1 # Quantifying the unquantifiable:

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

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14   **Abstract:** We challenge the oft-repeated claim that the beetles (Coleoptera) are the most species-

15   rich order of animals. Instead, we assert that another order of insects, the Hymenoptera, are more

16   speciose, due in large part to the massively diverse but relatively poorly known parasitoid wasps.

17   The idea that the beetles have more species than other orders is primarily based on their

18   respective collection histories and the relative availability of taxonomic resources, which both

19   disfavor parasitoid wasps. Since it is unreasonable to directly compare numbers of described

20   species in each order, we present a simple logical model that shows how the specialization of

21   many parasitic wasps on their hosts suggests few scenarios in which there would be more beetle

22   species than parasitic wasp species. We couple this model with an accounting of what we call the

23   "genus-specific parasitoid-host ratio" from four well-studied genera of insect hosts, a metric by

24   which to generate extremely conservative estimates of the average number of parasitic wasp

25   species attacking a given beetle or other insect host species. Synthesis of these two approaches

26   suggests that the Hymenoptera may have 2.5 - 3.2x more species than the Coleoptera.

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34   "…if the micro-hymenopterists would get off their lazy asses

35   and start describing species, there would be more micro-

36   Hymenoptera than there are Coleoptera."

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38   – Terry Erwin (in Rice, 2015)

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40   The beetles (order Coleoptera), have historically (Kirby & Spence, 1818; Westwood, 1833;

41   Hutchinson, 1959) and contemporaneously (Farrell, 1998; Hunt et al., 2007; McKenna & Farrell,

42   2009; Zhang, 2011; Wiens, Lapoint & Whiteman, 2015; Zhang et al., 2018) been described as

43   the most speciose order of animals on Earth. The great diversity of beetles was sufficiently

44   established by the middle of last century such that J.B.S. Haldane (possibly apocryphally[1])

45   quipped that an intelligent creator of life must have had "…an inordinate fondness for beetles"

46   (Gould, 1993). However, what evidence underlies the claim that the Coleoptera are more

47   species-rich than the other insect orders? Certainly, more species of beetles (>350,000) have

48   been *described* than any other order of animal, insect or otherwise (Bouchard et al., 2009), but

49   does this reflect their actual diversity relative to other insects?

50   Why are beetles thought to be so diverse in the first place? In part, historical biases in beetle

51   collecting and an associated accumulation of taxonomic resources for the Coleoptera may have

52   had an outsized influence on our perception of diversity. In the mid-to-late 1800s, beetles were

53   prized among insects for their collectability. Many landed gentlemen - including, notably,

54   Charles Darwin - collected beetles for sport and would make a great show of comparing the sizes

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[1] Whether or not Haldane ever actually said it exactly in this way is unresolved (Gould, 1993). 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   of their respective collections (Browne, 1996; Sheppard, 2004). This preconception was then

56   reinforced by studies that extrapolated from specific, targeted collections of insect diversity that

57   focused on beetles. Of these, perhaps the highest in profile was a study conducted by Terry

58   Erwin. Erwin (1982) used an insecticide to fog the canopies of 19 individual *Luehea seemannii*

59   trees in a Panamanian rainforest and then collected and identified the insect species that fell out

60   of those trees. After having identified the proportion of the beetle species that were apparently

61   host-specific to *L. seemannii* (163 of 955), he estimated that there might be as many as 12.2

62   million beetle species in the tropics. Similar studies seeking to estimate global insect diversity

63   have also tended to emphasize beetles (e.g., Ødegaard, 2000; Stork et al., 2015).

64   Nevertheless, some previous work has challenged the canon, with various authors suggesting –

65   though never quite insisting – that the Hymenoptera may be more speciose than the Coleoptera

66   (LaSalle, 1993; LaSalle & Gauld, 1993; Gaston, 1993; Austin & Dowton, 2000). The premise

67   behind this suggestion is that most of the larvae of the Parasitica (one of the two infraorders of

68   apocritan Hymenoptera; the other is the Aculeata, which includes ants, bees, and wasps), are

69   obligate parasites of insect and other arthropod hosts that feed on the host's tissue until the host

70   dies (≈ "parasitoids"). Why is this parasitic life history relevant to the Hymenoptera's

71   proportional contribution to insect diversity? Simply put, species of parasitoid Hymenoptera

72   (including the Parasitica, as well as some other groups such as the Orussidae and some

73   Chrysidoidea) attack all orders of insects as well as some non-insect arthropods (Gibson, Huber

74   & Woolley, 1997; Wharton, Marsh & Sharkey, 1997; Noyes, 2017), and, reciprocally, most

75   holometabolous insect species are attacked by at least one – and often many more than one –

76   species of hymenopteran parasitoid (Schoenly, 1990; Memmott & Godfray, 1993). For instance,

77   Hawkins and Lawton (1987) examined parasitoid communities associated with 158 genera of

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78   British insects across five different orders, and found that parasitoid species richness ranged from

79   2.64 – 9.40 per host species across different host insect orders.

80   If parasitoid wasps are ubiquitous and most hosts are attacked by many different species, why is

81   there any debate at all about the Hymenoptera being more diverse than other orders? One reason

82   may be that estimates of the regional and global species-richness of parasitoid wasps remain

83   elusive. Their small size and a relative paucity of taxonomic resources have left the parasitoid

84   Hymenoptera relatively under-described compared to other insect orders (Gaston, 1993; Huber,

85   2009). As a consequence, when collection-based estimates of regional insect diversity have been

86   attempted, they have often excluded all but the largest and easiest-to identify families of parasitic

87   Hymenoptera (e.g., Novotny et al., 2002; Pietsch et al., 2003; Basset et al., 2012; though see

88   Gaston, 1991; Stork, 1991).

89   A second reason for uncertainty regarding the species richness of the parasitoid Hymenoptera is

90   that their host ranges are often unknown. While it may be true that most insects harbor many

91   parasitoid species, the question remains whether these parasitoid communities are exclusively

92   composed of oligophagous or polyphagous wasps that attack many hosts, or if instead the

93   average insect host tends to have some number of specialist wasps among its many predators

94   (**Figure 1**). Only in the latter case would one be able to confidently assert that the Hymenoptera

95   is the largest of the insect orders.
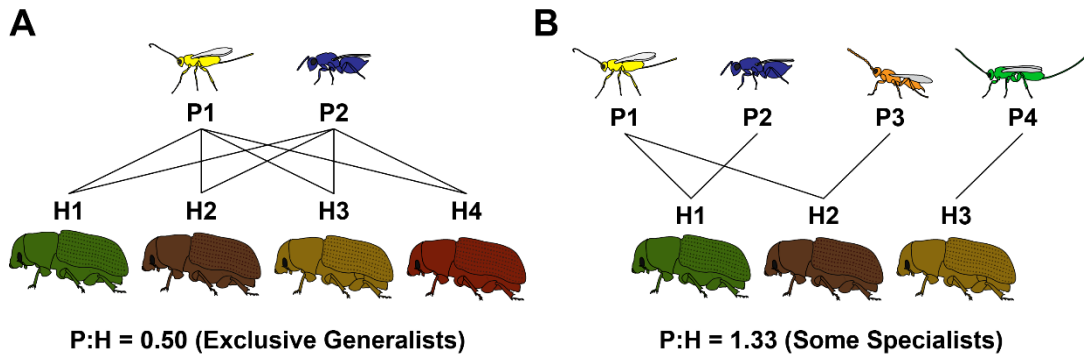
Figure 1. An illustration of how uncertainty about specialist vs. generalist behaviors might lead to misleading conclusions about parasitoid species richness. In panel A, each host species (differently colored beetles) is attacked by two parasitoids. However, because all parasitoids attack all four beetles 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?

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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: $\qquad I = 1 - (P + C)$

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: $\qquad P = C(p_C) + I(p_I)$

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.

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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

142   species-specialist parasitoid for every four beetle species), coupled with a p_I of 0.50, results in P

143    $= C$ (and the many tens of thousands of non-parasitoid Hymenoptera will then tip the scale in

144   their favor). Even if the Coleoptera amount to 40% of the insects, which reflects the percentage

145   of 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).
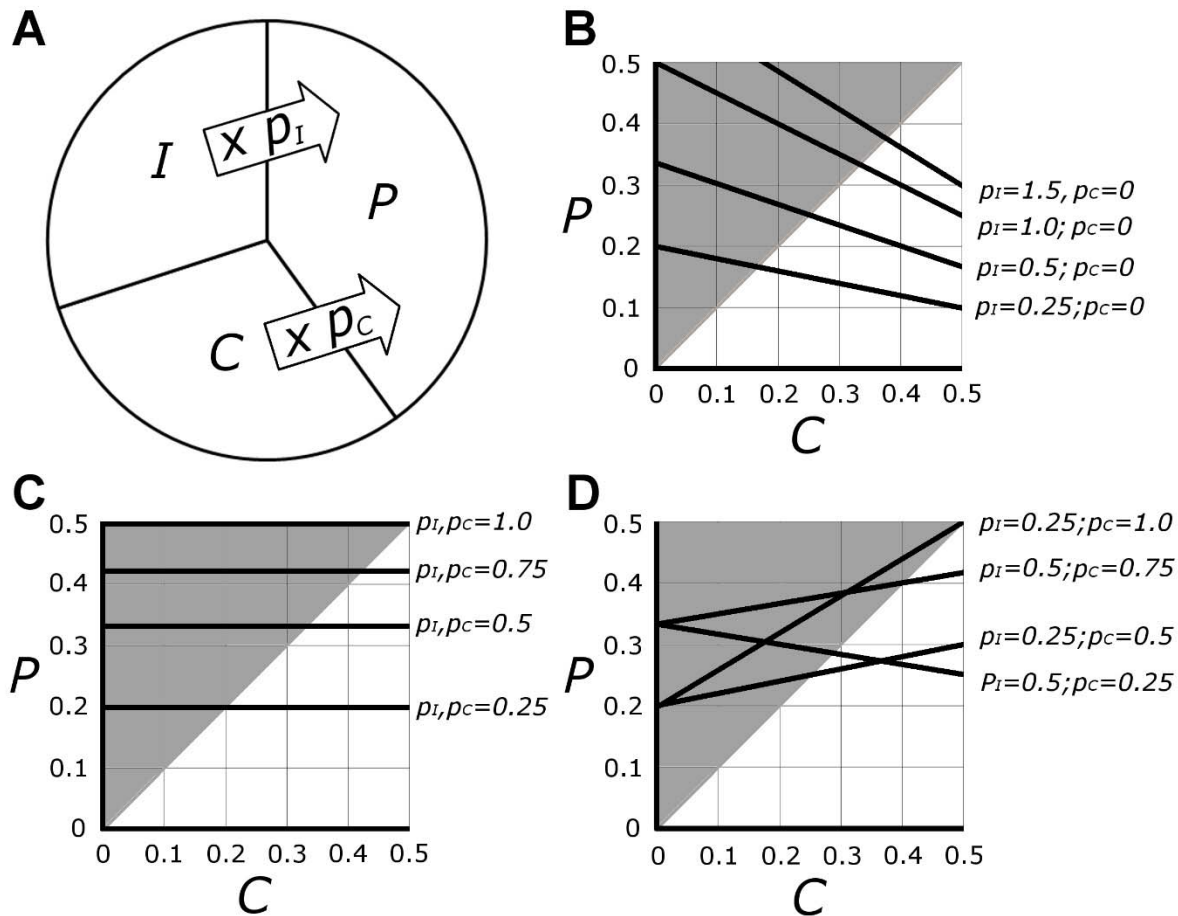
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Figure 2. Representations of the space where the number of parasitoid wasp species would outnumber the Coleoptera, given different parasitoid-to-host ratios for coleopteran hosts and for other insect hosts. A) Pictorial representation of the model, 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
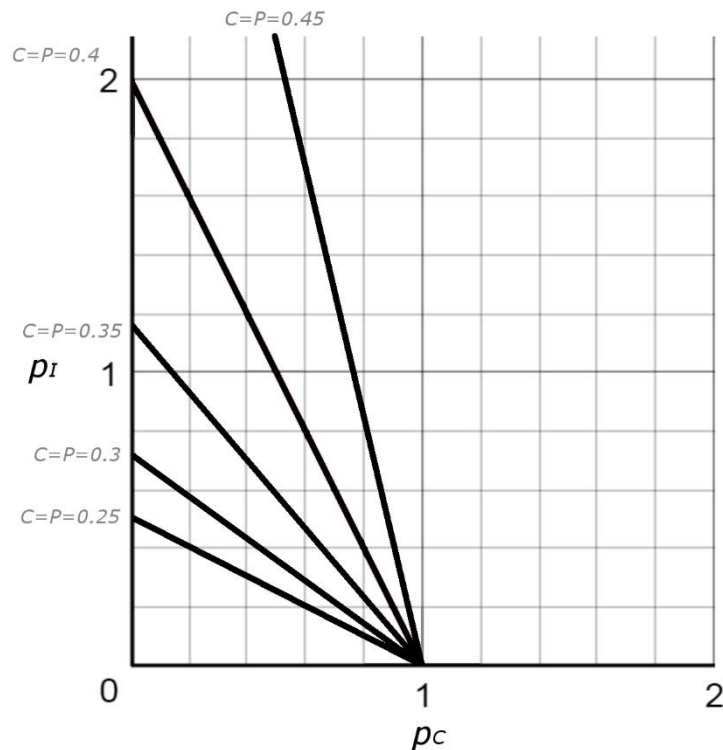
159   p_C and p_I are equal; D) Some additional combinations of p_C and p_I. Though

160   both axes could continue to 1.0, some high values of P and C are not

161   mathematically possible or biologically likely, and at P or C values above 0.5

162   the question about relative species-richness becomes moot.

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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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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 $C > P$.

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

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

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

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

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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.

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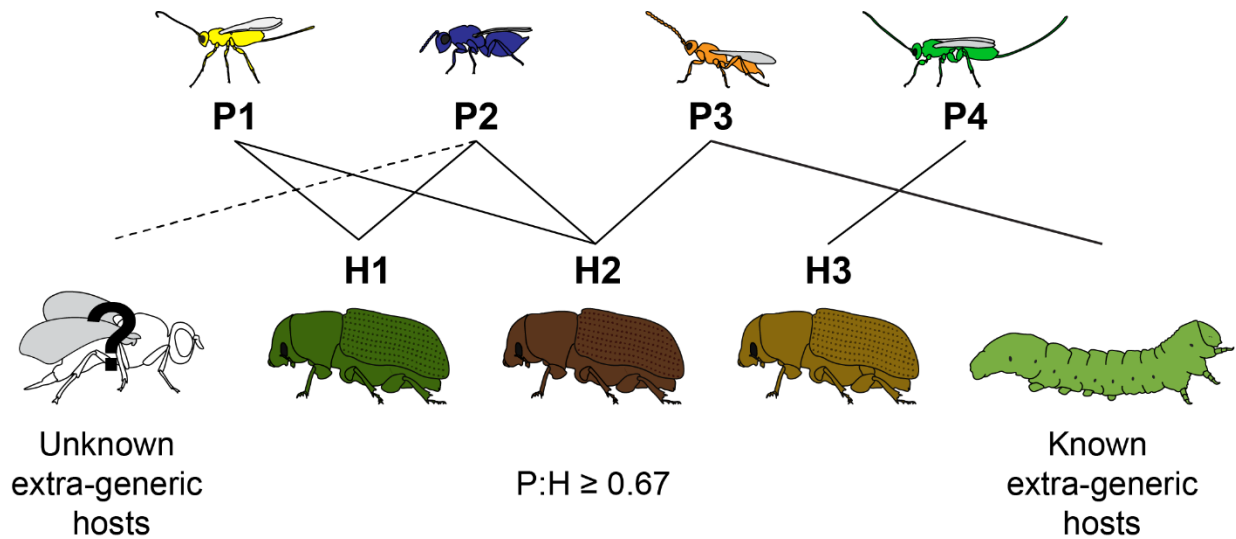
198   **Figure 4**. Known genus-specialist parasitoids can be used to calculate a

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-

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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).

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210   Below, we present four case studies, representing host-parasitoid systems with records

211   sufficiently complete to allow for calculation of genus-specialist parasitoid:host ratios. For each

212   system, we focus on a single host genus in North America. We restricted geography so that

213   parasitoid numbers would not be inflated by large biogeographic differences between hosts in

214   their parasitoid assemblages. North America was chosen because sampling is relatively strong,

215   and several robust resources exist for Nearctic parasitoids (e.g., Peck, 1963; Krombein et al.,

216   1979; Noyes, 2017).

217   For each system, we searched for all literature that mentioned the name of the host genus (or

218   historical synonyms) and either "parasite" or "parasitoid" and compiled a database of records,

219   performing reticulated searches on each parasitoid species name as it was added to the database

220   in order to determine known parasitoids host ranges. From among all parasitoid records, we

221   classified parasitoids as "genus-specialists" if they had only ever been reared from hosts in this

222   same genus. We then split these "genus-specialists" into two groups: those for which an

223   argument can be made that they do not have unknown extra-generic hosts, and those that were

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224   "possible genus-specialists" but for which records were less complete. Non-hymenopteran

225   parasitoids (e.g., Tachinidae) were excluded, but in any case were only present for two of the

226   four hosts we examined (*Malacosoma* and *Neodiprion*), and generally do not have the

227   taxonomically cosmopolitan host ranges of the hymenopteran parasitoids. For cases where host

228   genera were found on multiple continents, only host species in North America were included in

229   the study, and to be conservative, a parasitoid was still considered "generalist" if it occurred on

230   an extra-generic host species outside of North America. Introduced host species were noted but

231   not counted in host lists, as they do not represent long-term host-parasite relationships.

232   Introduced parasitoid species were included in generalist lists, regardless of whether they were

233   specialists on that genus in North America or elsewhere. We describe each system below and

234   refer the reader to Supplemental Materials for species lists, specialist / generalist classifications,

235   and citations. A summary of data across the four genera can be found in **Table 1**.

236   **System 1: *Rhagoletis* (Diptera: Tephritidae)**

237   Many North American *Rhagoletis* flies are pests of agriculturally-important fruits. Eggs are

238   deposited in ripening fruits by the female fly, and larvae develop through several instars while

239   feeding on fruit pulp (Bush, 1966). For most species, larvae then exit the fruit and pupate in the

240   soil. Parasitoids are known from egg, larval and pupal stages of many *Rhagoletis* species.

241   Several studies have described the parasitoid communities associated with *Rhagoletis*

242   agricultural pest species (e.g., Lathrop & Newton, 1933; Bush, 1966; Cameron & Morrison,

243   1974; Wharton & Marsh, 1978; Feder, 1995), though records of parasitoids of non-pest species

244   also exist (e.g., Rull et al., 2009; Forbes, Hood & Feder, 2010; Forbes et al., 2012). Moreover,

245   many of the associated parasitoid species are well-studied in their own right, with robust records

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246   of their biology, ecology, and host-ranges (Wharton & Marsh, 1978; Muesebeck, 1980; Forbes et

247   al., 2009; Wharton & Yoder, 2017).

248   Of the 24 species of North American *Rhagoletis* flies, 16 have a published record of parasitoid

249   associations. Across these 16 flies, we found records of 39 parasitoid species, among which 24

250   "genus-specialists" have been described only from North American *Rhagoletis* and no other

251   insect host (**Supplemental Table 1**). Of these, we set aside three "possible" genus-specialist

252   species that did not have a strong collection record and for which host records may possibly be

253   incomplete. The remaining set of genus-specialists included 14 braconids (genera *Diachasma*,

254   *Diachasmimorpha*, *Utetes*, and *Opius*), six diapriids (genus *Coptera*), and a pteromalid (genus

255   *Halticoptera*). The genus-specialist P:H ratio for *Rhagoletis* is therefore either 1.31 (21/16), or

256   1.50 (24/16), depending on whether "possible genus-specialists" are included. An extra-

257   conservative P:H ratio might also include the eight *Rhagoletis* hosts that have no record of

258   parasitoids (P:H = 21/24 = 0.88), though this almost certainly ignores some number of unknown

259   genus-specialist parasitoids.

260   Some of the 15 "generalist" parasitoids of *Rhagoletis* have been reared from a diverse set of

261   extra-generic hosts, but in some cases only from one other fruit-infesting tephritid (e.g.,

262   *Phygadeuon epochrae* and *Coptera evansi*, both of which have only been reared from *Rhagoletis*

263   and from *Epochra canadensis* [Diptera: Tephritidae]). These 15 "generalists" are listed in

264   **Supplemental Table 1**.

265   **System 2: *Malacosoma* (Lepidoptera: Lasiocampidae)**

266   The tent caterpillars (genus *Malacosoma*) are shelter building, cooperatively-foraging moths that

267   damage both coniferous and deciduous trees across at least 10 families. Most species use >1 host

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268   tree genus, though some (e.g., *Malacosoma constrictum*; *Malacosoma tigris*) are more

269   specialized (Fitzgerald, 1995). There are six North American species of *Malacosoma*, some with

270   overlapping geographic distributions (Fitzgerald, 1995). Female moths lay eggs in a mass

271   wrapped around a branch of the host tree. Larvae of most species (*M. disstria* is an exception)

272   live colonially inside "tents" made of spun silk and make regular excursions to feed on host

273   leaves. The caterpillar stage is eaten by birds, mammals and several insect predators, but the

274   most taxonomically diverse natural enemies are the parasitoids (Fitzgerald, 1995). Of these,

275   approximately one third are Dipteran (family Tachinidae), while the remaining two thirds are

276   Hymenopteran parasitoids. Parasitoids attack all immature life stages, but most appear to emerge

277   during the pre-pupal or pupal stage. Parasitoids of the North American tent caterpillars have been

278   well documented, and often in the context of other available forest caterpillar hosts, such that it is

279   reasonable to assert that some parasitoid species are *Malacosoma*-specific (e.g., Langston, 1957;

280   Stacey, Roe & Williams, 1975; Shaw, 2006).

281   All six of the North American *Malacosoma* species have at least one known parasitoid

282   association, and we compiled a total of 78 different parasitoid species across all hosts

283   (**Supplemental Table 2**). Of these, eleven had only been reared from *Malacosoma*. Five of these

284   eleven species we assigned to the "possible genus-specialists" category, as they had not been

285   assigned a specific name (which makes it hard to determine whether other hosts exist), or

286   because they had only been reared a single time from the host. The remaining six "genus-

287   specialists," were from four different hymenopteran families. The genus-specialist P:H ratio for

288   *Malacosoma* is therefore between 1.00 and 1.83.

289   *Malacosoma* have many more "generalists" than *Rhagoletis*: 68 species have been reared from

290   both *Malacosoma* and at least one other extra-genetic host (**Supplementary Table 2**). Many of

291   these appear to be specific to Lepidopteran hosts.

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

293   Approximately 14 species of *Dendroctonus* bark beetles are found in North America (Six &

294   Bracewell, 2015). *Dendroctonus* are specific to conifers in family Pinaceae, and can be highly

295   destructive to their host trees. Female beetles construct nuptial chambers in trees where they

296   mate with males and then deposit eggs in tunnels in the phloem. Larvae feed on phloem and

297   outer bark and leave the tree only after pupation and adult emergence (Six & Bracewell, 2015).

298   Most species are tree genus- or species-specific.

299   Parasitoids have been described for eight of the 14 North American *Dendroctonus* species,

300   though for two of these (*D. adjunctus* and *D. murryanae*) only one or two parasitoid species are

301   known. The total list of *Dendroctonus*-associated parasitoids is long, but the records are also

302   often problematic, as *Dendroctonus* share their habitat with several other genera of bark beetles,

303   which may or may not be attacked by the same parasitoids. In many studies, parasitoids are listed

304   as "associates" of either *Dendroctonus*, or of one of the other species, or of both, but this does

305   not always necessarily mean that a parasitoid attacks that beetle (Overgaard, 1968; Langor, 1991;

306   Berisford, 2011). We have here again tried to be conservative, though in one case (*Meterorus*

307   *hypophloei*) we have ignored a claim of "association" with *Ips* beetles (Kulhavy et al., 1989) as it

308   did not seem to be well justified and other authors describe *M. hypophloei* as a *Dendroctonus*

309   *frontalis* specialist (Stein & Coster, 1977; Berisford, 2011). In total, we found nine

310   *Dendroctonus* genus-specialists, two possible genus-specialists, and 48 "generalists"

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311 (**Supplemental Table 3**). The genus-specific P:H ratio for *Dendroctonus* is therefore between

312 1.13 and 1.38.

313 **System 4: *Neodiprion* (Hyemenoptera: Diprionidae)**

314 *Neodiprion* is a Holarctic genus of pine-feeding sawflies specializing on conifers in the family

315 Pinaceae (Smith, 1993). These sawflies have close, life-long associations with their tree hosts.

316 The short-lived, non-feeding adults mate on the host plant shortly after eclosion, after which the

317 females deposit their eggs into pockets cut within the host needles. The larvae hatch and feed

318 externally on the host needles throughout development, and then spin cocoons on or directly

319 beneath the host (Coppel & Benjamin, 1965; Knerer & Atwood, 1973; Knerer, 1993). Many

320 species also have highly specialized feeding habits, and feed on a single or small handful of host-

321 plant species in the genus *Pinus*. Since many of the ~33 *Neodiprion* species native to North

322 America are considered economic pests (Arnett, 1993), considerable effort has gone into

323 describing their natural history and exploring potential methods to control *Neodiprion* outbreaks.

324 Despite the wealth of natural history information, compiling a list of parasitoids attacking

325 *Neodiprion* is complicated by a history of accidental and intentional introductions. In addition to

326 the native species, the European pine sawfly, *Neodiprion sertifer,* and three species from the

327 closely related genera *Diprion* and *Gilpinia* were introduced in the past ~150 years and have

328 spread across the United States and Canada (Britton, 1915; Gray, 1938; Balch, 1939; Schaffner

329 Jr., 1939). In an attempt to control these invasive pests, several parasitoids have been introduced,

330 and now attack both native and invasive diprionids (Finlayson & Reeks, 1936; Finlayson, 1963;

331 MacQuarrie et al., 2016).

332   We found 20 genus-specialist parasitoid species associated with the 21 species of North

333   American *Neodiprion* for which parasitoid records exist. An additional seven parasitoids were

334   classified as "possible" genus-specialists. The genus-specific P:H ratio for *Neodiprion* is

335   therefore between 0.95 and 1.29. An additional 51 species had been reared from both *Neodiprion*

336   and an extra-generic host, with nine introduced parasitoids. We also compiled a list of 14

337   introduced parasitoids, nine hyperparasitoids, and 28 tachinid (Diptera) parasitoids of *Neodiprion*

338   (**Supplemental Table 4**), but these were not included in any analyses.

339

340   **Synthesis**

341   Upon considering our model together with actual estimates of P:H ratios from natural host

342   systems (**Table 1**), there appear to be few conditions under which the Hymenoptera would not be

343   the largest order of insects. If, for instance, the P:H ratios for *Rhagoletis*, *Malacosoma*,

344   *Dendroctonus*, and *Neodiprion* are at all representative of other hosts in those respective orders,

345   and we use them to calculate relative species richness based on recent counts of only the

346   *described* species in each order (Adler & Foottit, 2009), the Hymenoptera exceed the Coleoptera

347   by 2.5-3.2 times (**Table 2**). Recall that these calculations ignore all hyperparasitoids, and also

348   omit parasitoids of other insect orders (e.g., Hemiptera, Orthoptera) and of non-insect

349   arthropods. Even if we use half of the lowest P:H ratio estimate for each of the four largest

350   orders, the Hymenoptera would outnumber the Coleoptera by more than 1.3 times.

351   Note that P:H ratios might be measured more accurately and / or calculated in different ways,

352   most of which we would expect to increase the estimates of P:H reported here. For instance,

353   rather than ignoring all of the so-called "generalist" parasitoids, one could identify those for

19

354 which host ranges are known (e.g., **Figure 4**), divide each by the total number of host genera

355 attacked, and add that fraction to the numerator of the P:H ratio for the focal host genus. As one

356 example, the "generalist" parasitoids *Phygadeuon epochrae* and *Coptera evansi* both attack only

357 *Rhagoletis* flies and the currant fly *Epochra canadensis*. These would each add an additional 0.5

358 to the other 24 "genus-specialist" parasitoids of *Rhagoletis*, giving a revised P:H of 1.56. For

359 *Malacosoma*, *Dendroctonus*, and *Neodiprion,* which all have many "generalist" parasitoids with

360 host ranges that include only a few other extra-generic hosts in the same respective family, such

361 additions should increase P:H ratio estimates by a considerable margin.

362 Another way to calculate P:H would be to focus not on a host genus but on hosts sharing the

363 same habitat. For instance, *Dendroctonus* bark beetles share their habitat niche with several other

364 species of beetle, and many of their parasitoids are "specialists" in the sense that they attack

365 more than one bark beetle, but all within the same tree habitat (Berisford, 2011). One could,

366 therefore, calculate a P:H where H is the number of potential beetle host species in the habitat,

367 and P is the number of "habitat-specialist" parasitoid species (those that attack one or more of the

368 hosts in that habitat and no other hosts in other habitats).

369 Our analyses largely ignore the increasingly common finding that many apparently polyphagous

370 insects – both herbivores and parasitoids – show evidence of additional host-associated genetic

371 structure that might, if considered here as distinct lineages, change P:H ratios (e.g., Drès &

372 Mallet, 2002; Stireman et al., 2006; Smith et al., 2008; Condon et al., 2014; Forbes et al., 2017).

373 Indeed, all four of our focal host genera have named subspecies or show evidence for host-

374 associated, reproductively-isolated lineages (Stehr & Cook, 1968; Powell et al., 2014; Six &

375 Bracewell, 2015; Bagley et al., 2017). Though we chose to "lump" subspecies and other

376 reproductively isolated lineages together for this analysis, it is interesting to consider how a

377 detailed study of genetic diversity and reproductive isolation among a host genus and all of its

378 associated parasitoids might change P:H ratios. Studies of the flies in the *Rhagoletis pomonella*

379 species complex and three of their associated parasitoids suggest that where additional host-

380 associated lineages are found in a phytophagous insect, this cryptic diversity may be multiplied

381 many times over in its specialist parasitoid community (Forbes et al., 2009; Hood et al., 2015). If

382 broadly true, this implies that genus-specific P:H ratios may often be much higher than we report

383 here.

384 One sensible criticism will surely be: to what extent are the P:H ratios for these four genera

385 reflective of global P:H ratios for their respective orders (Coleoptera, Lepidoptera, Diptera, and

386 the non-parasitoid Hymenoptera)? Surely some insect genera escape parasitism, and perhaps the

387 examples chosen here simply have exceptionally large, or unusually specialized, parasitoid

388 communities. As to the former, it may be that such escape artists exist, but they also may be

389 relatively rare. After all, there are parasitoids that attack aquatic insects (Juliano, 1981; Elliott,

390 1982), that parasitize insects in Arctic communities (e.g., Fernandez-Triana et al., 2011), and

391 even those that dig down into soils to unearth and oviposit into pupae (Muesebeck, 1980). The

392 list of potential hosts for parasitoids also extends to many non-insect arthropods, including

393 spiders, mites, and nematodes (Lasalle, 1994; Finch, 2005). As to the four example genera being

394 representative of overly large parasitoid communities, all of their "overall" P:H numbers (**Table**

395 **1**) are actually below the means found for their respective orders in an extensive study of

396 parasitoid communities in Britain (Hawkins & Lawton, 1987), suggesting that these communities

397 are of average, or slightly below-average, size.

398

399 **Concluding Thoughts**

400 While it may indeed be premature to claim that the Hymenoptera is the largest order of insects

401 based solely on what we present here, other studies offer support for the same conclusion. In

402 fact, the preponderance of evidence suggests that the common wisdom about the Coleoptera

403 being the most speciose is the more dubious claim. Studies of insect diversity that reduce

404 taxonomic biases have found the Hymenoptera to be the most species-rich in both temperate

405 (Gaston, 1991) and tropical (Stork, 1991) forests, as well as in other habits (e.g., Kimsey et al.,

406 2017). In addition, a mass-barcoding study of Canadian insects found both Hymenoptera and

407 Diptera more diverse than Coleoptera (Hebert et al., 2016). Moreover, other historically-accepted

408 ideas about diversity of parasitoid hymenopterans have recently been questioned, including the

409 apparent myth that parasitoids are one of only a few groups whose diversity decreases towards

410 the tropics (Veijalainen et al., 2012; Eagalle & Smith, 2017). In any case, we hope this

411 commentary results in a redoubled effort to understand and describe natural histories of

412 parasitoid wasps, including host ranges and cryptic host-associated diversity, such that estimates

413 of P:H can be made for additional host genera. We also hope to see similar efforts in other

414 animal groups that may harbor great diversity but for which far too little is known about host

415 ranges, such as particularly speciose orders of mites and nematodes (e.g., Grucmanová &

416 Holuša, 2013; Walter & Proctor, 2013). In other words, and to again quote Erwin (1982), we

417 hope that "…someone will challenge these figures with more data."

418

419 **Competing Interests**

420 We have no competing interests.

421

Authors' Contributions

423 AAF conceived of the study. All authors helped formulate a framework for addressing the

424 questions in the paper, developed the logical model, and collected and analyzed data from the

425 four host genera. AAF and RKB wrote the manuscript. All authors gave final approval for

426 publication.

427

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

679 **genera.** Shown for each host genus are: the total number of North American (NAm) species, as

680 well as the number with parasitoid records; the overall P:H, which includes generalist species;

681 the genus-specialist P:H; and the genus-specialist P:H when "possible genus-specialists" were

682 included. Parasitoid families that were among each group of genus-specialists are also listed.

683

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

36

					Proctotrupidae; Pteromalidae; Platygastridae
Neodiprion (Hymenoptera: Diprionidae)	33 (21)	3.48	0.95	1.29	Ichneumonidae; Chrysididae

684

685 **Table 2**. **Calculations of hymenopteran species richness, given numbers of described insect**

686 **species in other orders and P:H ratios estimated in this paper.** Combining conservative P:H

687 ratio estimates from four case studies with numbers of described species in the four largest insect

688 orders (Adler and Foottit 2009; Huber 2009) offers an idea of how species richness of the

689 Hymenoptera may compare with that of other orders. [a]Parastioids attack hosts in all other insect

690 orders, but these are omitted as we did not estimate P:H ratios for any hosts in these orders. Total

691 numbers therefore exclude large numbers of hymenopteran species.

	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[a]	0[a]	0[a]
TOTAL PARASITOID HYMENOPTERA	1,107,487	833,590	416,795
Non-parasitoid Hymenoptera (to add to calculated parasitoid numbers)	62,000	62,000	62,000
TOTAL HYMENOPTERA	**1,152,127**	**883,810**	**472,905**

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38

693   **Figure Captions.**

694   **Figure 1**. An illustration of how uncertainty about specialist vs. generalist behaviours might lead

695   to misleading conclusions about parasitoid species richness. In panel A, each host species

696   (differently colored beetles) is attacked by two parasitoids. However, because all parasitoids

697   attack all four beetles the overall species richness of hosts exceeds that of the parasitoids (i.e.,

698   P:H < 1). In panel B, while some hosts have only one parasitoid, overall parasitoid richness

699   exceeds host richness (P:H > 1) because some parasitoids are more specialized.

700

701   **Figure 2**. Representations of the space where the number of parasitoid wasp species would

702   outnumber the Coleoptera, given different parasitoid-to-host ratios for coleopteran hosts and for

703   other insect hosts. A) Pictorial representation of the model, wherein the total number of

704   parasitoid species (*P*) will be the sum of the number of species of Coleoptera (*C*) and of other

705   insects (*I*), each first multiplied by their respective overall parasitoid-to-host ratio (p_C or p_I); B)

706   Black lines show results of the model for four different values of p_I and with p_C held at zero (i.e.,

707   when the average coleopteran has no specialist parasitoids). Where black lines overlap with gray

708   shaded areas represents space where *P* > *C;* C) Results of four different scenarios in which p_C

709   and p_I are equal; D) Some additional combinations of p_C and p_I. Though both axes could

710   continue to 1.0, some high values of *P* and *C* are not mathematically possible or biologically

711   likely, and at *P* or *C* values above 0.5 the question about relative species-richness becomes moot.

712

713   **Figure 3.** Plot based on Equation 4, with five representations of moments when *C* and *P* are

714   equal proportions (solid black lines). p_I = overall P:H ratio for non-coleopteran insect hosts; p_C =

715   overall P:H ratio for the Coleoptera. Space above and to the right of each line represents values

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

717    $C > P$.

718

719   **Figure 4.** Known genus-specialist parasitoids can be used to calculate a minimum P:H ratio for

720   an insect host genus. The focal beetle genus H (three species) has four known parasitoids, P1-P4.

721   P1 and P4 are relatively well-studied, and known to be genus-specialists, attacking only hosts in

722   this beetle genus. P3 has some known extra-generic hosts, while the host range of P2 is poorly

723   studied and unknown extra-generic hosts may exist. For the purposes of estimating a genus-

724   specialist P:H, one would therefore use only P1 and P4, such that a minimum P:H for this beetle

725   genus would be 2/3, or 0.67. Note that if the total number and identities of extra-generic hosts

726   were known for P2 and P3, a "true" P:H for the genus could be calculated (see Synthesis, below).

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