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Parmentier T[1,2,3], De Laender F[3], Wenseleers T[2], Bonte D[1]

[1] Terrestrial Ecology Unit (TEREC), Department of Biology, Ghent University, K.L. Ledeganckstraat 35, B-9000 Gent, Belgium

[2] Laboratory of Socioecology and Socioevolution, KU Leuven, Naamsestraat 59, B-3000 Leuven, Belgium

[3] Research Unit of Environmental and Evolutionary Biology, Namur Institute of Complex Systems, and Institute of Life, Earth, and the Environment, University of Namur, Rue de Bruxelles 61, 5000 Namur, Belgium

*Correspondence: Thomas.Parmentier@ugent.be

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22 **Abstract**

23 Indirect interactions occur when a species affects another species by altering the density

24 (density-mediated interactions) or influencing traits (trait-mediated interactions) of a third

25 species. We studied variation in these two types of indirect interactions in a network of red

26 wood ants and symbiotic arthropods living in their nests. We tested whether the ant workers

27 indirectly affected survival of a symbiotic prey species (*Cyphoderus albinus*) by changing the

28 density and/or traits of three symbiotic predators, i.e. *Mastigusa arietina*, *Thyreosthenius*

29 *biovatus* and *Stenus aterrimus*, provoking respectively low, medium and high ant aggression.

30 An ant nest is highly heterogeneous in ant worker density and the number of aggressive

31 interactions towards symbionts increase with worker density. We therefore hypothesized that

32 varying ant density could indirectly impact prey-predator interactions of the associated

33 symbiont community.

34 Ants caused trait-mediated indirect effects in all three prey-predator interactions, by affecting

35 the prey-capture rate of the symbiotic predators at different worker densities. Prey capture rate

36 of the highly and moderately aggressed spider predators *M. arietina* and *T. biovatus* decreased

37 with ant density, whereas the prey capture rate of the weakly aggressed beetle predator *S.*

38 *aterrimus* increased. Ants also induced density-mediated indirect interactions as high worker

39 densities decreased the survival rate of the two predatory spider species.

40 These results demonstrate for the first time that a host can indirectly mediate the trophic

41 interactions between associated symbionts. In addition, we show that a single host can induce

42 opposing indirect effects depending on its degree of aggression towards the symbionts.

43

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Introduction

Community dynamics are propelled by a complex set of antagonistic, neutral and mutualistic interactions. Direct interactions as found in symbiosis and predation have been traditionally studied to understand the structuring of communities. However, theoretical and empirical evidence increasingly show that indirect interactions are abundant and strongly shape community dynamics as well (Strauss 1991; Wootton 1994; Guimarães et al. 2017). Indirect interactions between two species arise when the effect of one species on another is mediated by a third species. Indirect effects can be subdivided into two categories. Density-mediated indirect effects arise when a species indirectly affects another by changing the survival of a third species (Abrams et al. 1996). A typical example is a predator that indirectly promotes the growth of plants by decreasing the density of herbivores (Hebblewhite et al. 2005). Trait-mediated indirect effects, on the other hand, emerge when a species affects another species by altering the foraging behavior, refuge use, physiology or other traits of a third species (Abrams et al. 1996; Werner and Peacor 2003).

Indirect interactions are at the heart of food web dynamics by mediating both consumptive and competitive interactions (Abrams et al. 1996; Werner and Peacor 2003). A diverse array of key ecological processes such as trophic cascades, trait-mediated cascades and competition are induced by indirect interactions (Abrams et al. 1996; Levine et al. 2017). Ultimately, these types of interactions have a structuring role in communities and may promote species coexistence (van Veen et al. 2005; Levine et al. 2017).

While the study of indirect interactions is tightly linked with food web networks, a cumulative number of studies also recorded them in host-symbiont networks (Dunn et al. 2012; Guimarães et al. 2017). Symbionts are species that live in close association with a host on which they may have beneficial, neutral or adverse effects. Indirect effects between species may govern to a large degree coevolution in mutualistic networks (Guimarães et al. 2017). Guimarães et al.

72   (2017) showed that large and nested mutualistic networks are expected to have more indirect

73   effects than small and modular networks shaped by specialized mutualisms. Empirical studies

74   on indirect interactions in host-symbiont networks typically reported that these interactions

75   could alter the competitive outcome of two susceptible hosts (Hambäck et al. 2006; van

76   Nouhuys and Kraft 2012) or of two competing parasites (Waage and Davies 1986; Bush and

77   Malenke 2008; Lebrun et al. 2009). Host-mediated competition between two parasites was for

78   example found in two feather-feeding lice in which the magnitude of competition was

79   dependent on the defense (preening) of the host bird (Bush and Malenke 2008). Indirect effects

80   can also mediate trophic interactions rather than competitive interactions in this type of

81   networks as demonstrated in symbiont communities associated with pitcher plants (terHorst

82   2010).

83

84   Red wood ants (*Formica rufa* group) also form such host-symbiont networks. These

85   widespread ants are keystone arthropods in European forest ecosystems (Gösswald 1989;

86   Stockan et al. 2016). They exert wide-range effects on the forest fauna and flora and drive

87   biogeochemical processes (Wardle et al. 2011). The above ground part of a red wood ant nest

88   is a conspicuous mound of organic thatch (Rosengren et al. 1987), which is tightly regulated

89   and provides an ideal habitat for a diverse community of associated symbionts, known as

90   myrmecophiles (Parmentier et al. 2014). The majority of these red wood ant myrmecophiles

91   directly interact with their host by feeding on their eggs and larvae and stealing prey carried

92   into the nest (Parmentier et al. 2016a). In addition, many red wood ant myrmecophiles hunt on

93   smaller myrmecophiles in the red wood ant nest microcommunity (Parmentier et al. 2016a).

94   Ants also directly interact with their myrmecophile guests. If detected, ants try to deter or hurt

95   them by showing aggression. Red wood ants show a highly variable degree of aggression

96   towards myrmecophiles ranging from almost complete ignorance to heavy persecution,

97   depending on the identity of the myrmecophile species (Parmentier et al. 2016b). In addition,

98   the aggression response will be more prominent in densely crowded chambers in the nest,

99   such as the chambers with brood, compared to the nest periphery, because of an increase in

100   aggressive events and fewer opportunities to hide. Interestingly, myrmecophiles show

101   preferences for particular nest locations and corresponding worker densities (Parmentier et al.

102   2016b), likely reflecting their tolerance to different degrees of ant aggression.

103   We thus anticipate the density of red wood ant workers to indirectly affect the survival of a

104   myrmecophilous prey species by altering the behavior or survival of its myrmecophilous

105   predator. Red wood ants vary greatly in their degree of aggression towards different

106   myrmecophilous predators. The prey capture rate of those predators is as a result expected to

107   change differently with increasing worker densities. We compared the effect of worker density

108   on the prey capture rate among three different myrmecophilous predators, i.e. the rove beetle

109   *Stenus aterrimus* Erichson, 1839 and the spiders *Thyreosthenius biovatus* (O. Pickard-

110   Cambridge, 1875) and *Mastigusa arietina* (Thorell, 1871). They provoke respectively low,

111   medium and high levels of ant aggression (Parmentier et al. 2016b). The myrmecophilous

112   springtail *Cyphoderus albinus* Nicolet, 1842 was used as the shared prey of the three

113   myrmecophilous predators (Fig. 1). The increase of aggressive events caused by increased

114   worker densities will likely change the behavior of persecuted myrmecophilous predators,

115   whereas the behavior of myrmecophilous predators that provoke little or no aggression is

116   expected not to alter (Fig. 1). Therefore we hypothesized that increasing worker densities

117   would have the strongest negative effect on the prey capture rate of the myrmecophilous

118   predator that provoked the highest degree of aggression.

Material & Methods

Study system and sampling

119   Myrmecophiles, ant workers, and organic nest material were repeatedly collected in a colony

122   of the red wood ant *Formica rufa* Linnaeus, 1761 in Boeschepe, France, from June until

123   September 2017. This supercolony was headed by many queens (polygynous) and consisted

124   of multiple mounds which constantly exchanged workers and resources (polydomous).

125   Myrmecophiles were collected by spreading out nest material into a large plastic tray. The

126   white springtail *Cyphoderus albinus* is an obligate ant symbiont that may reach high densities

127   in ant nests (Parmentier et al. 2015). Ant workers pay little or no attention to its presence

128   (Parmentier et al. 2016b). This springtail is likely to be the principal prey for many

129   myrmecophilous predators and was therefore used as the myrmecophilous prey in the

130   experiment (Parmentier et al. 2016a). We selected three predators which were obligate ant

131   symbionts as well. *Stenus aterrimus* is a rove beetle specialized to capture springtails (Koerner

132   et al. 2012). Ants show weak rates of aggression (aggression in 13% of encounters; see

133   Parmentier et al. 2016a) towards this species and are distributed throughout the nest

134   (Parmentier et al. 2016b). The two other selected predators were the spiders *Thyreosthenius*

135   *biovatus* and *Mastigusa arietina*. The former can be found throughout the nest and is

136   occasionally attacked (aggression in 24% of encounters), whereas the latter is strongly

137   persecuted (aggression in 73% of encounters) and is restricted to the sparsely occupied

138   periphery of the nest (Parmentier et al. 2016b). The three tested myrmecophilous predators

139   predate on the springtail and interact with their host by kleptoparasitism and brood predation

140   (so far only recorded for *T. biovatus* and *M. arietina*, Parmentier et al. 2016a). The ants do not

141   predate on the myrmecophilous predators and prey, but only negatively interact with them by

142   an aggression response.

143   Ant workers were kept in a container with a plaster-filled bottom and given access to water and

144   sugar water ad libitum prior to the experiment. The myrmecophilous prey *C. albinus* was

145   cultured in a container with organic nest material and some hundreds of workers of the

146 supercolony. Myrmecophilous predators were individually placed in small snap-lid containers

147 (diameter 4.5 cm) filled with moistened plaster in the lab. Next, we offered to all predators three

148 *C. albinus* prey to level out differences in feeding status. Subsequently, the beetle *S. aterrimus*

149 and the spider *M. arietina* were starved for a period of 4 days and the spider *T. biovatus* for 10

150 days. We opted for a longer starvation period in *T. biovatus,* as the proportion of surviving prey

151 in presence of *T. biovatus* starved for four days (mean = 0.92, *N* = 10) was close to prey

152 survival without predators. Starving *T. biovatus* for a period of 10 days considerably increased

153 its prey capture rate. Nest material was stored in a freezer (-21 °C) to kill tiny and hidden

154 organisms such as mites, and which could potentially serve as additional prey for the

155 myrmecophilous predators. We reconciled the extensive search effort to find the relatively rare

156 predators with the need for a high number of replicates, by reusing the predators in subsequent

157 trials. Before using a predator again, it was first re-isolated, fed with three individuals of *C.*

158 *albinus* prey and starved as before. All spider individuals were female.

159 *Experiment: Prey-predator interactions under different worker densities*

160 We aimed with this experiment to test the effect of increasing density of ant workers on the

161 prey capture success of symbiotic predators (Fig. 1). The experiment was done in plastic

162 containers (diameter 5 cm, height = 5.5 cm) with a 1-cm bottom of plaster of Paris. The side of

163 the container was coated with fluon to prevent ants and myrmecophiles to climb on. The

164 container was closed with a lid in which there was a hole (diameter 2 cm) covered with fine

165 mesh. This prevented myrmecophiles from escaping by rare flying (*S. aterrimus)* or jumping

166 events (*C. albinus*). Approximately 5 mL of the defrosted organic material was then added to

167 the container together with 5 fully grown individuals of *C. albinus* collected in the stock colony.

168 The nest material and plaster was moistened. As we wanted to test prey-predation under

169 differing worker densities, we assigned 0 (0W: control), 5 (5W: low density), 15 (15W: medium

170 density) or 45 (45W: high density) ant workers to a container. Finally, one starved predator

171 individual of *S. aterrimus, T. biovatus* or *M. arietina* was introduced (Fig. 2). The introduction

172 of the predator in the container was approximately 30 min. later than the prey giving the latter

173 time to hide. After 48h, the number of surviving prey individuals out of 5 was recorded. To test

174 the effect of predation, we need to control for natural mortality of the prey. Therefore we

175 counted the number of prey out of 5 that survived without predators under the 4 levels of worker

176 density (number of replicates: 0W = 37, 5W = 39, 15W = 37, 45W = 40). All containers were

177 kept at 20-22 °C in complete darkness. The experiment was conducted from July until October

178 2017. The number of trials for each treatment is summarized in Table 1. We did not test the

179 effect of 45 workers on the prey capture rate and survival of *M. arietina*. In 4 preliminary tests

180 with this species, all individuals died within a couple of hours. The spider is expected not to

181 survive these stressful conditions, which was already suggested by another lab experiment

182 (Parmentier et al. 2016b). As it was difficult to obtain large numbers of *M. arietina*, we chose

183 to allocate the spiders only to 0W, 5W and 15W to assess their prey capture rate.

184

185 *Statistical analyses*

186 <u>Myrmecophile survival under different levels of worker density</u>

187 In some trials, predators were dead before the end of the 48h test period. This could be

188 explained by natural mortality, starvation, through increased stress or inflicted injuries by the

189 ants (Parmentier 2016). The effect of ant worker density on predator survival was compared

190 by calculating the proportion of trials in which the predator survived. Here, we only based on

191 trials in which the predator was used for the first time so that the exposure time to the ants was

192 comparable. We compared pairwise the effect of different levels of ant density on predator

193 survival by employing Fisher exact tests and subsequently controlled the false discovery rate

194 of the corresponding P-values using the Benjamini-Hochberg (BH) procedure (Benjamini and

195 Hochberg 1995).

196 To test the effect of ant density on the proportion of surviving *Cyphoderus albinus* in absence

197 of predators, a quasibinomial error distributed (to account for overdispersion) GLM was used

198   with logit link function. We assessed the significance of these baseline data with a likelihood-

199   ratio test using the 'Anova' function of the R-package car (Fox and Weisberg 2011).

200   <u>Prey-predator interactions under different worker densities</u>

201   Capture success under different worker densities was based on trials where the predators

202   survived until the end. One trial was excluded, because the predator was visibly hurt at the

203   end and which may have affected its prey capture success. In all other trials, predators showed

204   normal behavior at the end. For each predator separately, we modelled the proportion of

205   surviving prey under different densities of ant workers using a GLMM (generalized linear mixed

206   model) with binomial error distribution and logit link function. Treatment (= different levels of

207   worker ant density: 0 workers, 5 workers, 15 workers and 45 workers) was included as a fixed

208   factor. To account for re-using predator individuals in subsequent trials (max. 4 trials per

209   individual), we included predator identity as a random factor. This factor was nested in

210   treatment as an individual was always exposed to the same treatment level (i.e. identical

211   worker ant density) in all of its replicates. We also added an observation level random factor

212   to correct for overdispersion (Browne et al. 2005). The GLMMs were run using the 'glmer'

213   function in R-package lme4 (Bates et al. 2015) and significance was tested using a likelihood-

214   ratio test implemented in the 'Anova' function of the R-package car (Fox and Weisberg 2011).

215   Subsequently, the different levels of ant density in these GLMM-models were pairwise

216   compared with the glht function of the 'multcomp' package (Hothorn et al. 2008). Within each

217   series of pairwise tests, we controlled the false discovery rate using the BH-procedure.

218

Results

Myrmecophile survival under different levels of worker density

The prey *Cyphoderus albinus* was rarely noticed by the host ant and freely foraged in the nest material. Survival of this species was correspondingly very high after 48h across all treatments. It was seemingly not affected by the presence of ants, ranging from low to high density of ant workers (quasibinomial GLM, Chisq = 3.60, *P* = 0.31; Fig. 3). Survival rate of the predator *Stenus aterrimus* was high and equal across different levels of ant density (*P-values* of 6 BH corrected Fisher Exact tests *P* = 1.00, proportions survivals see Table 1). Survival of the predator *Thyreosthenius biovatus* declined with increasing worker density (Table 1, Fig. 3), but the 6 pairwise BH corrected Fisher Exact tests were not significantly different. Survival of the spider *Mastigusa arietina* steeply declined with increasing worker density (Table 1, Fig. 3). Survival at medium worker densities (15 workers) was significantly lower than survival without ants (BH corrected Fisher Exact test *P* = 0.002) and survival at low (5 workers) worker densities (BH corrected Fisher Exact test *P* = 0.029).

Prey-predator interactions under different worker densities

To compare prey capture rate among predators and worker densities, we here only included trials in which the predator survived till the end (48h-period) (Table 1). Natural mortality was very low and constant across all 4 levels of ant density (see above). Therefore, we directly compared the effect of the predator on the survival of the prey under different worker densities without controlling for natural mortality. All three predators efficiently captured the prey *C. albinus* in absence of ants. Indeed, the proportion of surviving prey *C. albinus* in absence of ants and predators was reduced from 0.97 ± 95% CI [0.94-0.99] to 0.46 [0.40-0.52], 0.54 [0.48-0.60], and 0.41 [0.35-0.47] in presence of *S. aterrimus*, *T. biovatus,* and *M. arietina,* resp. Survival of *C. albinus* in presence of the spiders *T. biovatus* and *M. arietina* was significantly higher with increasing ant density (GLMM$_{T. biovatus}$: Chisq = 28.27, *P* < 0.001; GLMM$_{M. arietina}$:

245   Chisq = 31.61, *P* < 0.001), indicating a lower capture rate of both spiders in higher ant

246   densities. BH controlled post hoc tests on the survival of *C. albinus* with *T. biovatus* indicated

247   that *C. albinus* survival without ants and with low ant density was significantly higher than in

248   the treatments with medium and high ant densities (Table 2). Higher worker density thus

249   negatively affected prey capture success of the two spiders (Fig. 3). In contrast, survival of *C.*

250   *albinus* with *S. aterrimus* was significantly higher in the absence and low densities of ants

251   compared to medium and high worker densities (GLMM: Chisq = 31.96, *P* < 0.001, Table 2),

252   reflecting a higher prey capture rate of the beetle in medium and high worker densities.

253

Discussion

While it is widely accepted that symbionts can impose strong antagonistic to mutualistic direct effects on their partners (Thrall et al. 2007) it is predicted that indirect interactions may be equally pervasive in host-symbiont networks (e.g. Lebrun et al. 2009, van Nouhuys and Kraft 2012). These indirect effects may mediate competitive and trophic interactions between different symbionts or change the competitive outcome of different hosts. Here, we showed that indirect effects can radically alter trophic interactions between symbionts in a host-ant community. We surprisingly found that the host caused contrasting indirect effects on the survival of the prey symbiont *Cyphoderus albinus* by inducing different responses in its predators. The symbiotic predator species responded differently to increasing worker densities and their response was tightly linked with the level of aggression they provoked in the host colony. The prey capture rate of the heavily persecuted predator *Mastigusa arietina* declined sharply, the poorly attacked spider *Thyreosthenius biovatus* became moderately less successful, whereas the tolerated rove beetle *Stenus aterrimus* even captured a higher proportion of *C. albinus* prey with increasing worker densities of their red wood ant host.

Increasing ant densities differently altered the prey capture rate of the three symbiotic predators. The contrasting indirect effects of the ants on the symbiotic prey here are trait-mediated as they arise from changes in the behavior of the symbiotic predators, which in turn affect the survival of the myrmecophilous prey. Worker density in ant nests is highly heterogeneous, typically low at the periphery and high in the brood chambers (Hölldobler and Wilson 1990). The frequency of aggressive interactions towards symbionts will be much higher in densely crowded chambers. Consequently, the center of the nest may not be a safe microhabitat for the myrmecophilous predators *T. biovatus* and *M. arietina*, which is underlined by their increased mortality risk in the crowded chambers. The increasing harassment with higher ant densities is likely to promote hiding behavior in the two spiders, a typical behavior seen in many animals to avoid predation or injury risks (Blanchard et al. 1990, Cooper and

281   Blumstein 2015, see for myrmecophilous beetles in von Beeren et al. 2010), and will eventually

282   decrease their prey capture rate (Abrams et al. 1996; Preisser 2005; Cooper and Blumstein

283   2015). In line with the prediction that the defense behavior of animals will increase with higher

284   levels of risk (Lima and Bednekoff 1999), we found that negative effect of increasing worker

285   density was more pronounced in the spider *M. arietina*. As this species provokes aggression

286   much more frequently and severely than *T. biovatus*, it is expected to show a stronger defense

287   response and its foraging behavior will consequently be more affected. The reduced prey

288   capture rate observed in the spiders could also result from a more timid prey instead of a more

289   timid predator in presence of more ants. But this mechanism is unlikely because the prey's

290   foraging behavior and survival seemed not to be affected by ant density (pers. observations

291   TP). *Stenus aterrimus* is hardly noticed by the ants and could freely forage in the crowded nest

292   chambers. We did a priori not expect a change in its predation rate (Fig. 1), but our results

293   surprisingly showed that the beetle captured more prey in denser nest chambers. No

294   convincing explanation has yet been found to explain this pattern. It is possible that the

295   increased prey capture rate of *S. aterrimus* in densely populated chambers could be driven by

296   a higher encounter rate between prey and predator. Higher ant densities may stimulate either

297   the activity of the predator, prey or even both leading to more prey captures.

298

299   While trait-mediated effects were omniprevalent, we also found evidence of density-mediated

300   indirect effects, which are caused by a lethal effect of increasing ant density on two predators.

301   Survival of *M. arietina* was significantly lower in chambers with higher worker densities. A

302   negative, yet non-significant, trend in survival was detected in *T. biovatus*. As in many other

303   networks, trait-mediated and density-mediated indirect effects act thus simultaneously in our

304   study system (Abrams et al. 1996; Banerji et al. 2015). Reduced survival of the spiders with

305   increasing ant density could be caused by starvation or higher levels of stress. Additionally,

306   crowded nest chambers offer fewer hiding places and could make the spiders more vulnerable

307   to lethal ant attacks. We found no evidence of reduced survival of the beetle *S. aterrimus* in

308   denser nest chambers. It should be noted that the 48h test period was relatively short and we

309   cannot exclude long-term detrimental effects of high worker densities on beetle fitness.

310   Nevertheless, aggression towards the beetles is extremely low, which hints that the long-term

311   impact of living in high worker densities is low for this species.

312

313   Indirect effects can have a major effect on competitive interactions. Plants are well known to

314   mediate competitive interactions between herbivores (Inbar and Gerling 2008; Utsumi et al.

315   2010). Typically, a herbivore induces morphological or chemical defences in the host plant

316   which in turn will hamper the fitness of a competing herbivore (Inbar and Gerling 2008).

317   Likewise, host-mediated interspecific competition in parasite communities has been reported

318   in multiple studies focusing both on micro- and macroparasites (Waage and Davies 1986;

319   Chilcutt and Tabashnik 1997; Bush and Malenke 2008; Lebrun et al. 2009; Ulrich and Schmid-

320   Hempel 2012). Both theoretical (Levine et al. 2017) and empirical work (van Veen et al. 2005)

321   underline the role of indirect effects in host-symbiont network stability and shaping species

322   coexistence. Multiple studies already reported niche partitioning in host-symbiont networks

323   (Proffit et al. 2007, Hechinger et al. 2009, von Beeren et al. 2010), but did not report indirect

324   effects as a mechanism of the symbiont community assembly so far. We suggest that indirect

325   effects may shape the competitive interactions between the three symbiotic predators in our

326   study system. The host ant differently affected the prey capture rate of competing predators,

327   resulting in a competitive advantage for predators that induce lower aggression by the host

328   than their competitors. The springtail *C. albinus* is generally the most abundant

329   myrmecophilous prey in red wood ant nests. It can be found throughout the nest, but it reaches

330   its highest densities in the center of the nest (Parmentier et al. 2016a, pers. observations TP).

331   Densities of other prey species are low in the core of the nest, but a group of facultative

332   symbionts can be found at the periphery of the nest (unpublished results). These species

333   (mites, flies, spiders …) mostly live away from ant nests (Robinson and Robinson 2013;

334   Parmentier et al. 2014), but may occupy the nest periphery in high numbers. The spider

335   *Mastigusa arietina* cannot compete with the other predators in the core of the nest. It strictly

336   lives at the periphery of the nest and it is readily killed in dense nest chambers (Parmentier et

337 al. 2016b). *Mastigusa arietina* is likely to have a broader dietary niche than the two other

338 predators as it may feed on the diverse community of facultative symbionts as well. The

339 predators *S. aterrimus* and *T. biovatus*, in contrast to *M. arietina*, can be found throughout the

340 nest (Parmentier et al. 2016b). Based on our results, the beetle *S. aterrimus* will have a strong

341 competitive advantage to *T. biovatus* in the more crowded parts of the nest, because of higher

342 tolerance to high worker densities and an increased predation response.

343

344

345 Our results contribute to a deeper understanding of the dynamics occurring in host-symbiont

346 networks. We showed that variable conditions in a host environment determine interaction

347 strength of associated symbionts by inducing density- and trait-mediated indirect effects.

348 Fitness balances of the symbionts may shift with the variation in host conditions. Further

349 research is needed to understand whether the interplay of indirect effects facilitate species

350 coexistence and explain the spatial niche partitioning of the myrmecophile symbiont

351 community.

352

356

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Tables

Table 1. Number of replicates and number of surviving predators for each treatment.

	0 workers	5 workers	15 workers	45 workers	
Stenus aterrimus					
total different individuals tested	$N = 16$	$N = 28$	$N = 18$	$N = 22$	$N_{tot} = 84$
total predators survived in first replicate (dead)	16 (0)	26 (2)	17 (1)	21 (1)	
total replicates predator survived (dead)	36 (8)	39 (5)	42 (3)	40 (6)	
Thyreosthenius biovatus					
total different individuals tested	$N = 24$	N = 32	$N = 34$	$N = 37$	$N_{tot} = 129$
total predators survived in first replicate (dead)	23 (1)	26 (6)	27 (7)	27 (10)	
total replicates predator survived (dead)	38 (3)	35 (9)	39 (11)	38 (13)	
Mastigusa arietina					
total different individuals tested	$N = 16$	$N = 24$	$N = 33$		$N_{tot} = 73$
total predators survived in first replicate (dead)	16 (0)	21 (3)	19 (14)		
total replicates predator survived (dead)	41 (1)	42 (5)	31 (20)		

Table 2. Benjamini-Hochberg corrected post-hoc tests comparing pairwise the effect of different worker density levels on prey capture rate of the three predators: *Stenus aterrimus*, *Thyreosthenius biovatus* and *Mastiguas arietina*.

	Stenus aterrimus			*Thyreosthenius biovatus*			*Mastigusa arietina*	
	5 workers	15 workers	45 workers	5 workers	15 workers	45 workers	5 workers	15 workers
0 workers	0.654	**<0.001**	**0.003**	0.218	**<0.001**	**<0.001**	**0.001**	**<0.001**
5 workers	-	**<0.001**	**<0.001**	-	**0.009**	**0.004**	-	**0.009**
15 workers	-	-	0.319	-	-	0.697	-	-
45 workers	-	-	-	-	-	-	-	-

Figures

Fig. 1. Overview of the ant-symbiont and symbiont-symbiont interactions in the red wood ant microcosm. Black arrows depict prey-predator interactions between myrmecophiles, grey arrows denote aggressive interactions between ant and myrmecophiles. The thickness of the lines corresponds with the provoked level of aggression (proportion of aggressive interactions) as reported in Parmentier et al. (2016a). No effect on the prey capture rate of tolerated (ignored) predators is a priori expected. A medium negative effect on prey capture rate is expected in moderately attacked predators (thin red dotted line), a strong negative effect in heavily persecuted predators (thick red dotted line).

Fig. 2. A. Top view of a container used in the experiments. In this trial, the rove beetle *Stenus aterrimus* (indicated by arrow) is introduced in a container with 45 red wood ant workers. B. The springtail *Cyphoderus albinus* captured by *T. biovatus*. C. The springtail *Cyphoderus albinus* captured by *S. aterrimus*. D. Detailed view of a test container with *Mastigusa arietina* and *Cyphoderus albinus* (indicated by arrows). Note that all trials were conducted in complete darkness.

Fig. 3. Multipanel displaying at 4 densities (0, 5, 15 and 45) of host ant workers: (i) proportional survival of *Cyphoderus albinus* in absence of a myrmecophilous predator (white points) (ii) proportional survival of a myrmecophilous predator (grey points) and (iii) proportional survival of *C. albinus* in presence of the myrmecophilous predator (black points). Data are given in three separate boxes for the three different myrmecophilous predators, i.e. left: *Stenus aterrimus*, middle: *Thyreosthenius biovatus*, right: *Mastigusa arietina*. Survival of prey without a predator was determined in a single series of trials, but is depicted in all three figures as a baseline. Error bars represent 95% confidence intervals. Means of a treatment (i.e. same color code and with same predator) labelled with different letters are significantly different at the α = 0.05 level (corrected for multiple testing using Benjamini-Hochberg procedure).
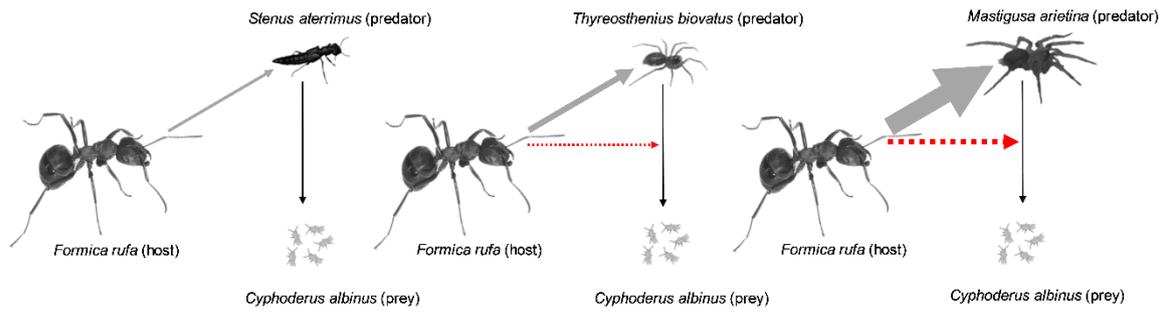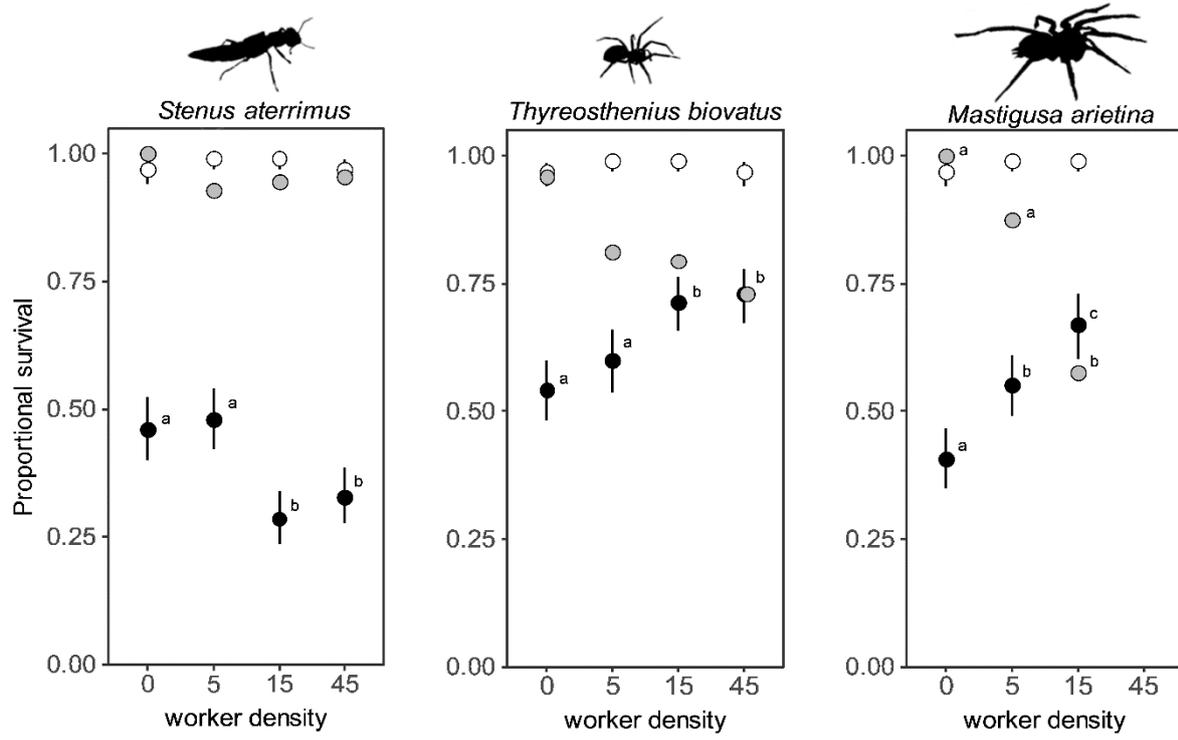
Fig. 1

Fig. 2

Fig. 3