus-specific P:H ratio for *Neodiprion* is  
334 therefore between 0.95 and 1.29. An additional 51 species had been reared from both *Neodiprion*  
335 and an extra-generic host, with nine introduced parasitoids. We also compiled a list of 14  
336 introduced parasitoids, nine hyperparasitoids, and 28 tachinid (Diptera) parasitoids of *Neodiprion*  
337 (**Supplemental Table 4**), but these were not included in any analyses.

338

### 339 **Synthesis**

340 Upon considering our model together with actual estimates of P:H ratios from natural host  
341 systems (**Table 1**), there appear to be few conditions under which the Hymenoptera would not be  
342 the largest order of insects. If, for instance, the P:H ratios for *Rhagoletis*, *Malacosoma*,  
343 *Dendroctonus*, and *Neodiprion* are at all representative of other hosts in those respective orders,  
344 and we use them to calculate relative species richness based on recent counts of only the  
345 *described* species in each order (Adler and Foottit 2009), the Hymenoptera exceed the  
346 Coleoptera by 2.5-3.2 times (**Table 2**). Recall that these calculations ignore all hyperparasitoids,  
347 and also omit parasitoids of other insect orders (e.g., Hemiptera, Orthoptera) and of non-insect  
348 arthropods. Even if we use half of the lowest P:H ratio estimate for each of the four largest  
349 orders, the Hymenoptera would outnumber the Coleoptera by more than 1.3 times.

350 Note that P:H ratios might be measured more accurately and / or calculated in different ways,  
351 most of which we would expect to increase the estimates of P:H reported here. For instance,  
352 rather than ignoring all of the so-called “generalist” parasitoids, one could identify those for  
353 which host ranges are known (e.g., **Figure 4**), divide each by the total number of host genera  
354 attacked, and add that fraction to the numerator of the P:H ratio for the focal host genus. As one  
355 example, the “generalist” parasitoids *Phygadeuon epochrae* and *Coptera evansi* both attack only  
356 *Rhagoletis* flies and the currant fly *Epochra canadensis*. These would each add an additional 0.5  
357 to the other 24 “genus-specialist” parasitoids of *Rhagoletis*, giving a revised P:H of 1.56. For  
358 *Malacosoma*, *Dendroctonus*, and *Neodiprion*, which all have many “generalist” parasitoids with  
359 host ranges that include only a few other extra-generic hosts in the same respective family, such  
360 additions should increase P:H ratio estimates by a considerable margin.

361 Another way to calculate P:H would be to focus not on a host genus but on hosts sharing the  
362 same habitat. For instance, *Dendroctonus* bark beetles share their habitat niche with several other  
363 species of beetle, and many of their parasitoids are “specialists” in the sense that they attack  
364 more than one bark beetle, but all within the same tree habitat (Berisford 2011). One could,  
365 therefore, calculate a P:H where H is the number of potential beetle host species in the habitat,  
366 and P is the number of “habitat-specialist” parasitoid species (those that attack one or more of the  
367 hosts in that habitat and no other hosts in other habitats).

368 Our analyses largely ignore the increasingly common finding that many apparently polyphagous  
369 insects – both herbivores and parasitoids – show evidence of additional host-associated genetic  
370 structure that might, if considered here as distinct lineages, change P:H ratios (e.g., Dres and  
371 Mallet 2002; Stireman et al. 2006; Smith et al. 2008; Condon et al. 2014; Forbes et al. 2017).  
372 Indeed, all four of our focal host genera have named subspecies or show evidence for host-  
373 associated, reproductively-isolated lineages (Stehr and Cook 1968; Powell et al. 2014; Six and  
374 Bracewell 2015; Bagley et al. 2017). Though we chose to “lump” subspecies and other  
375 reproductively isolated lineages together for this analysis, it is interesting to consider how a  
376 detailed study of genetic diversity and reproductive isolation among a host genus and all of its  
377 associated parasitoids might change P:H ratios. Studies of the flies in the *Rhagoletis pomonella*  
378 species complex and three of their associated parasitoids suggest that where additional host-  
379 associated lineages are found in a phytophagous insect, this cryptic diversity may be multiplied  
380 many times over in its specialist parasitoid community (Forbes et al. 2009; Hood et al. 2015). If  
381 broadly true, this implies that genus-specific P:H ratios may often be much higher than we report  
382 here.

383 One sensible criticism will surely be: to what extent are the P:H ratios for these four genera  
384 reflective of global P:H ratios for their respective orders (Coleoptera, Lepidoptera, Diptera, and  
385 the non-parasitoid Hymenoptera)? Surely some insect genera escape parasitism, and perhaps the  
386 examples chosen here simply have exceptionally large, or unusually specialized, parasitoid  
387 communities. As to the former, it may be that such escape artists exist, but they also may be  
388 relatively rare. After all, there are parasitoids that attack aquatic insects (Julinao 1981; Elliott  
389 1982), that parasitize insects in Arctic communities (e.g., Fernandez-Triana et al. 2011), and  
390 even those that dig down into soils to unearth and oviposit into pupae (Muesebeck 1990). The  
391 list of potential hosts for parasitoids also extends to many non-insect arthropods, including  
392 spiders, mites, and nematodes (LaSalle 1994; Finch 2005). As to the four example genera being  
393 representative of overly large parasitoid communities, all of their “overall” P:H numbers (**Table**  
394 **1**) are actually below the means found for their respective orders in an extensive study of  
395 parasitoid communities in Britain (Hawkins and Lawton 1987), suggesting that these  
396 communities are of average, or slightly below-average, size.

397

### 398 **Concluding Thoughts**

399 While it may indeed be premature to claim that the Hymenoptera is the largest order of insects  
400 based solely on what we present here, other studies offer support for the same conclusion. In  
401 fact, the preponderance of evidence suggests that the common wisdom about the Coleoptera  
402 being the most speciose is the more dubious claim. Studies of insect diversity that reduce  
403 taxonomic biases have found the Hymenoptera to be the most species-rich in both temperate  
404 (Gaston 1991) and tropical (Stork 1991) forests. Moreover, other historically-accepted ideas  
405 about diversity of parasitoid hymenopterans have recently been questioned, including that

406 parasitoid diversity decreases towards the tropics (Veijalainen et al. 2012; Eagalle and Smith  
407 2017). In any case, we hope this commentary results in a redoubled effort to understand and  
408 describe natural histories of parasitoid wasps, including host ranges and cryptic host-associated  
409 diversity, such that estimates of P:H can be made for additional host genera. In other words, and  
410 to again quote Erwin (1982), we hope that “...someone will challenge these figures with more  
411 data.”

412

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418

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632 **Table 1.** Summary of estimates of parasitoid to host (P:H) ratios for four host insect genera.

Focal Host Genus	# NAm Species (# with parasitoid records)	P:H (overall)	P:H		
			(genus- specialists only)	(specialist) [including possible genus- specialists]	Genus-specialist families
<i>Rhagoletis</i> (Diptera: Tephritidae)	24 (16)	2.44	1.31	1.50	Braconidae; Diapriidae; Pteromalidae
<i>Malacosoma</i> (Lepidoptera: Lasiocampidae)	6 (6)	13.00	1.00	1.83	Braconidae; Eulophidae; Ichneumonidae; Platygastridae
<i>Dendroctonus</i> (Coleoptera: Curculionidae)	14 (8)	6.50	1.13	1.38	Braconidae; Ichneumonidae; Gasteruptiidae; Proctotrupidae; Pteromalidae; Platygastridae
Neodiprion (Hymenoptera: Diprionidae)	33 (21)	3.48	0.95	1.29	Ichneumonidae; Chrysididae

633 Table 1 note: Shown for each host genus are: the total number of North American (NA)   
634 species, as well as the number with parasitoid records; the overall P:H, which includes generalist   
635 species; the genus-specialist P:H; and the genus-specialist P:H when “possible genus-specialists”   
636 were included. Parasitoid families that were among each group of genus-specialists are also   
637 listed.   
638

639 **Table 2. Calculations of hymenopteran species richness, given numbers of described insect**  
 640 **species in other orders and P:H ratios estimated in this paper.**

	High P:H estimates from case studies	Low P:H estimates from case studies	Half of lowest estimates from case studies
Diptera (152,244)	228,366	199,440	99,720
Lepidoptera (156,793)	286,931	156,793	78,397
Coleoptera (359,891)	494,850	406,677	203,338
Non-parasitoid Hymenoptera (~62,000)	79,980	58,900	29,450
All other insect orders (335,970)	0 <sup>a</sup>	0 <sup>a</sup>	0 <sup>a</sup>
<b>TOTAL PARASITOID</b>	<b>1,107,487</b>	<b>833,590</b>	<b>416,795</b>
<b>HYMENOPTERA</b>			
Non-parasitoid Hymenoptera (to add to calculated parasitoid numbers)	62,000	62,000	62,000
<b>TOTAL HYMENOPTERA</b>	<b>1,152,127</b>	<b>883,810</b>	<b>472,905</b>

641 Table 2 note: Combining conservative P:H ratio estimates from four case studies with numbers  
 642 of described species in the four largest insect orders (Adler and Foottit 2009; Huber 2009) offers  
 643 an idea of how species richness of the Hymenoptera may compare with that of other orders.  
 644 <sup>a</sup>Parasitoids attack hosts in all other insect orders, but these are omitted as we did not estimate  
 645 P:H ratios for any hosts in these orders. Total numbers therefore exclude large numbers of  
 646 hymenopteran species.