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1 **The topology and drivers of ant–symbiont networks across**
2 **Europe**

3
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16
17 **ABSTRACT**

18 Intimate associations between different species drive community composition across
19 ecosystems. Understanding the ecological and evolutionary drivers of these symbiotic
20 associations is challenging because their structure eventually determines stability and
21 resilience of the entire species network. Here, we compiled a detailed database on naturally
22 occurring ant–symbiont networks in Europe to identify factors that affect symbiont network
23 topology. These networks host an unrivalled diversity of macrosymbiotic associations,
24 spanning the entire mutualism–antagonism continuum, including: (1) myrmecophiles –

25 commensalistic and parasitic arthropods; (2) trophobionts – mutualistic aphids, scale insects,
26 planthoppers and caterpillars; (3) social parasites – parasitic ant species; (4) parasitic
27 helminths; and (5) parasitic fungi. We dissected network topology to investigate what
28 determines host specificity, symbiont species richness, and the capacity of different symbiont
29 types to switch hosts.

30 We found 722 macrosymbionts (multicellular symbionts) associated with European ants.
31 Symbiont type explained host specificity and the average relatedness of the host species.
32 Social parasites were associated with few hosts that were phylogenetically highly related,
33 whereas the other symbiont types interacted with a larger number of hosts across a wider
34 taxonomic distribution. The hosts of trophobionts were the least phylogenetically related
35 across all symbiont types. Colony size, host range and habitat type predicted total symbiont
36 richness: ant hosts with larger colony size, a larger distribution range or with a wider habitat
37 range contained more symbiont species. However, we found that different sets of host factors
38 affected diversity in the different types of symbionts. Ecological factors, such as colony size,
39 host range and niche width predominantly determined myrmecophile species richness,
40 whereas host phylogeny was the most important predictor of mutualistic trophobiont, social
41 parasite and parasitic helminth species richness. Lastly, we found that hosts with a common
42 biogeographic history support a more similar community of symbionts. Phylogenetically
43 related hosts also shared more trophobionts, social parasites and helminths, but not
44 myrmecophiles.

45 Taken together, these results suggest that ecological and evolutionary processes structure host
46 specificity and symbiont richness in large-scale ant–symbiont networks, but these drivers may
47 shift in importance depending on the type of symbiosis. Our findings highlight the potential of
48 well-characterized bipartite networks composed of different types of symbioses to identify
49 candidate processes driving community composition.

50 *Key words:* ant guests, commensalism, ecological network, Formicidae, host–parasite
51 network, host switching, inquiline, microcosm, mutualism, parasite species richness.

52

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76

77 **I. INTRODUCTION**

78 Close associations between different species, known as symbioses, are crucial components of
79 communities in all ecosystems. These intricate associations display a high diversity, ranging
80 from mutually beneficial partnerships to parasitic interactions in which one species exploits
81 another (Paracer & Ahmadjian, 2000). Interactions among species are central to ecological
82 and evolutionary dynamics in assemblages of species that belong to different guilds and
83 trophic levels. They are thus essential elements of the ‘entangled bank’ – Darwin’s metaphor
84 for the complexity and connectedness of natural systems (Darwin, 1859) – and can give rise
85 to important stabilising feedbacks that eventually maintain diversity and ecosystem
86 functioning (Thrall *et al.*, 2007; Bastolla *et al.*, 2009). To date, insights are derived from
87 theory and empiricism focusing on either competition and predator–prey interactions (e.g.
88 Hairston, Smith & Slobodkin, 1960; Pimm, 1979; Tilman, 1982) or more recently mutualistic
89 interactions (Bascompte, Jordano & Olesen, 2006; Bascompte & Jordano, 2007; Barabás,
90 D’Andrea & Stump, 2018; Johnson & Bronstein, 2019; Spaak & De Laender, 2020).
91 Communities contain a wide variety of interactions, rendering the ecological network
92 extremely complex (Newman, 2003). One important feature of complex systems is the
93 presence of properties that emerge from interactions among the specific components of the
94 system (Solé & Bascompte, 2006). Typically, these emergent properties result from the
95 interaction between different network components across time and space and are difficult to
96 predict from the specific (isolated) pairwise interactions (Vázquez, Chacoff & Cagnolo, 2009;
97 Grilli *et al.*, 2017). Generally speaking, modular networks that are characterized by a high
98 connectance tend to be more robust to species loss, and are less affected by disturbance (Solé
99 & Bascompte, 2006; Olesen *et al.*, 2007). While theoretical progress has been made (Solé &

100 Montoya, 2001), the field is suffering from a lack of comprehensive and manageable
101 empirical systems. This limits empirical tests of theory (Valdovinos, 2019) and thus hampers
102 the development of effective management tools to safeguard the biodiversity and ecosystem
103 functions of natural ecosystems (De Laender *et al.*, 2016).

104 The study and interpretation of the drivers and consequences of the topology in host–
105 symbiont networks sheds light on the evolution of the strategies and traits of hosts and
106 symbionts. Moreover, this network approach may unravel general rules in community
107 assembly processes which can be compared across different types of symbionts and different
108 systems. While network studies at local scales will be informative on the local community
109 assembly processes, those reconstructed at regional or global scales will allow inference of
110 macro-ecological and evolutionary processes (Trøjelsgaard & Olesen, 2013).

111 In contrast to trophic networks, bipartite host–symbiont networks contain different kinds of
112 links, with interactions between hosts and symbionts ranging from antagonistic to mutualistic
113 (Ings *et al.*, 2009). Examples of such networks include plant–mycorrhiza and host–
114 microbiome associations. The complexity of these networks is enormous, and their
115 description is merely based on one interaction type, either antagonistic or mutualistic,
116 although theory predicts that the diversity of interaction types may be essential for community
117 stability (Fontaine *et al.*, 2011; Mougi & Kondoh, 2012; Allesina & Tang, 2015). The
118 topology of bipartite host–symbiont networks can be dissected by adopting two different
119 perspectives, i.e. that of each of the individual sets of species (hosts and symbionts). Asking
120 what factors cause a given topology is equivalent to asking, for each of the sets, what explains
121 the number of links per species and the specificity of these links, i.e. how the links are
122 distributed among species from the focal set. An example of this approach is found in studies
123 on predator–prey networks, where average web vulnerability (i.e. the average number of

124 predators per prey) and generality (i.e. the average number of prey eaten per predator) link the
125 specificity of the two interacting species sets (Schoener, 1989).

126 A determining feature of the ecology of symbionts is host specificity, which can be quantified
127 in host–symbiont networks by the number of links departing from a symbiont node. Yet, a
128 measure of host specificity should ideally consider the relatedness of the targeted host species
129 as well (Poulin & Mouillot, 2003). Generalist symbionts target multiple, unrelated host
130 species and may gain low to high benefits in any host. Specialist symbionts, in turn, engage
131 with one or only a few related species, and achieve high benefits with their hosts by resorting
132 to advanced morphological, physiological and behavioural adaptations (Bronstein, Alarcón &
133 Geber, 2006; Thrall *et al.*, 2007). Their strong specialization, however, is offset by lower
134 population densities and higher extinction risks due to the lower availability of hosts. Several
135 studies in host–symbiont systems clearly found that host specificity is tightly linked with
136 fundamental ecological processes and evolutionary history. Typically, host specificity is
137 different among cohabiting symbionts, as for example demonstrated in parasites of primates
138 (Pedersen *et al.*, 2005) and in parasitic mites on mussels (Edwards & Malcolm, 2006). A
139 study on moths and plants indicated that host specificity can be dependent on the type of
140 symbiotic interaction, with pollinating moths being more specific than their parasitic leaf-
141 feeding relatives (Kawakita *et al.*, 2010).

142 From the perspective of the host, it is fundamental to understand the ecological, evolutionary
143 and environmental drivers that promote the number of associated symbionts, i.e. the number
144 of links departing from a host node to symbiont nodes. Studies on different host–symbiont
145 systems reported multiple host variables which correlate with parasite species richness.
146 Generally, the makeup of symbiont communities is orchestrated by both ecological and
147 evolutionary host factors. Body size has been identified as a key ecological factor that favours
148 species richness (Lindenfors *et al.*, 2007) and species interactions (Werner & Gilliam, 1984).

149 Host species may be conceptualized as island habitats for symbionts and, in line with island
150 theory (MacArthur & Wilson, 1967), larger host species tend to support more symbionts
151 (Kuris, Blaustein & Alió, 1980). Symbiont richness is also expected to increase with other
152 ecological factors such as the number and variety of microhabitats offered by the host, host
153 longevity, host range, and interaction probability with other host species (Kamiya *et al.*, 2014;
154 Stephens *et al.*, 2016). Evolutionary processes may affect symbiont species richness in
155 different ways. Related hosts often show traits that are correlated throughout evolution
156 (phylogenetic correlation) which lead to similar values in species richness. However, related
157 host species may have diverged with time, whether or not in a common spatial evolutionary
158 ancestry (biogeography), but may still attract a similar fauna of symbionts as unrelated host
159 species with a similar ecology (Poulin, 1995).

160 Another pattern that emerges in host–symbiont networks is the sharing/transmission of
161 symbiont species across host species. The degree of symbiont sharing is vital as symbiont
162 transmission can connect eco-evolutionary dynamics across hosts as a result of rapid
163 symbiont spread in host populations [e.g. Jaenike *et al.*, 2010; Himler *et al.* (2011) in
164 endosymbionts]. While little is known about the proximate mechanisms by which single
165 symbionts switch between hosts, we can anticipate that host species with similar ecological
166 niches and/or a shared evolutionary history tend to have similar symbiont communities. The
167 pervasive effect of phylogenetic relatedness on symbiont sharing has for example been
168 demonstrated in bat parasites (Luis *et al.*, 2015) and in plant–mycorrhiza (Veresoglou &
169 Rillig, 2014).

170 Ant–symbiont networks are ideally suited to study which factors drive bipartite network
171 topology (Ivens *et al.*, 2016). The diversity of symbiotic associations found in ants (Kistner,
172 1982; Hölldobler & Wilson, 1990; Rettenmeyer *et al.*, 2010; Parmentier, 2020) is thought to
173 be promoted by their omnipresence in terrestrial ecosystems, their stable and climate-

174 controlled nest fortresses and the high number of available resources in the nest (Kronauer &
175 Pierce, 2011). Ants interact with different types of symbionts spanning the entire parasitism–
176 mutualism gradient. They include parasitic ants, different groups of arthropods living in the
177 nests, mutualistic aphids and caterpillars, endoparasitic helminths, plants, bacteria and fungi
178 (Hölldobler & Wilson, 1990). Therefore, they are promising systems to study different
179 interaction types within a single biological system (Fontaine *et al.*, 2011).

180 Ant–symbiont networks that have been studied recently typically deal with local interaction
181 networks and mostly focus on one kind of symbiotic interaction in isolation, such as
182 mutualistic plant–ant networks (Guimarães *et al.*, 2006; Blüthgen *et al.*, 2007; Dáttilo,
183 Guimarães & Izzo, 2013; Cagnolo & Tavella, 2015), mutualistic aphid–ant networks (Ivens *et*
184 *al.*, 2018) or parasite–ant networks (Elizalde *et al.*, 2018). Some studies have already covered
185 different types of symbiotic interactions in a local network (Pérez-Lachaud & Lachaud, 2014;
186 Rocha, Lachaud & Pérez-Lachaud, 2020) and a recent study tested different types of ant–
187 symbiont interactions on a large scale (Glasier, Poore, & Eldridge, 2018). However, the latter
188 study only included a limited set of interaction types and pooled interactions of well-studied
189 bioregions with those of very poorly studied regions.

190 Here, we ask what factors explain the topology of ant–symbiont networks across Europe. We
191 firstly provide a quantitative and systematic meta-analysis of the diversity of European ant–
192 symbiont interactions. By adopting the symbiont perspective, we test the hypothesis that the
193 type of symbiosis explains the number and identity of their host species (host specificity).

194 More specifically, we expect that parasitic ants are more specific than the other types of
195 symbionts. Secondly, we follow a trait-based host perspective to identify the major drivers
196 that promote the diversity of ant–symbiont interactions and facilitate symbiont sharing. We
197 test the hypothesis that the number of symbionts with which an ant species interacts and the
198 number of symbionts it shares with other ant hosts depend on ecological factors (colony size,

199 nest type, distribution, habitat, degree of sympatry, worker size) and evolutionary drivers
200 (phylogeny, biogeography) associated with the host species.

201

202 **II. MATERIALS AND METHODS**

203 **(1) Ant symbionts**

204 Symbionts are species that engage in a close association with a host species on which they
205 may have beneficial, neutral or adverse effects. We limited our analyses to Europe (excluding
206 the Canary Islands and Madeira), as knowledge of ant–symbiont interactions on other
207 continents is extremely fragmentary and poorly understood. Moreover myriad unknown
208 symbionts presumably await discovery and description in these continents (Parmentier, 2020).
209 By contrast, a firm body of knowledge on the distribution and diversity of ant symbionts in
210 Europe has been recorded and has grown steadily from a long tradition of studying ant
211 symbionts since the end of the 19th century (Wasmann, 1894; Janet, 1897). We focused on all
212 types of macrosymbionts (multicellular organisms) associated with European ants. We did not
213 include microsymbionts (unicellular microorganisms such as bacteria), as only a few case
214 studies are available. In addition, these symbionts differ completely in their strategies and
215 dynamics. Depending on the intimacy of the relationship between ants and symbionts, we can
216 distinguish obligate and facultative interactions. An obligate interaction occurs when a
217 symbiont lives permanently inside or near an ant nest. Obligate symbionts depend completely
218 on ants and cannot be found without them. Facultative myrmecophiles may associate with
219 ants, but regularly (or mostly) occur without ants. This study focuses on obligate symbionts.
220 We categorized five types of symbionts: (1) myrmecophiles; (2) trophobionts; (3) social
221 parasites; (4) helminths; and (5) fungi (Table 1). Myrmecophiles were further subdivided into
222 three functional groups: unspecialized myrmecophiles, specialized myrmecophiles and
223 myrmecophilous parasitoids (Table 1).

224 Plants engaging in mutualistic relationships (e.g. myrmecochory) were not included in our
225 analyses. Contrary to the tropics, ant–plant relationships tend to be loose in Europe and are at
226 best facultative (Rico-Gray & Oliveira, 2007).

227

228 **(2) Ant–symbiont data set compilation**

229 We compiled documented ant–symbiont interactions in Europe. Our database of ant–symbiont
230 interactions was assembled from 269 published references, including faunistic notes, research
231 articles, reviews and books. In a first round of searches, we scanned reference works (e.g.
232 Wasmann, 1894; Donisthorpe, 1927; Evans & Till, 1966; Uppstrom, 2010; Tykarski, 2017;
233 Molero-Baltanás *et al.* 2017) for associations between ant hosts and symbionts. Next, we
234 searched for ant–symbiont interactions *via Google Scholar* using the terms: “myrmecophile”
235 or “ant associate” or “inquiline” or “ant guest” or “ant symbiont”. We also found host–
236 symbiont interactions within the reference lists of the retrieved publications. In a second
237 phase, each symbiont occurring in Europe was searched by its Latin binomial name and its
238 common taxonomic synonyms combined with a search string with the names of all ant genera
239 ($N = 56$; AntWiki, 2019) found in Europe (for example “*Phengaris alcon*” AND *Acropyga*
240 OR *Anochetus* OR *Aphaenogaster* OR *Bothriomyrmex* OR *Camponotus* OR ...) using *Google*
241 *Scholar*. We chose *Google Scholar* over ISI Web of Science, as the latter does not retrieve
242 faunistic notes or other types of grey literature. We omitted symbionts from our data set when
243 they were reported not to be associated with ants. Note that some species with a poorly
244 studied biology, such as parasitoid wasps and mites, were included in our data set, although
245 they may not be completely dependent on ants. Ultimately, we obtained a binary host–
246 symbiont matrix (see online Supporting information Appendix S1, references used to compile
247 this table are listed in Appendix S2) filled with interactions (1) and non-interactions (0)
248 between ants (columns) and symbionts (rows). We included some references on ant–

249 trophobiont interactions reported in the non-European part of Russia (e.g. Novgorodova,
250 2005) to increase the relatively modest number of reported interactions in this type of
251 association. The reported ants and trophobionts in these references have a widespread
252 Palearctic distribution and they are expected to interact in Europe as well.

253

254 **(3) Host specificity in different symbiont types**

255 We first determined the host range of the different symbiont types. A second analysis
256 compared host relatedness across symbiont types. We used two approaches to estimate host
257 relatedness: taxonomic and phylogenetic relatedness.

258 In the first analysis, we compared the number of host species across seven different types of
259 host symbionts, i.e. unspecialized myrmecophiles, specialized myrmecophiles,
260 myrmecophilous parasitoids, trophobionts, social parasites, parasitic fungi and helminths
261 (Table 1). Symbionts with hosts only identified at the genus level were not included in all
262 subsequent analyses. Note that we found evidence of one mutualistic fungus (*Cladosporium*
263 *myrmecophilum*) (Table 1), but we only analysed parasitic fungi to ensure a coherent
264 functional group of symbionts. Studies are uneven across symbionts, potentially meaning that
265 better studied symbionts have a higher number of recorded host species. To account for
266 differences in sampling effort, we therefore first performed a regression of the total number of
267 host species against the $(\ln+1)$ -transformed number of *Google Scholar* hits for the binomial
268 species name (and commonly used synonyms) of the symbionts. The residuals of this
269 regression were not normally distributed. Therefore we used a non-parametric Kruskal-Wallis
270 test to compare these residuals across symbiont types. This test was followed by *post-hoc*
271 Dunn tests with the Benjamini–Hochberg adjustment for multiple testing.

272 In the second analysis, we compared the relatedness of targeted host species across the seven
273 different symbiont types. For each symbiont, we estimated the average taxonomic distance

274 between the different hosts by using the specificity index, S_{TD} proposed by Poulin & Mouillot
275 (2003). Host ant species (all ants belong to the family Formicidae) were classified following
276 Linnaean classification into subfamilies, tribes, genera and species groups/subgenera. The
277 taxonomic distance between two hosts is then defined as the number of hierarchical steps that
278 are needed to reach a common node in the taxonomic tree. The taxonomic distance between
279 two species of the same subgenus/species group equals 1; the distance between two species of
280 the same genus, but from a different subgenus/species group equals 2. A distance of 3 or 4
281 was assigned to a pair of species belonging to the same tribe or subfamily, respectively. A
282 taxonomic distance of 5 is reached between two ant host species from different subfamilies
283 (largest possible distance). S_{TD} was estimated by averaging the taxonomic distance across all
284 pairs of host species. However, S_{TD} cannot be calculated for symbionts with a single host
285 species, although this can be addressed by excluding these ‘singletons’ from the analyses
286 (Poulin & Mouillot, 2005). The single host species for many of our symbionts (e.g. mites)
287 likely reflects undersampling, rather than true specificity to a single host species, because
288 even extremely specialized species (e.g. *Microdon*, *Claviger*, social parasites) often have
289 more than one host species. Since these singletons were equally distributed over all groups of
290 symbionts, we argue they could be omitted from further analyses; a total of 392 symbionts
291 were retained in our analysis. Note that the S_{TD} is not affected by uneven sampling when dealt
292 with in this way. We modelled the S_{TD} as a response variable against the predictor symbiont
293 type with a non-parametric Kruskal-Wallis test, followed by *post-hoc* Dunn tests with the
294 Benjamini–Hochberg adjustment for multiple testing. Alternatively, we can assign a default
295 taxonomic distance of 1 to the singletons, which is the lowest possible value (Poulin &
296 Mouillot, 2005). We repeated the analysis with this approach and compared it with the
297 analysis without singletons.

298 Next, we compared the relatedness of the targeted host species across the symbiont types with
299 a phylogenetic- instead of a taxonomic-distance matrix. The phylogenetic-distance matrix was
300 based on the phylogenetic tree of European ants (Arnan, Cerdá & Retana, 2017). Distances
301 between species were estimated by node count (number of nodes along the branches of the
302 tree from one species to another) and were retrieved using Mesquite v.3.5. Phylogenetic
303 distances are more accurate than taxonomic distances to assess relatedness, but unfortunately
304 we do not possess phylogenetic information at the species level for all ants in our data set (the
305 phylogeny was known for 108 out of 181 ant species). We decided to exclude the 73 ant
306 species without phylogenetic information and their interactions with their symbionts from
307 subsequent analyses. We believe that this is acceptable as the retained 108 species cover
308 87.8% of the interactions in our host species–symbiont data set. In addition, symbionts that
309 interacted with only one ant species were omitted, as no specificity index could be calculated
310 for these species. Ultimately, we retained 362 symbiont species and 108 ant species in this
311 analysis (host–symbiont matrix in Appendix S3). As the residuals meet the assumptions of a
312 general linear model (GLM), we ran a GLM using phylogenetic distance as the response
313 variable and symbiont type as predictor. Significance of the model was assessed with a
314 likelihood ratio test (ANOVA function implemented in the package *car*), pairwise *post-hoc*
315 tests were conducted with the Benjamini–Hochberg adjustment for multiple testing.

316

317 **(4) Predictors of symbiont diversity in European ants**

318 A central question in this study is why some ant species host more symbionts than other ant
319 species. Therefore, we first compiled for the European ant species several predictors based on
320 Arnan *et al.* (2017), Boulay *et al.* (2017), Seifert (2007) and AntWiki (2019). We selected
321 traits of the host that could affect symbiont diversity. These predictors were colony size
322 (number of workers), average worker size (mm), nest type [levels: (a) arboreal; (b)

323 diverse; (c) soil; and (d) organic mound] and phylogeny as a proxy for trait similarity, and
324 factors reflecting differences in the functional role of the host species, including habitat
325 [levels: (a) eurytope: – a broad range of niches, including anthropogenic habitats; (b) open;
326 (c) open/sylvicolous; and (d) sylvicolous], distribution range, the number of sympatric ants
327 and biogeographic region [levels: (a) atlantic; (b) boreo-mountain; (c) continental; (d)
328 Mediterranean; and (e) wide-ranging]. Ants were assigned to the biogeographical region
329 where they were found proportionally the most in sampled biogeographical regions based on
330 the observations of Arnan *et al.* (2017). If the proportional occurrence in the most preferred
331 region was less than double the proportional occurrence in another region, the ant species was
332 grouped under the ‘wide-ranging’ category. We also estimated the distribution range [the
333 number of countries where the host species has been reported, based on records on AntWiki
334 (2019)], the number of sympatric ants [number of ant species with symbionts which share at
335 least one country in the distribution range, based on AntWiki (2019)] and the number of hits
336 for their binomial name (and common synonyms) on *Google Scholar* as a proxy for sample
337 effort for every ant species. Next we correlated total symbiont diversity with the host
338 predictors described above, while correcting for the phylogenetic relatedness of the different
339 ant species. The phylogenetic relatedness of host species should be accounted for as closely
340 related host species cannot be treated as independent observations. For that reason, we
341 modelled a phylogenetic generalized least-squares regression (PGLS) with total number of
342 symbionts per ant species as the dependent variable. A PGLS model incorporates a
343 phylogenetic variance–covariance matrix in its error structure. We used the variance–
344 covariance matrix based on the pairwise node counts retrieved from the phylogenetic tree of
345 European ants by Arnan *et al.* (2017). The phylogenetic relatedness of 108 out of the 181 ant
346 species found in our data set was determined in this tree (see Appendix S3). From this subset
347 of 108 species, we were able to find values for all predictors for 96 species. Consequently, the

348 PGLS model was based on these 96 ant species (Appendix S4). This data set reduction is
349 acceptable as these 96 ant species interact with 620 symbionts and cover 86.5% of the
350 recorded interactions in the host species–symbiont data set. The phylogenetic covariance
351 matrix was multiplied by Pagel’s λ , a widely used parameter that scales and corrects for the
352 expected degree of phylogenetic covariance (Pagel, 1999). This multiplier spans from 0,
353 which corresponds to the complete absence of a phylogenetic signal in the residuals of the
354 model (the model is then similar to a regular GLM with an ordinary least-squares error
355 structure) to 1, when the covariance of the model residuals follows a Brownian motion model
356 of evolution (Pagel, 1999; Freckleton, Harvey, & Pagel, 2002). The λ parameter
357 characterizing the phylogenetic signal was estimated through maximum likelihood estimation
358 within the PGLS model. We analysed this model using the *pgls* function embedded in the R
359 3.5.1-package ‘caper’. We transformed the variables to meet the normality assumptions of the
360 residuals. Number of symbionts was square–root transformed, the predictors colony size, the
361 number of sympatric ants and *Google Scholar* hits ln-transformed, and the distribution range
362 was square-root transformed. Finally, all continuous predictors were scaled to unit variance.
363 In addition to this analysis on the drivers of total symbiont diversity, we ran similar PGLS
364 models with subsets of symbiont species richness as dependent variables (overall number of
365 myrmecophiles, trophobionts, social parasites and helminths, separately) and predictors of the
366 subset of ant species that engage with these symbionts as predictors. Identical transformations
367 of predictors and subsets of symbiont richness were applied as in the analysis on total
368 symbiont richness described above. Diversity of fungi was not regressed against ant predictors
369 in separate PGLS models as the number of host ants is relatively low in these groups.
370 Models were ranked per analysis with the *dredge* function in the ‘MuMIn’ R-package
371 according to their corrected Akaike Information Criterion (AICc) value. We retained the best

372 models identified with $\Delta AICc < 2$. Significance levels of the predictors of the retained models
373 were assessed using Wald χ^2 tests.

374

375 **(5) Predictors of symbiont sharing in European ants**

376 Studying the factors that facilitate or constrain the transmission of a symbiont from one host
377 to another is pivotal to understanding the ecological and co-evolutionary processes in host–
378 symbiont networks (Okuyama & Holland, 2008; Pilosof *et al.*, 2013). For example, symbionts
379 that are only shared by closely related hosts may indicate host–symbiont co-evolution in the
380 network (Guimarães, Jordano & Thompson, 2011). Predictors were similar to the previous
381 analysis and encompassed traits of the ant species and variables related to their habitat and
382 distribution, including colony size, worker size, nest type, phylogeny as a proxy for trait
383 similarity, habitat, distribution range, biogeographic region and allopatric distribution. We
384 used multiple regression on distance matrices (MRM), an extension of partial Mantel analysis,
385 to test the association between different distance matrices (Lichstein, 2007). The symbiont
386 dissimilarity matrix contained the pairwise Jaccard distances between each pair of host ants
387 based on the presence–absence data of the symbionts they supported. This matrix was
388 regressed against multiple distance/dissimilarity matrices giving dissimilarities in the
389 aforementioned predictors. Worker size difference was the absolute difference for this trait
390 between every pair of ant species. The pairwise differences in colony size were ln-
391 transformed. For the allopatric distribution matrix, we first calculated the degree of overlap in
392 distribution (sympatry) between each pair of species (ln-transformed number of countries in
393 the distribution range that are shared between each pair of ant species). We standardized this
394 matrix between 0 and 1 and subtracted it from 1 to obtain a dissimilarity matrix. Entries in the
395 distance matrices of habitat, nest type and biogeographic region were coded 0 when the pair
396 of ants occupy the same habitat, nest type or biogeographic region, respectively, and 1 when

397 the pair of ants show differences in these variables. The phylogenetic distances were the
398 pairwise node counts. Again, we focused our analysis on the subset of 96 ants for which the
399 phylogenetic relationship was resolved by Arnan *et al.* (2017) and for which we possessed
400 values for all predictors. We also included a matrix of sampling effort in which we pairwise
401 multiplied the $(\ln+1)$ -transformed hits on *Google Scholar* of one ant species with the $(\ln+1)$ -
402 transformed hits on *Google Scholar* of another ant species. All matrices were standardized
403 between 0 and 1 and MRM analyses were conducted in the R package ‘ecodist’ using the
404 MRM function. Significance of the predictor matrices was tested using 9999 permutations.
405 We removed non-significant predictors, and reran the MRM analysis until all predictors were
406 significant (Martiny *et al.*, 2011). The relative importance of the significant predictor matrices
407 was calculated with the lmg metric, which uses unweighted averages of sequential R^2 of
408 different orderings of the model predictors. The calculation and visualization of the lmg
409 metrics was conducted with the R-package ‘relaimpo’.

410 We conducted similar MRM analyses on subsets of the symbiont community, where the
411 response variable was the dissimilarity (pairwise Jaccard indices) in the set of myrmecophiles,
412 trophobionts, social parasites, helminths and parasitic fungi of the host ants, respectively.

413 All statistical tests were conducted in R 3.5.2.

414

415 **III. RESULTS**

416 **(1) Ant–symbiont networks display a diversity of species interactions**

417 We identified 722 obligate ant symbionts interacting with 181 ant species in Europe
418 (Appendix S1). The references we used to compile the host–symbiont interaction matrix are
419 listed per symbiont species in Appendix S2. Myrmecophiles ($N = 535$) outnumbered the four
420 other types of ant symbionts ($N = 80$, $N = 71$, $N = 22$ and $N = 14$ for trophobionts, social
421 parasites, parasitic helminths and fungi, respectively). One fungus was mutualistic, the other

422 13 species were parasitic. Within the group of myrmecophiles, beetles and mites were the
423 most species-rich groups (Fig. 1). The subdivision of myrmecophiles into parasitoids ($N =$
424 33), unspecialized myrmecophiles ($N = 413$) and specialized myrmecophiles ($N = 89$) can be
425 found in Appendix S1. The hosts of 75 symbionts were not identified at the species level in
426 the literature record. The distribution of the number of host species per symbiont was right-
427 skewed (mean = 3.58, median = 2). The highest frequency (39%) of symbionts interacted with
428 one host species and a maximum number of 34 host species was documented in the
429 myrmecophilous silverfish *Proateturina pseudolepisma*.

430 European ant genera contained a highly variable number of species (proportional to the genus
431 font size in Fig. 2; Fig. S1), ranging from 1 to 82, in the genera that interact with symbionts.
432 Generally, the species-rich ant genera, such as the Formicinae genera *Lasius*, *Formica* and
433 *Camponotus* and the Myrmicinae genera *Messor* and *Myrmica* attracted a higher diversity of
434 all five types of symbionts (Pearson's product-moment correlation: $r = 0.59$, $P < 0.001$, d.f. =
435 30; Fig. S1). A notable exception was the European ant genus *Temnothorax*, which contained
436 the most species while supporting a relatively moderate number of symbionts. Myrmecophiles
437 were the dominant group in most ant genera. Trophobionts were generally the second most
438 diverse group, but were absent or nearly absent in some genera such as *Monomorium*,
439 *Aphaenogaster*, *Leptothorax*, *Messor*, *Temnothorax* and *Cataglyphis*. Social parasites
440 contributed slightly to total symbiont diversity in most ant genera, but were very diverse in
441 the ant genera *Temnothorax*, *Tetramorium* and *Leptothorax*. Helminths and fungi represent a
442 minor fraction of the symbiont fauna in almost all ant genera. However, fungi are well-
443 represented in *Myrmica*. Ant genera shared many symbionts with other genera (78.9% of the
444 hosted community on average), belonging to the same or different ant subfamilies (connecting
445 lines in Fig. 2). *Temnothorax*, *Leptothorax* and *Messor* are characterized by a relatively high
446 number of unique symbionts (see relatively large inner circles in Fig. 2).

447

448 **(2) Host specificity in different symbiont types**

449 After controlling for sampling effort, symbiont groups had significantly different host ranges
450 (Kruskal-Wallis chi-squared = 44.97, d.f. = 6, $P < 0.001$; Fig. 3). Social parasites had the
451 lowest number of host species (Fig. 3, *post-hoc* comparisons indicated with letter code). Other
452 symbiont types interacted with a higher number of ants, but we did not detect significant
453 differences among these other types (Fig. 3). Host range of symbiont groups without
454 controlling for sampling effort can be found in Fig. S2.

455 The average taxonomic distance between host species targeted by a symbiont was
456 significantly different among symbiont groups (Kruskal-Wallis chi-squared = 83.37, d.f. = 6 ,
457 $P < 0.001$; Fig. S3). The approach where we omitted the symbionts with one host species
458 (Fig. S3) and that where we assigned a taxonomic distance of 1 to these species (Fig. S4)
459 provided similar results (relative differences among symbiont groups are very similar in Figs
460 S3 and S4). Likewise, we found significant differences in average phylogenetic distance
461 between host species across the symbiont groups (GLM, $F = 17.27$, d.f. = 6, $P < 0.001$; Fig.
462 4). Patterns in the average host phylogenetic distance of the different symbiont groups closely
463 matched those of the average host taxonomic distance. Host species of social parasites were
464 very closely related to each other (Figs 4 and S3). Parasitic fungi also exploited related host
465 species. Helminths and myrmecophiles interacted with hosts that are much more unrelated on
466 average. We did not find differences in host relatedness among myrmecophilous parasitoids,
467 unspecialized and specialized myrmecophiles (Figs 4 and S3). Ants interacting with
468 trophobionts showed the lowest relatedness (Fig. 4).

469

470 **(3) Predictors of symbiont diversity in European ants**

471 The number of symbionts is highly variable in ant species. Here we report the host drivers that
472 affect total symbiont richness and diversity of four subsets of ant symbionts (myrmecophiles,
473 trophobionts, social parasites and helminths). Total symbiont diversity was clearly positively
474 correlated with colony size. This factor was highly significant (PGLS, $P < 0.001$) in the four
475 top-ranking models (Table 2, Fig. 5). Habitat and distribution range of the host were also
476 incorporated in most of the top-ranking models. In these models, symbiont richness increased
477 with the host distribution range and was highest in eurytopic habitats (PGLS, $P < 0.001$). As
478 expected, sample effort has a major effect on the reported total symbiont diversity and the
479 other subsets of symbiont diversity. Symbiont interactions were highest in ants that are
480 intensively studied. We controlled for sample effort by including the proxy $(\ln+1)$ -
481 transformed *Google Scholar* hits in our models. Myrmecophile richness was also positively
482 affected by colony size (PGLS, $P < 0.001$ in the five top-ranking models, Table 2, Fig. 5),
483 distribution and eurytopic habitat. Myrmecophiles were more abundant in larger ants (PGLS,
484 $P < 0.05$ in the retained models). Trophobiont diversity was positively correlated with
485 sampling effort and an eurytopic habitat in most models (Fig. 5, Table 2). Trophobiont
486 diversity was in some models also higher in ant species with a higher distribution. There were
487 no predictors consistently present in the top-ranking models explaining social parasite species
488 richness (Table 2) Helminth diversity was higher in eurytopic ant species, but no other
489 predictors were consistently retained in the top models (PGLS, $P < 0.001$, Table 2).

490 We found a phylogenetic signal in the predictors of the PGLS models ($\Delta AICc < 2$) with total
491 symbiont richness as dependent variable (Pagel λ ranged from 0.41 to 0.54 Table 2). The
492 residuals of the models showed different degrees of phylogenetic covariance. The largest
493 phylogenetic signal was found in the models with social parasites (Pagel λ ranged from 0.83
494 to 1.00) and helminths (Pagel λ ranged from 0.85 to 0.94) as dependent variable. By contrast,

495 phylogenetic relatedness of the hosts did not explain additional variation (Pagel's $\lambda = 0$) in
496 most retained models with myrmecophiles as dependent variable (Table 2).

497

498 **(4) Predictors of symbiont sharing in European ants**

499 The dissimilarity matrices of the host predictors (indicated with Δ in Fig. 6) were positively
500 correlated with dissimilarity in symbiont composition (Fig. 6). This shows that ant species
501 with a higher similarity in these predictors display a higher similarity in symbiont
502 composition. The most important predictors of similarity in ant symbiont communities in the
503 European ant data set were phylogenetic relatedness of the ant hosts (MRM, $\text{img} = 0.40$, $P <$
504 0.001) and similarity in biogeographic region (MRM, proportional contribution to the total r^2
505 $= \text{img} = 0.35$, $P < 0.001$) (Fig. 6). Similarities in worker size ($\text{img} = 0.07$, $P = 0.01$), colony
506 size ($\text{img} = 0.04$, $P = 0.02$) and habitat ($\text{img} = 0.01$; $P = 0.03$) also facilitated the sharing of
507 symbionts (Fig. 6). Better studied ant pairs shared more similar symbiont communities
508 (MRM, $\text{img} = 0.13$, $P < 0.001$). Well-studied ant pairs also shared more trophobionts,
509 myrmecophiles and parasitic fungi (MRM-analyses, img ranging from 0.14-0.60, all $P < 0.05$,
510 Fig. 6). Trophobiont sharing was also positively correlated with phylogenetic relatedness and
511 similarity in biogeographic regions of the ant hosts (MRM, $\text{img} = 0.22$, $P < 0.001$ and $\text{img} =$
512 0.13 , $P < 0.001$, respectively). The similarities in social parasite communities was largely
513 explained by phylogenetic relatedness (MRM, $\text{img} = 0.76$, $P < 0.001$). Similarities in
514 biogeography (MRM, $\text{img} = 0.04$, $P = 0.04$) explained additional variation in the sharing of
515 social parasites. Helminth sharing was also strongly facilitated in phylogenetically related ant
516 hosts (MRM, $\text{img} = 0.71$, $P < 0.001$). Interestingly, phylogenetic relatedness of the hosts did
517 not promote the sharing of myrmecophiles. The similarity of myrmecophile communities
518 between ant hosts was mainly driven by living in a similar biogeographic region (MRM, img

519 = 0.68, $P < 0.001$), Lastly, ants in the same biogeographic region tend to share more parasitic
520 fungi (MRM, $\text{Im}g = 0.44$, $P < 0.01$) (Fig. 6).

521

522 **IV. DISCUSSION**

523 Understanding community composition and stability is an important challenge in ecology.

524 Network analysis has approached this challenge, using community structure and species

525 interactions as fundamental building blocks. Yet, studies that explain the detailed topology of

526 large-scale ecological networks encompassing a diversity of interaction types are limited. We

527 here provide a complete tally of the distribution of ant symbiont groups over European ants

528 and compare host specificity, symbiont richness, host switching and its drivers for different

529 ant symbiont groups.

530

531 **(1) Characterization of the European ant–symbiont network**

532 It is widely acknowledged that the group of obligate ant symbionts is hyperdiverse

533 (Wasmann, 1894; Kistner, 1979, 1982; Hölldobler & Wilson, 1990; Rettenmeyer *et al.*, 2010),

534 although exact species numbers at a regional scale are lacking. Rough estimates of the global

535 diversity of parasites living in ant nests reach 10,000 to 20,000 species (Thomas, Schönrogge

536 & Elmes, 2005), which is higher than mammal and bird diversity. We here identified 722

537 symbionts distributed over 181 ant species in Europe. The majority of these symbionts were

538 classified as myrmecophiles, which are commensalistic-to-parasitic arthropods mostly living

539 inside the ant nest (Kronauer & Pierce, 2011; Parmentier *et al.*, 2016a; Parmentier, 2020).

540 Beetle and mite communities were the most diverse groups. In other regions, beetles and

541 mites also outnumber other myrmecophilous arthropod groups (Kistner, 1982; Hölldobler &

542 Wilson, 1990). Social parasites and mutualistic trophobionts are medium-sized groups;

543 endoparasitic helminths and parasitic fungi are relatively species-poor, but understudied.

544 Mutualistic ant symbionts are thus clearly overshadowed by the diversity of commensalistic
545 and parasitic ant symbionts in Europe. Species-rich ant genera and subfamilies generally
546 supported higher numbers of ant symbionts. Host–symbiont networks are characterized by an
547 asymmetrical organization of interactions with host-specific symbionts and symbionts that
548 interact with multiple host taxa (Guimarães *et al.*, 2006). Overall, a large proportion of the
549 symbionts were shared among heterogeneric ant species (Fig. 2). Some ant genera interacted
550 with a relatively low number of symbionts, but most of their symbionts were not found in
551 association with other ant genera. The highly specific group of social parasites was much
552 more represented in the symbiont community of these hosts. In addition, the group of
553 trophobionts is diverse in some ant genera, but is marginal or even absent in others (Fig. 2).
554 The distribution of trophobiont interactions across the ant genera echoed the dietary
555 preferences of the host. The diet of genera such as *Formica*, *Lasius* and *Myrmica* consists of a
556 significant proportion of honeydew, whereas genera with few or no trophobiotic interactions
557 are known to be predatory (e.g. *Temnothorax*, *Cataglyphis*) or granivorous (e.g. *Messor*)
558 (Seifert, 2007). Mutualistic interactions are much more diverse in tropical systems than those
559 observed in the European network and include ant-cultivated plants, ant-defended plants and
560 ant-cultivated fungi (Rico-Gray & Oliveira, 2007). The uneven distribution of the five types
561 of symbionts among the European ant genera suggests that some ant lineages are more
562 predisposed to associate with particular types of symbionts. Ant–host associations are thus
563 shaped by deep evolutionary processes as determined by biotic and environmental drivers of
564 speciation and extinction (Aguilée *et al.*, 2018).

565

566 **(2) Host specificity in different symbiont types**

567 Host specificity is a key feature of host–symbiont networks, and is moulded by the ecological
568 and evolutionary interactions between the host and symbiont (Poulin & Mouillot, 2003).

569 Patterns in host specificity have been studied in a wide range of host–symbiont systems.
570 Generally, parasites are thought to have a tendency to evolve to extreme host specialization as
571 they need complex adaptations to bypass host defences (Kawakita *et al.*, 2010). The drivers
572 favouring host specificity in mutualist partners are far less understood and both low and high
573 degrees of specificity are widespread (e.g. plant–seed dispersers and fig–fig wasps,
574 respectively). Ant symbioses are ideal to unravel patterns in host specificity. They occupy the
575 complete mutualism–parasitism continuum and allow comparison of host specificity in
576 different types of symbionts. We here demonstrate that average host range in European ant
577 symbionts was much broader than previously assessed in a study on host specificity of
578 myrmecophiles at a global scale (Glasier *et al.*, 2018) which found that obligate ant symbionts
579 occurred on average with *ca.* 1.20 host species. We, however, found that European symbionts
580 were reported with three times this number of host species (3.58) on average. The much lower
581 number of detected hosts in Glasier *et al.* (2018) is probably the result of their searching
582 method. They did not include data from faunistic notes, grey literature and books, which
583 report the majority of interactions between ants and their symbionts. Moreover, the symbiont
584 fauna, let alone the range of their interactions, is poorly documented outside Europe, which
585 makes hard predictions at a global scale unreliable (Parmentier, 2020). Ant symbionts were
586 extremely variable over the host-ant range. After controlling for sampling effort, social
587 parasites clearly targeted the lowest number of host species, which is in line with expectations
588 as they are the most specialized group of parasites (Buschinger, 2009). Apart from the number
589 of hosts, the relatedness of host species is also a vital aspect of host specificity. It is well
590 described that social parasites colonize nests of related hosts (Emery’s rule; Buschinger,
591 2009). However, this has not been compared with other types of symbiont groups. We showed
592 that the hosts of social parasites were clearly the most related of all symbiont types. The hosts

593 of myrmecophiles, parasitic fungi and helminths showed moderate to poor relatedness on
594 average. Trophobionts were associated with the most distantly related ant species.
595 There is a large body of literature that explains the constraints of host switching in social
596 insect symbionts. Generally, it is thought that specialized myrmecophiles and social parasites
597 rely on chemical deception, by mimicking the colony recognition cues or some key
598 pheromones (overview in Parmentier, Dekoninck & Wenseleers, 2017). They are completely
599 integrated into the host colony and are treated as a true colony member. Because of this strict
600 mimicking of the host's communication system, they are not able to colonize unrelated host
601 species. Unspecialized myrmecophiles are typically poorly integrated into the colony, but host
602 switching is more common in this group. This is facilitated by the use of general defensive
603 chemicals, chemical insignificance or behavioural strategies (Stoeffler, Tolasch & Steidle,
604 2011; Parmentier *et al.*, 2017, 2018). Consequently, we predicted that specialized
605 myrmecophiles would display much higher degrees of host specificity than unspecialized
606 myrmecophiles. Surprisingly, we did not find differences in the number of host species and
607 host relatedness among unspecialized myrmecophiles, specialized myrmecophiles and
608 parasitoids. A limitation of the present study is that we do not have information on the relative
609 importance of the recorded host species for a symbiont. It is likely that some of the listed host
610 species of specialized symbionts rarely act as hosts, resulting in an overestimation of the
611 actual species range and host species relatedness of symbionts. Additionally, the biology of
612 most myrmecophiles is poorly known, which makes a functional grouping according to
613 specialization challenging and open for refinement. The processes which make trophobionts
614 attractive to one host, but not to another are hitherto unexplored. Likewise, the mechanisms of
615 host switching and the factors that facilitate or constrain host switching in endoparasitic
616 helminths and fungi are unknown.
617

618 **(3) Predictors of symbiont diversity in European ants**

619 Associations between ant hosts and their symbionts are not random and are structured
620 according to both ecological and evolutionary factors that act at different spatiotemporal
621 scales. From the perspective of ant symbionts, ant nests can be conceptualized as habitat
622 islands. Ant species with larger ant nests interact with more symbiont species. Nest size of ant
623 species has been repeatedly hypothesized as an important driver of ant symbiont diversity
624 (Hughes, Pierce & Boomsma, 2008; Kronauer & Pierce, 2011), and here was formally tested
625 for the first time. Previous studies across very different host–symbiont systems [e.g.
626 ectoparasites of fishes (Guégan *et al.*, 1992), parasites of hoofed mammals (Ezenwa *et al.*,
627 2006), parasites of carnivores (Lindenfors *et al.*, 2007), feather mites of finches (Villa *et al.*,
628 2013)] identified the size of the host species as one of the key factors in determining symbiont
629 species richness (Kamiya *et al.*, 2014). This positive association results from the fact that
630 larger host species provide more niches and are less ephemeral (Lindenfors *et al.*, 2007).
631 Analogously, ant species with larger nests provide more space to allow larger population
632 sizes, thereby reducing the extinction risk of symbionts (*cf.* island theory; MacArthur &
633 Wilson, 1967). In addition, ant species with larger nests provide a higher diversity of
634 microhabitats, including refuge areas that eventually facilitate species coexistence (Barabás *et*
635 *al.*, 2018). Larger ant nests are also expected to be more persistent (Kaspari & Vargo, 1995).
636 The colony size of ant species is thus a strong local driver of total symbiont richness, and
637 myrmecophile richness in particular.
638 Total symbiont diversity, myrmecophile diversity, helminth and trophobiont diversity are
639 additionally determined by more regional ecological factors like range size and niche width of
640 the host ants. In that respect, eurytopic ants, such as *Lasius niger* and *Myrmica rubra* that can
641 live in a wide variety of habitats including urban regions, hosted more symbionts,
642 myrmecophiles, trophobionts and helminths. An effect of both distribution and habitat reflects

643 that more symbionts occur in widely distributed ant species with high densities. Symbionts
644 associated with widely distributed ants are less prone to extinction as predicted by life-history
645 theory and metacommunity ecology (Nosil, 2002; Leibold *et al.*, 2004).

646 Host density has widely been demonstrated as a key factor explaining parasite species
647 richness (Lindenfors *et al.*, 2007). Interestingly, we found that species with larger workers
648 engaged with more myrmecophiles than ant species with small workers. This pattern in
649 myrmecophile diversity was previously hypothesized based on experimental work, showing
650 that the survival of three myrmecophilous beetles gradually increased in laboratory nests of
651 larger ant species (Parmentier, Dekoninck & Wenseleers, 2016b). This positive relationship
652 between ant size and myrmecophile diversity suggests that species with small workers detect,
653 attack and deter myrmecophiles more easily and efficiently.

654 Sampling effects appear highly relevant in most models of symbiont diversity among different
655 hosts. Trophobiotic and more specialized parasitic interactions as seen in the group of
656 helminths and social parasites are more determined by evolutionary drivers than
657 myrmecophiles. Indeed, affinity with their hosts is strongly shaped by the phylogeny of the
658 host. The effect of phylogeny is echoed in the high Pagel's lambda values of the
659 corresponding PGLS models, implying that much of the residual variation in trophobiont and
660 especially helminth and social parasite richness could be explained by the phylogeny of the
661 hosts. This strong phylogenetic driver for social parasite richness is in line with our previous
662 results that social parasites mainly target closely related ant species (referred to as Emery's
663 rule; Buschinger, 2009) belonging to a small number of ant genera. Symbiont network
664 structure thus shifts from more neutral ecological drivers related to regional species
665 abundance to co-evolutionary drivers related to ancestry. The uniqueness and tightness of
666 species interactions are known to be both a driver and consequence of co-evolutionary
667 dynamics. Interestingly, we here show that these evolutionary drivers overrule any ecological

668 one in the most specialized interactions (social parasites), hence demonstrating the integrated
669 nature of symbiont network formation according to the prevailing interaction strengths. Other
670 predictors, which were not considered in the analyses, may also positively affect the diversity
671 of symbionts. The availability of larvae and pupae rather than colony size may be more
672 important for parasitoid species (Rocha *et al.*, 2020). The tolerance level of ant species to
673 intruders and the colonial organization (either single nests or multiple connected nests, either
674 a single queen or multiple queens) are also possible determinants of diversity, but sufficient
675 information is lacking to test these hypotheses.

676 Ant–symbiont networks are unique in the sense that the host-associated network that is
677 studied covers a wide array of interactions, from putatively mutualist to strictly antagonistic.
678 We found that evolutionary processes are pivotal in networks of the most specialized ant
679 symbionts (social parasites), whereas less-specialized networks, as found in the group of
680 myrmecophiles, were mostly determined by ecological factors. The same pattern was found in
681 other symbiont systems. Studies on specialized host–parasite networks equally point at the
682 dominance of evolutionary drivers (phylogeny and biogeography) of these associations (Feliu
683 *et al.*, 1997; Rosas-Valdez & de Pérez-Ponce de León, 2011), while less-obligatory animal
684 parasitic (Nunn *et al.*, 2003; Ezenwa *et al.*, 2006; Lindenfors *et al.*, 2007; Nava &
685 Guglielmone, 2013) or plant mutualistic interactions (Sanders, 2003; Wagner, Mendieta-
686 Leiva, & Zotz, 2015) are more affected by ecological factors related to distribution and
687 abundance patterns that enhance contact and hence transmission of their diversity and host-
688 association patterns.

689

690 **(4) Predictors of symbiont sharing in European ants**

691 We hypothesized that the shared evolutionary history of related ant species would promote the
692 sharing of similar symbiont communities. A positive correlation between phylogenetic

693 relatedness of the hosts and symbiont sharing was demonstrated in previous studies on orchid
694 mycorrhiza (Jacquemyn *et al.*, 2011) and bat viruses (Luis *et al.*, 2015), but no such
695 relationship was found in arbuscular mycorrhiza (Veresoglou & Rillig, 2014) and primate
696 parasites (Cooper *et al.*, 2012). Consistent with our prediction, we found that the main factor
697 that promoted symbiont sharing in European ants was the relatedness of the hosts. It indicates
698 that many symbionts pass more easily to related host species. As related ant species employ
699 nearly identical defence structures (nestmate recognition cues, physiological and behavioural
700 defences), it enables symbionts, especially specialized parasites, to bypass the host defence
701 systems of related hosts. Another key factor that may facilitate the cross-species transmission
702 of symbionts is the overlap in geographical distribution of the hosts (*cf.* bat viruses in Luis *et*
703 *al.*, 2015). We showed that ant species living in the same biogeographical region possessed
704 more similar symbiont communities. This suggests that both the spatial overlap and similarity
705 in climatic conditions facilitate the sharing of symbionts. Sampling effort also considerably
706 explained the sharing of symbionts. More shared symbionts were reported in well-studied
707 pairs of species. Focusing on the different subsets of ant symbionts, we found that the sharing
708 of trophobionts between host ant species was mainly determined by biogeography and
709 phylogenetic relatedness. Phylogenetic relatedness of the hosts was the most important driver
710 explaining the sharing of helminths and social parasites. The strong phylogenetic effect on the
711 sharing of social parasites is directly linked to the very low taxonomic/phylogenetic distance
712 between their hosts. Social parasites target a very narrow range of host species by hijacking
713 their communication system. This exploitation of host cues is facilitated by immediate
714 common ancestry (Buschinger, 2009). The biology of most helminths is unknown, but
715 probably immune evasion is only possible in related host species. Myrmecophiles and
716 parasitic fungi were more similar in ant species residing in the same biogeographical region.
717 Climatic conditions have a strong effect on the distribution of different groups of

718 myrmecophiles. One example is the large group of myrmecophilous silverfish which are
719 mainly confined to ants living in the Mediterranean region (Molero-Baltanás *et al.* 2017;
720 Appendix S1). Interestingly, host switching of myrmecophiles and parasitic fungi was not
721 positively correlated with host relatedness (*cf.* Cooper *et al.*, 2012; Veresoglou & Rillig,
722 2014).

723

724 **V. OUTSTANDING QUESTIONS**

725 Merging different interaction types into one ecological network framework is a key challenge
726 in ecology (Fontaine *et al.*, 2011). Diverse host–symbiont communities provide an
727 opportunity to test the relative contributions of ecology and evolution to network assembly.
728 For example, our study on ant–symbiont networks revealed different roles of ecological and
729 evolutionary processes depending on the type of symbiosis. Our insights may provide a basis
730 for theory development and across-ecosystem comparisons (e.g. plant- and coral-based
731 networks) and synthesis.

732 We lack theory on how the architecture and the interaction signs and sizes jointly affect the
733 stability and productivity of these diverse networks, much in contrast to trophic or mutualistic
734 networks. The relative ease with which one can manipulate ant–symbiont communities makes
735 them suited as empirical systems to test theory.

736 Host–symbiont networks offer an opportunity to understand both ecological and evolutionary
737 processes behind community assembly, from meso- to macro-ecological scales (see Vellend,
738 2016). More specifically, as hosts occur spatially structured at these scales, it remains an open
739 question how these assembly processes are determined by ecological and evolutionary
740 limitation of dispersal. One key question is whether and how symbionts are dispersing: to
741 what degree is horizontal transfer and subsequent symbiont sharing across hosts a facilitator
742 of symbiont community assembly, and to which degree is vertical transfer, i.e. co-dispersal of

743 symbiont and host, established across the antagonism–mutualism gradient of host–symbiont
744 networks? Mutualistic plant mycorrhizal fungi and plant diaspores, for instance, are passively
745 co-dispersed by birds (Correia *et al.*, 2019). Are similar processes equally prevalent in ant–
746 symbiont interactions, for instance are symbionts transported by their host during colony
747 relocation (Parmentier, 2019)?

748 Empirical data demonstrate that different host ants coexist regionally. The stabilizing and
749 equalizing mechanisms that underpin such coexistence are at present unknown. How do the
750 complex symbiont networks in which these hosts are embedded contribute to such
751 mechanisms? Addressing such questions with new analytical tools in coexistence research
752 (Saavedra *et al.*, 2017; Spaak & De Laender, 2020) could advance our basic understanding of
753 how a variety of direct and indirect interactions affect coexistence among hosts. For example,
754 do symbionts induce indirect interactions among ant hosts? Do ant density-dependent
755 interactions between symbionts (Parmentier *et al.*, 2018) represent a stabilizing higher-order
756 interaction (Grilli *et al.*, 2017)?

757 Insights from this review are restricted and applicable to networks as characterized at the
758 species level, thereby neglecting any intraspecific variation. Following the relevance of
759 ecological and evolutionary determinants, the question remains open as to what degree co-
760 evolutionary dynamics between hosts and their symbiont community occur. As strong
761 selection may act on ant symbionts to bypass host colony defence, cryptic speciation in ant
762 symbionts is expected to be high (Schönrogge *et al.*, 2002; Zagaja & Staniec, 2015; von
763 Beeren, Maruyama & Kronauer, 2015). Symbiont populations may be adapted to an
764 individual host population as was demonstrated in the ant-parasitic syrphid fly *Microdon* and
765 the butterfly *Phengaris* (Elmes *et al.*, 1999; Tartally *et al.*, 2019). Ultimately, population
766 divergence may result in cryptic symbiont species each targeting a different host species.

767 At a higher phylogenetic level, other hymenopteran and insect lineages (Isoptera) provide
768 similar niches to nest symbionts. None of the listed ant symbionts are shared with wasps,
769 solitary and eusocial bees and termites (note that the latter two groups are poorly represented
770 in Europe). Apparently only facultative symbionts (e.g. *Porcellio scaber* in wasp and bee
771 nests for instance) or very generalist entomopathogens such as *Beauveria bassiana* are able to
772 spread across different social insect lineages, but more study is needed to understand the
773 drivers of host–symbiont divergence at these deep phylogenetic levels.

774

775 VI. CONCLUSIONS

776 (1) Ant–symbiont networks are particularly interesting to study large-scale patterns and
777 drivers in host–symbiont network topology and symbiont richness as they are extremely
778 diverse and cover the entire mutualism–antagonism continuum. We assembled a complete
779 network of ant–symbiont interactions in Europe and studied the drivers of host specificity,
780 symbiont richness and symbiont sharing in the different interaction sub-networks.

781 (2) We identified 722 ant macrosymbionts which we categorized in five types: (1)
782 myrmecophiles – commensalistic and parasitic arthropods ($N = 535$); (2) trophobionts –
783 mutualistic aphids, scale insects, plant hoppers and mutualistic Lepidoptera ($N = 80$); (3)
784 social parasites – parasitic ant species ($N = 71$); (4) parasitic helminths ($N = 22$); (5) fungi –
785 parasitic ($N = 13$) and mutualistic ($N = 1$).

786 (3) The different types of ant symbionts significantly varied in host specificity. Apart from
787 quantitative differences in host range, we also found clear differences in the average
788 taxonomic/phylogenetic relatedness of the targeted host species for the different types of ant
789 symbionts. The most species rich and best-studied ant genera generally supported the largest
790 number of symbionts, but the different types of symbionts were unevenly distributed across
791 ant genera.

792 (4) We revealed that the ecological and evolutionary factors which drive symbiont species
793 richness may shift depending on the type of symbiosis. Myrmecophile species richness is
794 mainly determined by ecological drivers, such as colony size, host range and niche width of
795 the host. By contrast, species richness of social parasites is strongly determined by the
796 evolutionary factor host phylogeny.

797 (5) Ants living in the same biogeographic region shared more symbionts. The sharing of
798 trophobionts, helminths and social parasites, in particular, was also strongly facilitated in
799 phylogenetically related hosts.

800

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806

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1772

1773 **IX. SUPPORTING INFORMATION**

1774 **Appendix S1.** Host–symbiont matrix listing the associations between ants and ant symbionts
 1775 in Europe. Ant species are listed in columns and symbionts in rows. 1, interaction recorded; 0,
 1776 no interaction recorded.

1777 **Appendix S2.** List of literature used to reconstruct the host–symbiont matrix in Appendix S1.

1778 **Appendix S3.** Host–symbiont matrix for ant hosts with known phylogeny.

1779 **Appendix S4.** Predictor values of host ant species.

1780 **Fig. S1.** Correlation between the number of described European species in an ant genus and
1781 the number of associated symbionts.

1782 **Fig. S2.** Number of host species per symbiont type.

1783 **Fig. S3.** Mean \pm SE taxonomic distance of targeted host species for different types of ant
1784 symbionts. Symbionts with a single host species were omitted from this analysis. Letter codes
1785 refer to Tukey *post-hoc* test. Symbiont types with no letters in common are significantly
1786 different ($P < 0.05$).

1787 **Fig. S4.** Mean \pm SE taxonomic distance of targeted host species for different types of ant
1788 symbionts. Taxonomic distance of symbionts with a single host species was set at 1.

1789

1790

1791 **FIGURE LEGENDS**

1792 **Fig. 1.** Distribution of different types of ant symbionts. Total number of symbionts $N = 722$,
1793 number of symbionts per type given in parentheses. Trophobionts are mutualistic, social
1794 parasites and helminths are strictly parasitic. Fungi are parasitic, except for the mutualistic
1795 species *Cladosporium myrmecophilum*. Myrmecophiles range from commensals to parasites
1796 and include parasitoid wasps and flies. Note that three mutualistic Lepidoptera species are
1797 classified as trophobionts and six parasitic and commensalistic Lepidoptera species as
1798 myrmecophiles.

1799
1800 **Fig. 2.** Ant–symbiont network displaying the proportional distribution of symbionts across the
1801 European ant genera. A multilevel pie chart is given for each ant genus. The size of the outer
1802 pie chart corresponds to the total number of associated symbionts (circle size legend in right
1803 corner). The size of the inner pie chart is related to the number of symbionts that are not
1804 shared with other ant genera (unique symbionts). The proportional distribution of the five
1805 types of ant symbionts (see Fig. 1) is given for all associated symbionts (colour segments in
1806 outer pie charts) and for the symbionts that are not shared with other genera (colour segments
1807 in inner pie charts). The relative proportion of unique symbionts can be deduced by the
1808 relative size of the inner circle to the outer circle. The genera are organized in four groups,
1809 corresponding to the ant subfamily to which they belong. The genera are connected with lines,
1810 of which the width is directly proportional to the number of shared symbionts. The font size
1811 of a genus is proportional to its number of described species in Europe.

1812
1813 **Fig. 3.** Mean \pm SE number of host species per symbiont type, controlled for sampling effort.
1814 Letter codes refer to Tukey *post-hoc* test. Species with no letters in common are significantly
1815 different ($P < 0.05$).

1816

1817 **Fig. 4.** Mean \pm SE phylogenetic distance of targeted host species (based on the phylogenetic
1818 tree of Arnan *et al.*, 2017) for different types of ant symbionts. Letter codes refer to *post-hoc*
1819 test. Symbiont types with no letters in common are significantly different ($P < 0.05$).

1820

1821 **Fig. 5.** Ranking of the predictors from the five PGLS models by the corrected Akaike
1822 information criterion (AICc). The change in AICc (Δ AICc) when adding or removing a
1823 variable from the most optimal model is compared. Predictors included in the most optimal
1824 model are removed (Δ AICc positive), whereas those not included are added (Δ AICc negative)
1825 to the best model (lowest AICc). The ranking is given for the five PGLS analyses, i.e. with
1826 dependent variable the number of symbionts (best model: ~ sample effort + colony size +
1827 distribution + habitat), myrmecophiles (best model: ~ sample effort + colony size +
1828 distribution + habitat + worker size), trophobionts (best model: ~ sample effort + habitat),
1829 social parasites (best model: ~ distribution range) and helminths (best model: ~ sample effort
1830 + habitat), respectively. Note that myrmecophiles, trophobionts, social parasites and
1831 helminths are four subsets of all ant-associated symbionts.

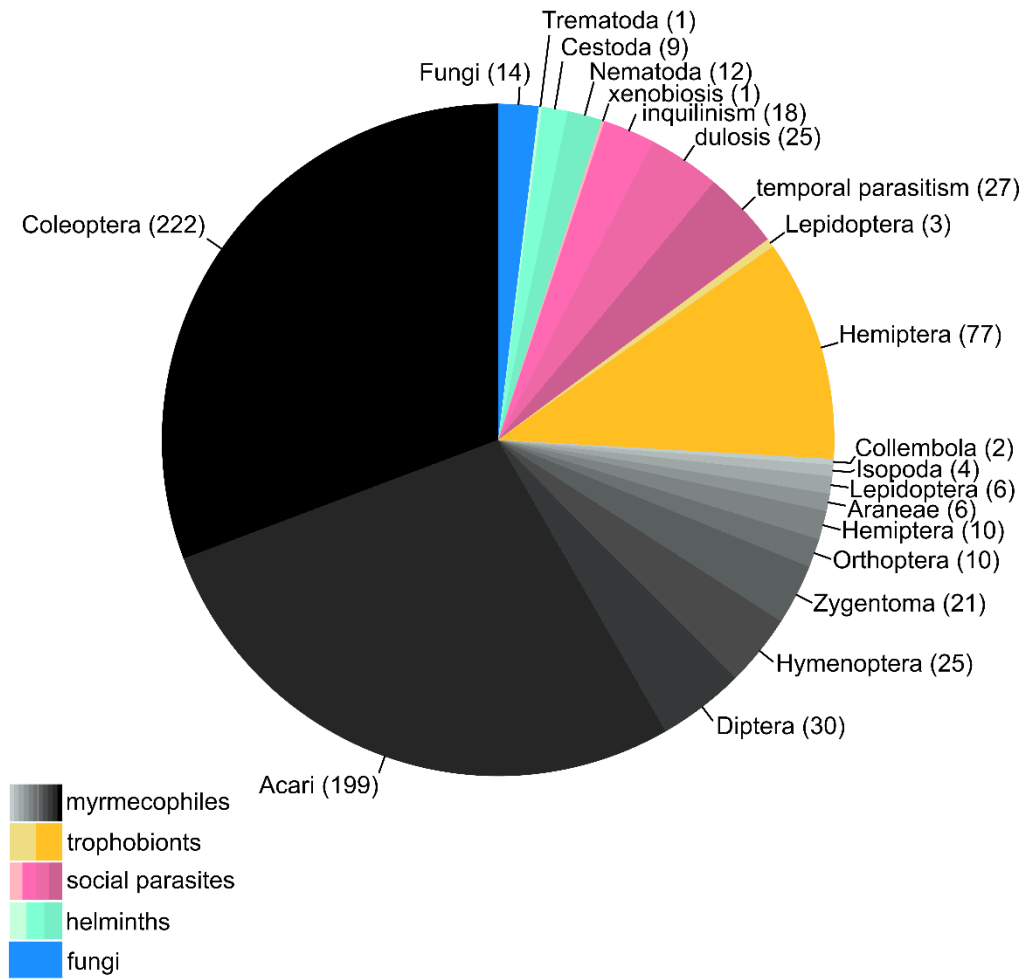
1832

1833 **Fig. 6.** Relative importance of the significant predictor matrices explaining the dissimilarity in
1834 symbiont communities across different ant species. Rankings are given for predictors
1835 explaining overall dissimilarity (1–similarity) in symbiont composition, and for dissimilarity
1836 in subsets of symbiont composition: myrmecophiles, trophobionts, social parasites, helminths
1837 and parasitic fungi, respectively. Note that myrmecophiles, trophobionts, social parasites,
1838 helminths and parasitic fungi are subsets of all ant-associated symbionts. The allocated
1839 contribution (sequential R^2) of the different distance matrices (indicated with Δ) or the matrix
1840 capturing the combined sample effort of a pair of host species to the explained variation of the

1841 MRM models is estimated with the lmg metric. The error bars are 95% confidence intervals
1842 produced using 1000 bootstrap replicates. The combined sample effort of a pair of host
1843 species was negatively correlated with their dissimilarity in symbiont composition. The
1844 dissimilarity matrices of all other predictors were positively correlated with dissimilarity in
1845 symbiont composition. Significance levels of the predictors were tested with a permutation
1846 test ($N = 9999$; ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; ·, $P < 0.10$).

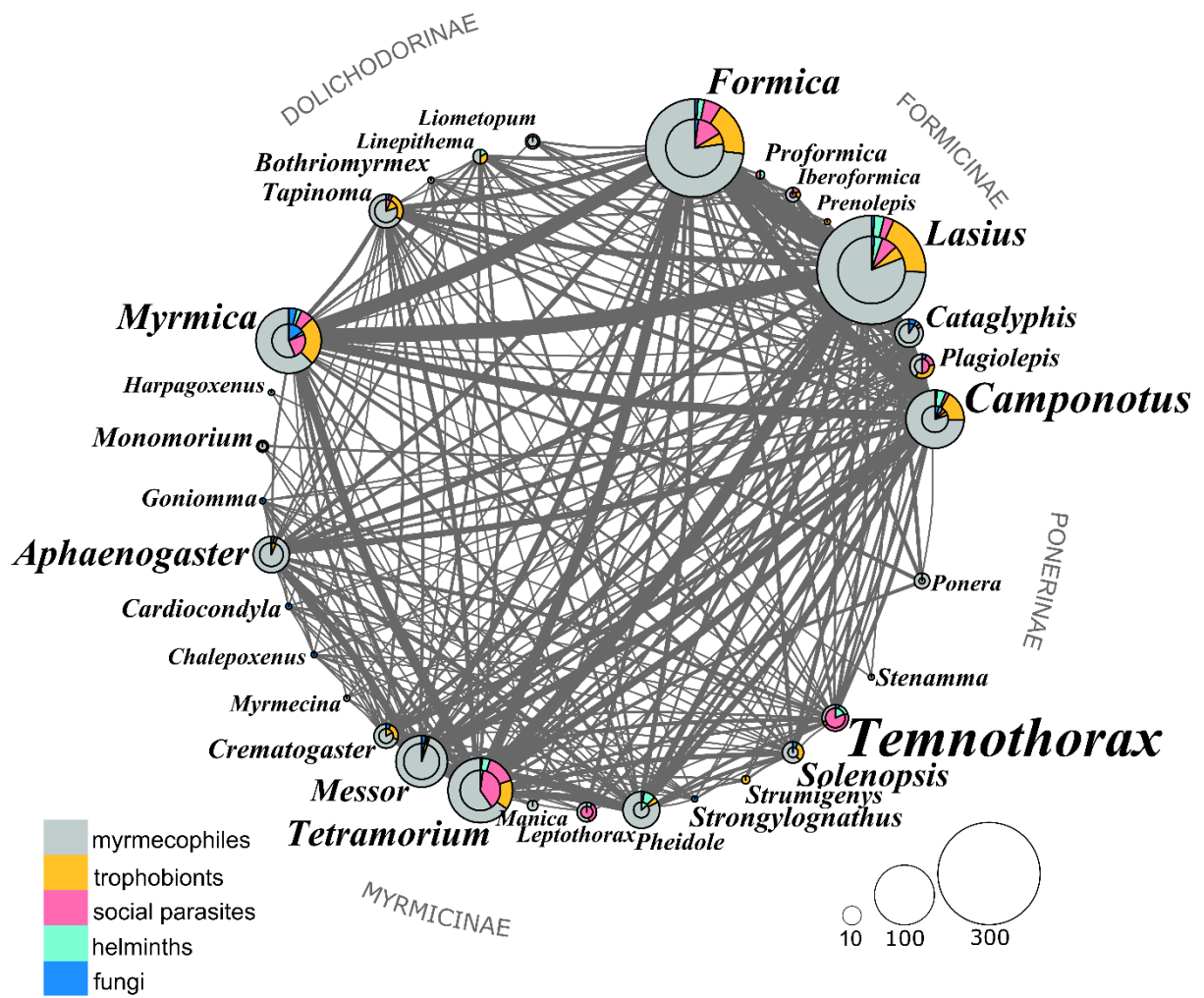
1847

1848 **FIGURES**
1849



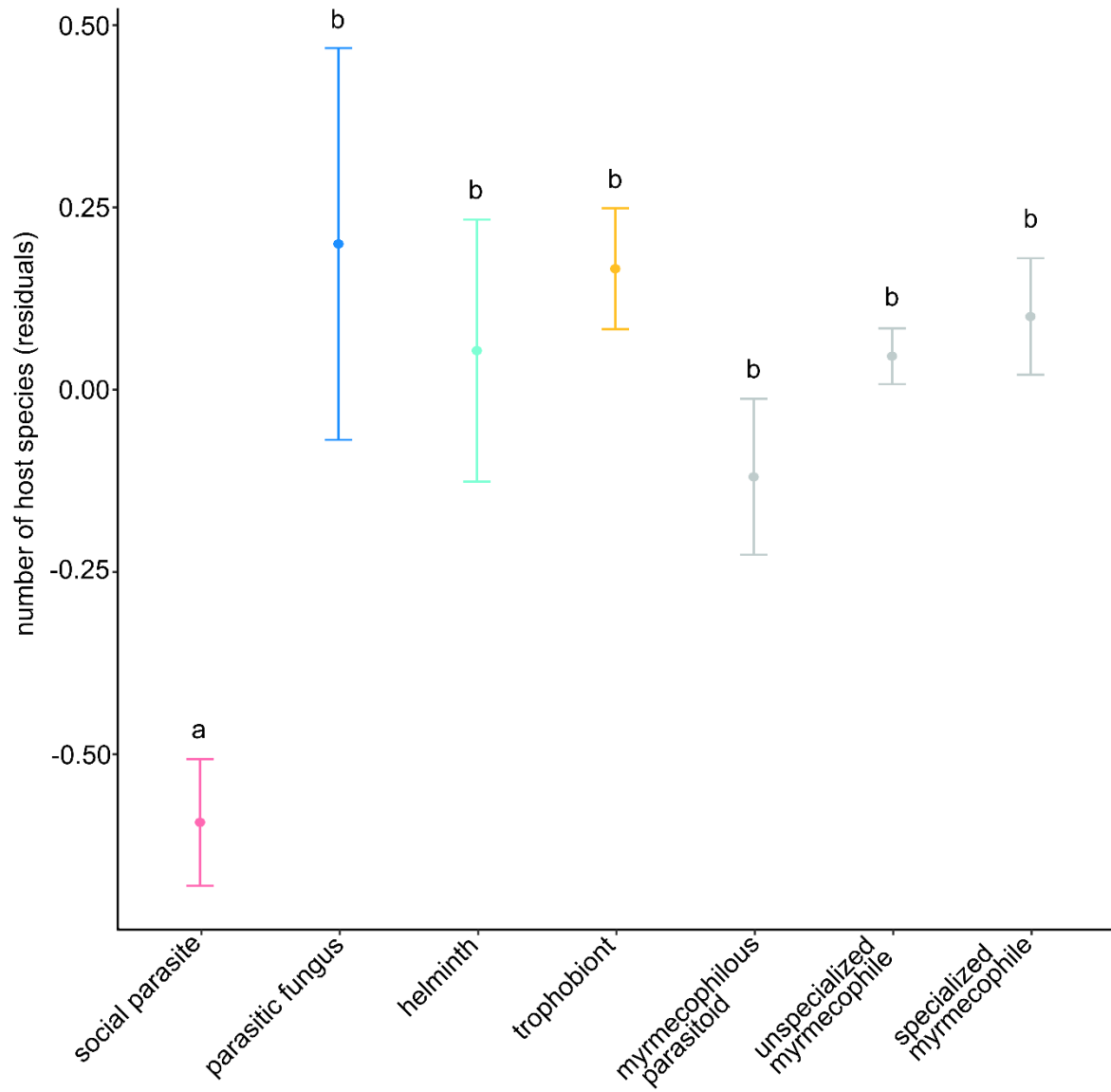
1850

1851 Fig. 1



1852

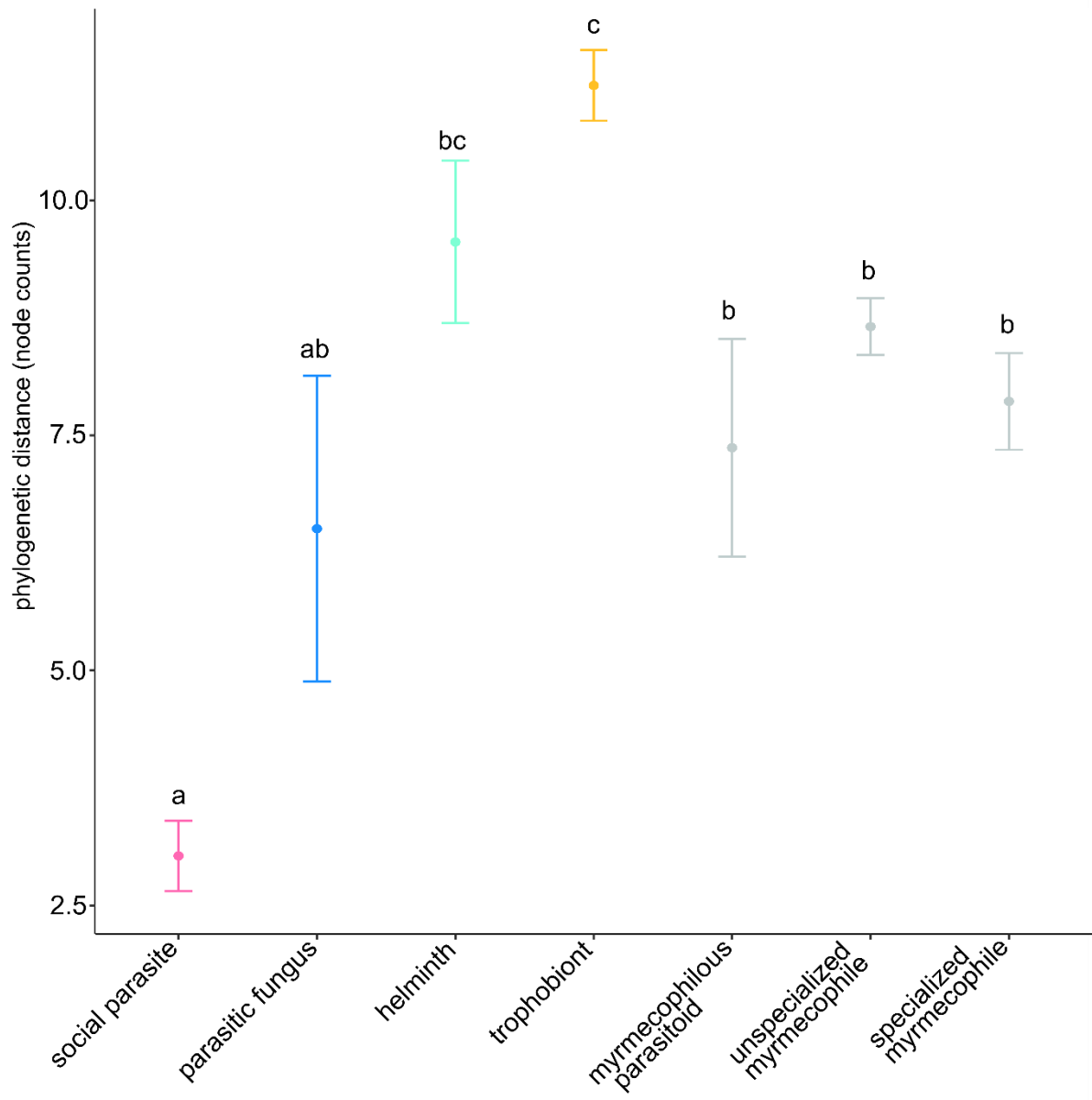
1853 Fig.2



1854

1855 Fig. 3

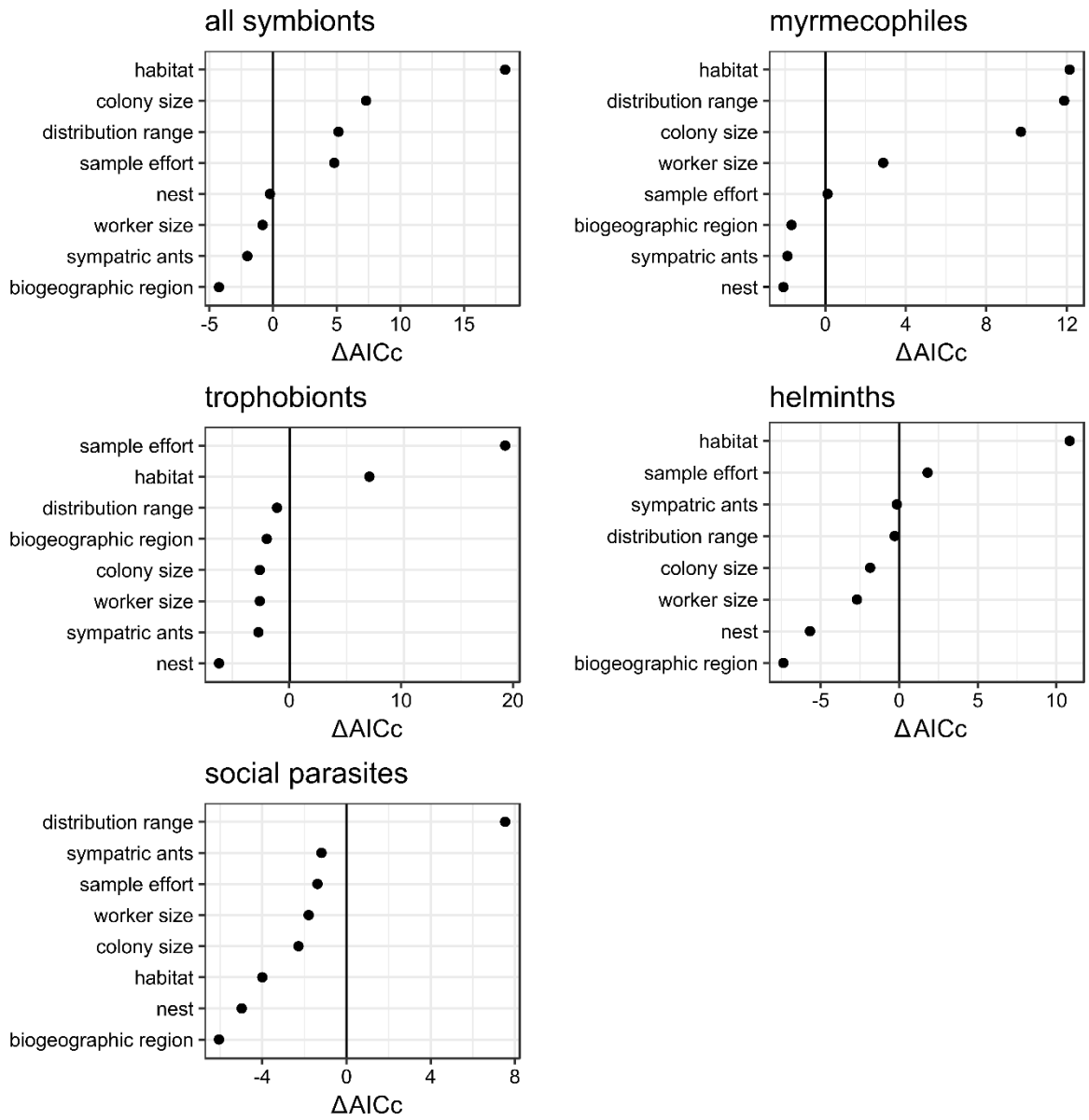
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1858 Fig. 4

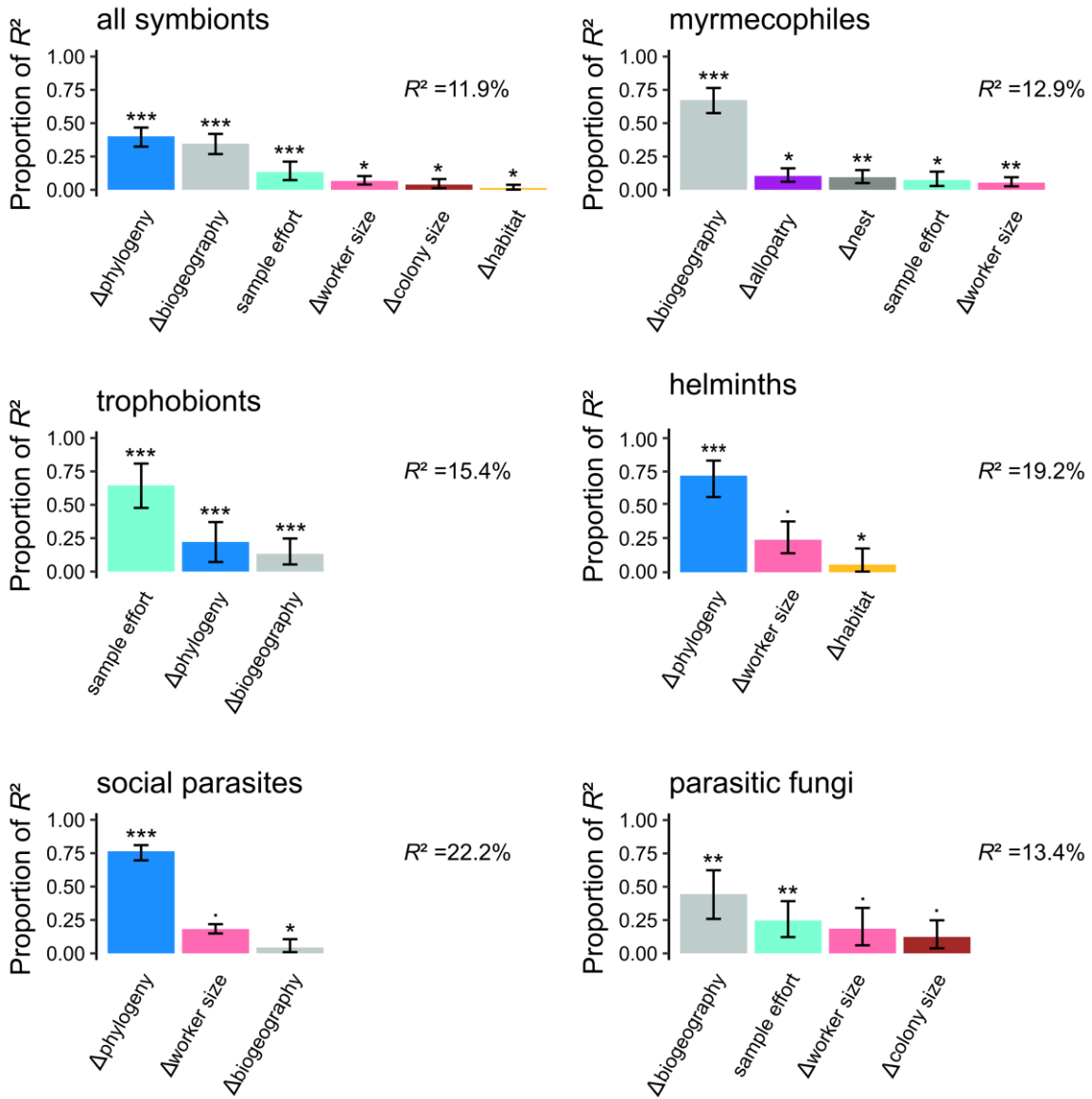
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1861 Fig. 5

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Fig. 6

1868 Table 1. Overview of the different types of ant symbionts found in Europe.

Symbiont type	General description	Representatives and strategies	Ref.
MYRMECOPHILE	A diverse group of arthropods that mostly live inside ant nests. The life strategies of these organisms range from commensalism to specialized parasitism; there are no mutualists in this group. Representatives in many arthropod orders, but beetles and mites are the most diverse. Also known as ant guests.	<ul style="list-style-type: none"> - unspecialized myrmecophiles: poorly integrated in the colony and may provoke aggression. Very similar in behaviour and morphology to free-living relatives. Do not rely on advanced chemical deception. - specialized myrmecophiles: accepted in the colony by being groomed, fed or transported. Typically possess advanced glandular structures (trichomes) or specialized behaviour to deceive the host. - myrmecophilous parasitoids: wasps and flies of which the larvae parasitize ant workers, ant larvae or possibly other myrmecophiles. Eventually kill the host. Adult parasitoids do not live in the nest. 	1–6
TROPHOBIONT	Mutualistic arthropods that provide sugary honeydew in exchange for protection and hygienic services. Mostly live outside the nest.	<ul style="list-style-type: none"> - Hemiptera: aphids, scale insects and planthoppers. - Lepidoptera: mutualistic caterpillars permanently living outside the nest. 	1
SOCIAL PARASITE	A group of ants that parasitize other ant species.	<ul style="list-style-type: none"> - xenobiosis: parasitic ants that construct a nest inside other ant nests, but raise their own brood. - temporary parasitism: a parasitic queen usurps a host colony and exploits the host work force to establish her own colony. Parasite workers gradually substitute the host worker force. - dulosis (slavery): a parasite colony is established as in temporary parasitism, but here the workers of the parasitic species will raid pupae of other ant species. Workers which will emerge from these pupae will do most of the tasks in the colony. - inquilinism: parasitic queens permanently exploit a host colony. The parasitic queen produces only sexuals, not workers. 	7
HELMINTH	Endoparasitic worms	<ul style="list-style-type: none"> - nematodes (Nematoda): the juveniles (dauers) of some groups, such as the Rhabditidae and Diplogastridae, live in the postpharyngeal glands of their ant host and are considered weak parasites. Mermithid nematodes develop in the haemocoel of the ant, may cause morphological changes in the host, and ultimately kill the host upon emergence. Other hosts, such as oligochaetes, may be necessary to complete the life cycle of mermithids. 	8–9

		<p>- flukes (Platyhelminthes: Trematoda): <i>Dicrocoelium</i> is a trematode whose definitive hosts are grassland vertebrates. The eggs are released along with the faeces and eaten by snails. Ants serve as the second intermediate host of the parasite and become infected by ingesting snail slime. The parasite induces behavioural changes in the ant which then climb to the top of grass stems where they are ingested by the definitive host.</p> <p>- tapeworms (Platyhelminthes: Cestoda): cestodes are infamous parasites that live in the digestive tract of vertebrates. These tapeworms have a life cycle with multiple hosts and ants may serve as an intermediate host.</p>	
FUNGUS	A diverse group of mainly ant-specific ecto- and endoparasites.	<p>- parasitic fungi: Laboulbeniales are ectoparasites that do not kill their host. They produce a multicellular thallus externally attached to the integument of the host ant. <i>Myrmicinosporidium durum</i> is an endoparasitic fungus which ultimately kills its host. <i>Pandora formicae</i> is a well-known entomopathogenic fungus, that manipulates its ant host to climb the vegetation. The ant attaches itself to the distal part of leaves with its mandibles and dies of the infection.</p> <p>- mutualistic fungi: <i>Cladosporium myrmecophilum</i> provides stability and structure to the carton nests of <i>Lasius fuliginosus</i>.</p>	10, 11

1869 1, Hölldobler & Wilson (1990); 2, Kronauer & Pierce (2011); 3, Elizalde *et al.* (2018); 4, Pérez-Lachaud *et al.* (2019); 5, Parmentier (2020); 6, Kistner (1982); 7, Buschinger
1870 (2009); 8, Poinar (2012); 9, Demartin (2018); 10, Espadaler & Santamaria (2012); 11, Maschwitz & Hölldobler (1970).

1871 Table 2. Estimates for the predictors of the top-ranked PGLS analyses ($\Delta AICc < 2$). The subset of best models is given for the analyses with total
 1872 number of (1) symbionts, (2) myrmecophiles, (3) trophobionts (4) social parasites and (5) helminths as dependent variable. Significant estimates
 1873 indicated in bold (***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; †, $P < 0.10$).
 1874

	intercept	colony size	sample effort	biogeo graphy	distribution	habitat	sympatric ants	nest type	worker size	d.f.	AICc	weight	lambda
all symbionts													
	6.48	0.82***	0.89**		0.70***	+***				7	375.3	0.33	0.54
	7.93	0.71***	0.84**		0.74***	+***		+		10	375.5	0.30	0.52
	6.85	0.82***	0.82**		0.77***	+***			0.31	8	376.0	0.22	0.44
	8.20	0.70***	0.77**		0.80***	+***		+	0.26	11	376.8	0.15	0.41
myrmecophiles													
	6.29	0.81***	0.43		0.95***	+***			0.45*	8	299.0	0.31	0.00
	6.64	0.94***			1.17***	+***			0.46*	7	299.1	0.29	0.00
	7.95	0.75***			1.20***	+***		+	0.44*	10	300.4	0.15	0.00
	7.56	0.57***	0.66*	+***	0.80***	+***			0.57*	12	300.7	0.13	0.32
	6.21	0.81***	0.45		1.10***	+***	-0.22		0.42*	9	300.9	0.12	0.00
trophobionts													
	2.93		0.77***			+***				5	131.2	0.42	0.73
	3.14		0.64***		0.20***	+***				6	132.3	0.24	0.60
	3.52	0.22**	0.42*		0.31***	+***				7	133.0	0.18	0.36
	3.06	0.11**	0.26***			+***				6	133.2	0.16	0.68
social parasites													
	1.34				0.27**					2	75.5	0.23	1.00
	1.19		0.26**							2	75.9	0.19	1.00
	1.25						0.22**			2	76.4	0.15	0.83
	1.30				0.17**		0.11			3	76.7	0.12	0.94
	1.27		0.13		0.16**					3	76.9	0.11	1.00
	1.21		0.16**				0.11			3	76.9	0.11	0.93
	1.29				0.26**				-0.10	3	77.3	0.09	0.98
helminths													
	1.81		0.14*			+***				5	31.7	0.18	0.91
	1.83		0.11*			+***	0.10			6	31.8	0.16	0.88
	2.01					+***	0.13*			5	31.9	0.16	0.85
	1.87		0.11		0.11**	+***				6	32.0	0.15	0.88
	2.07				0.14**	+***				5	32.1	0.14	0.87

2.07				+***		4	33.5	0.07	0.88
1.82	-0.06	0.16*		+***		6	33.5	0.07	0.94
1.83	-0.07	0.14*		+***	0.10	7	33.5	0.07	0.94

1875