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The topology and drivers of ant-symbiont networks across Europe

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

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

We found 722 macrosymbionts (multicellular symbionts) associated with European ants. 30 31 Symbiont type explained host specificity and the average relatedness of the host species. Social parasites were associated with few hosts that were phylogenetically highly related, 32 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 affected diversity in the different types of symbionts. Ecological factors, such as colony size, 38 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 related hosts also shared more trophobionts, social parasites and helminths, but not 43 44 myrmecophiles.

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

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77 I. INTRODUCTION

Close associations between different species, known as symbioses, are crucial components of 78 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 functioning (Thrall et al., 2007; Bastolla et al., 2009). To date, insights are derived from 86 87 theory and empiricism focusing on either competition and predator-prey interactions (e.g. Hairston, Smith & Slobodkin, 1960; Pimm, 1979; Tilman, 1982) or more recently mutualistic 88 89 interactions (Bascompte, Jordano & Olesen, 2006; Bascompte & Jordano, 2007; Barabás, D'Andrea & Stump, 2018; Johnson & Bronstein, 2019; Spaak & De Laender, 2020). 90 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 predict from the specific (isolated) pairwise interactions (Vázquez, Chacoff & Cagnolo, 2009; 96 97 Grilli et al., 2017). Generally speaking, modular networks that are characterized by a high connectance tend to be more robust to species loss, and are less affected by disturbance (Solé 98 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

predators per prey) and generality (i.e. the average number of prey eaten per predator) link the
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).

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

Host species may be conceptualized as island habitats for symbionts and, in line with island 149 150 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).

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

controlled nest fortresses and the high number of available resources in the nest (Kronauer & 174 175 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 (Hölldobler & Wilson, 1990). Therefore, they are promising systems to study different 178 179 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

symbionts. Secondly, we follow a trait-based host perspective to identify the major drivers
that promote the diversity of ant-symbiont interactions and facilitate symbiont sharing. We
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,

nest type, distribution, habitat, degree of sympatry, worker size) and evolutionary drivers
(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).

Plants engaging in mutualistic relationships (e.g. myrmecochory) were not included in our
analyses. Contrary to the tropics, ant–plant relationships tend to be loose in Europe and are at
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. Wasmann, 1894; Donisthorpe, 1927; Evans & Till, 1966; Uppstrom, 2010; Tykarski, 2017; 232 233 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 phase, each symbiont occurring in Europe was searched by its Latin binomial name and its 237 238 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) between ants (columns) and symbionts (rows). We included some references on ant-248

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

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

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

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

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

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 (2003). Host ant species (all ants belong to the family Formicidae) were classified following 275 276 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

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

PGLS model was based on these 96 ant species (Appendix S4). This data set reduction is 348 349 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 expected degree of phylogenetic covariance (Pagel, 1999). This multiplier spans from 0, 352 353 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 In-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 (In-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 of ants occupy the same habitat, nest type or biogeographic region, respectively, and 1 when 396

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 the literature record. The distribution of the number of host species per symbiont was right-426 427 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 Proatelurina pseudolepisma.

European ant genera contained a highly variable number of species (proportional to the genus

430

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).



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 top-ranking models (Table 2, Fig. 5). Habitat and distribution range of the host were also 475 476 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 (Δ 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 European ant data set were phylogenetic relatedness of the ant hosts (MRM, lmg = 0.40, P < 0.40503 504 0.001) and similarity in biogeographic region (MRM, proportional contribution to the total r^2 = lmg = 0.35, P < 0.001) (Fig. 6). Similarities in worker size (lmg = 0.07, P = 0.01), colony 505 506 size (lmg = 0.04, P = 0.02) and habitat (lmg = 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, lmg = 0.13, P < 0.001). Well-studied ant pairs also shared more trophobionts, 509 myrmecophiles and parasitic fungi (MRM-analyses, lmg 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, lmg = 0.22, P < 0.001 and lmg =512 0.13, P < 0.001, respectively). The similarities in social parasite communities was largely 513 explained by phylogenetic relatedness (MRM, lmg = 0.76, P < 0.001). Similarities in 514 biogeography (MRM, lmg = 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, lmg = 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, lmg

519 = 0.68, P < 0.001), Lastly, ants in the same biogeographic region tend to share more parasitic 520 fungi (MRM, lmg = 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.

Mutualistic ant symbionts are thus clearly overshadowed by the diversity of commensalistic 544 545 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 are known to be predatory (e.g. *Temnothorax*, *Cataglyphis*) or granivorous (e.g. *Messor*) 557 558 (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

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

Patterns in host specificity have been studied in a wide range of host-symbiont systems. 569 570 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 average. Trophobionts were associated with the most distantly related ant species. 594 595 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

additionally determined by more regional ecological factors like range size and niche width of
the host ants. In that respect, eurytopic ants, such as *Lasius niger* and *Myrmica rubra* that can
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

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

Host density has widely been demonstrated as a key factor explaining parasite species

646

richness (Lindenfors *et al.*, 2007). Interestingly, we found that species with larger workers engaged with more myrmecophiles than ant species with small workers. This pattern in myrmecophile diversity was previously hypothesized based on experimental work, showing that the survival of three myrmecophilous beetles gradually increased in laboratory nests of larger ant species (Parmentier, Dekoninck & Wenseleers, 2016*b*). This positive relationship between ant size and myrmecophile diversity suggests that species with small workers detect, 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

myrmecophiles. One example is the large group of myrmecophilous silverfish which are
mainly confined to ants living in the Mediterranean region (Molero-Baltanás *et al.* 2017;
Appendix S1). Interestingly, host switching of myrmecophiles and parasitic fungi was not

positively correlated with host relatedness (cf. Cooper et al., 2012; Veresoglou & Rillig,

722 2014).

723

724 V. OUTSTANDING QUESTIONS

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

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

736Host-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

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
- what degree is horizontal transfer and subsequent symbiont sharing across hosts a facilitator
- 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

(Saavedra *et al.*, 2017; Spaak & De Laender, 2020) could advance our basic understanding of

how a variety of direct and indirect interactions affect coexistence among hosts. For example,

do symbionts induce indirect interactions among ant hosts? Do ant density-dependent

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.

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

774

775 VI. CONCLUSIONS

(1) Ant–symbiont networks are particularly interesting to study large-scale patterns and

drivers in host–symbiont network topology and symbiont richness as they are extremely

diverse and cover the entire mutualism–antagonism continuum. We assembled a complete

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.

(2) We identified 722 ant macrosymbionts which we categorized in five types: (1)

myrmecophiles – commensalistic and parasitic arthropods (N = 535); (2) trophobionts –

mutualistic aphids, scale insects, plant hoppers and mutualistic Lepidoptera (N = 80); (3)

social parasites – parasitic ant species (N = 71); (4) parasitic helminths (N = 22); (5) fungi –

785 parasitic (N = 13) and mutualistic (N = 1).

(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

taxonomic/phylogenetic relatedness of the targeted host species for the different types of ant

symbionts. The most species rich and best-studied ant genera generally supported the largest

number of symbionts, but the different types of symbionts were unevenly distributed across

ant genera.

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

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

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801 VII. ACKNOWLEDGEMENTS

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- 1772

1773 IX. SUPPORTING INFORMATION

- 1774 Appendix S1. Host–symbiont matrix listing the associations between ants and ant symbionts
- 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
- the number of associated symbionts.
- 1782 Fig. S2. Number of host species per symbiont type.
- 1783 Fig. S3. Mean ± 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 ± 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

1791 FIGURE LEGENDS

1792Fig. 1. Distribution of different types of ant symbionts. Total number of symbionts N = 722,1793number of symbionts per type given in parentheses. Trophobionts are mutualistic, social1794parasites and helminths are strictly parasitic. Fungi are parasitic, except for the mutualistic1795species *Cladosporium myrmecophilum*. Myrmecophiles range from commensals to parasites1796and include parasitoid wasps and flies. Note that three mutualistic Lepidoptera species are1797classified as trophobionts and six parasitic and commensalistic Lepidoptera species as1798myrmecophiles.

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 shared with other ant genera (unique symbionts). The proportional distribution of the five 1804 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

1813Fig. 3. Mean \pm SE number of host species per symbiont type, controlled for sampling effort.1814Letter codes refer to Tukey *post-hoc* test. Species with no letters in common are significantly1815different (P < 0.05).

1817

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), social parasites (best model: ~ distribution range) and helminths (best model: ~ sample effort 1829 1830 + habitat), respectively. Note that myrmecophiles, trophobionts, social parasites and

Fig. 4. Mean \pm SE phylogenetic distance of targeted host species (based on the phylogenetic

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 capturing the combined sample effort of a pair of host species to the explained variation of the 1840

- 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

FIGURES 1849





1851 Fig. 1



1853 Fig.2















TABLES

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.	 <u>unspecialized myrmecophiles</u>: 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. <u>specialized myrmecophiles</u>: accepted in the colony by being groomed, fed or transported. Typically possess advanced glandular structures (trichomes) or specialized behaviour to deceive the host. <u>myrmecophilous parasitoids</u>: 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.	 <u>Hemiptera</u>: aphids, scale insects and planthoppers. <u>Lepidoptera</u>: mutualistic caterpillars permanently living outside the nest. 	1
SOCIAL PARASITE	A group of ants that parasitize other ant species.	 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	 <u>nematodes (Nematoda)</u>: 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

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

		 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. <u>tapeworms (Platyhelminthes: Cestoda)</u>: 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. 	
FUNGUS e	A diverse group of mainly ant-specific ecto- and endoparasites.	 <u>parasitic fungi</u>: 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. <u>mutualistic fungi</u>: <i>Cladosporium myrmecophilum</i> provides stability and structure to the carton nests of <i>Lasius fuliginosus</i>. 	10, 11

1870 (2009); 8, Poinar (2012); 9, Demartin (2018); 10, Espadaler & Santamaria (2012); 11, Maschwitz & Hölldobler (1970).

1871Table 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 total1872number 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).

	intercept	colony size	sample effort	bioge graph	distribution	habitat	t ^{sympatric} ants	nest type	worker size	d.f.	AICc	weigh	t 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