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Contrasting indirect effects of an ant host on prey–predator interactions of symbiotic arthropods

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Abstract

Indirect interactions occur when a species affects another species by altering the density (density-mediated interactions) or influencing traits (trait-mediated interactions) of a third species. We studied variation in these two types of indirect interactions in a network of red wood ants and symbiotic arthropods living in their nests. We tested whether the ant workers indirectly affected survival of a symbiotic prey species (*Cyphoderus albinus*) by changing the density and/or traits of three symbiotic predators, i.e., *Mastigusa arietina*, *Thyreosthenius biovatus* and *Stenus aterrimus*, provoking, respectively, low, medium and high ant aggression. An ant nest is highly heterogeneous in ant worker density and the number of aggressive interactions towards symbionts increases with worker density. We, therefore, hypothesized that varying ant density could indirectly impact prey–predator interactions of the associated symbiont community. Ants caused trait-mediated indirect effects in all three prey–predator interactions, by affecting the prey capture rate of the symbiotic predators at different worker densities. Prey capture rate of the highly and moderately aggressed spider predators *M. arietina* and *T. biovatus* decreased with ant density, whereas the prey capture rate of the weakly aggressed beetle predator *S. aterrimus* increased. Ants also induced density-mediated indirect interactions as high worker densities decreased the survival rate of the two predatory spider species. These results demonstrate for the first time that a host can indirectly mediate the trophic interactions between associated symbionts. In addition, we show that a single host can induce opposing indirect effects depending on its degree of aggression towards the symbionts.

Keywords Competition · Host mediated · Myrmecophile · Red wood ant · Trait-mediated

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

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diverse array of key ecological processes such as trophic cascades, trait-mediated cascades and competition is 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. (2017) showed that large and nested mutualistic networks are expected to have more indirect effects than small and modular networks shaped by specialized mutualisms. Empirical studies on indirect interactions in host–symbiont networks typically reported that these interactions could alter the competitive outcome of two susceptible hosts (Hambäck et al. 2006; van Nouhuys and Kraft 2012) or of two competing parasites (Waage and Davies 1986; Bush and Malenke 2008; Lebrun et al. 2009). Host-mediated competition between two parasites was for example found in two feather-feeding lice in which the magnitude of competition was dependent on the defense (preening) of the host bird (Bush and Malenke 2008). Indirect effects can also mediate trophic interactions rather than competitive interactions in this type of networks as demonstrated in symbiont communities associated with pitcher plants (terHorst 2010).

Red wood ants (*Formica rufa* group) also form such host–symbiont networks. These widespread ants are keystone arthropods in European forest ecosystems (Gösswald 1989; Stockan and Robinson 2016). They exert wide-range effects on the forest fauna and flora and drive biogeochemical processes (Wardle et al. 2011). The above ground part of a red wood ant nest is a conspicuous mound of organic thatch (Rosengren et al. 1987), which is tightly regulated and provides an ideal habitat for a diverse community of associated symbionts, known as myrmecophiles (Parmentier et al. 2014). The majority of these red wood ant myrmecophiles directly interact with their host by feeding on their eggs and larvae and stealing prey carried into the nest (Parmentier et al. 2016a). In addition, many red wood ant myrmecophiles hunt on smaller myrmecophiles in the red wood ant nest microcommunity (Parmentier et al. 2016a). Ants also directly interact with their myrmecophile guests. If detected, ants try to deter or hurt them by showing aggression. Red wood ants show a highly variable degree of aggression towards myrmecophiles ranging from almost complete ignorance to heavy persecution, depending on the identity of the myrmecophile species (Parmentier et al. 2016b). In addition, the aggression response will be more prominent in densely crowded chambers in the nest, such as the chambers with brood, compared to the nest periphery, because of an increase in aggressive events and fewer opportunities to hide. Interestingly, myrmecophiles show preferences for particular nest locations and corresponding worker densities (Parmentier et al. 2016b), likely reflecting their tolerance to different degrees of ant aggression.

We thus anticipate the density of red wood ant workers to indirectly affect the survival of a myrmecophilous prey species by altering the behavior or survival of its myrmecophilous predator. Red wood ants vary greatly in their degree of aggression towards different myrmecophilous predators. The prey capture rate of those predators is as a result expected to change differently with increasing worker densities. We compared the effect of worker density on the prey capture rate among three different myrmecophilous predators, i.e., the rove beetle *Stenus aterrimus* Erichson, 1839 and the spiders *Thyreosthenius biovatus* (O. Pickard-Cambridge, 1875) and *Mastigusa arietina* (Thorell, 1871). They provoke, respectively, low, medium and high levels of ant aggression (Parmentier et al. 2016b). The myrmecophilous springtail *Cyphoderus albinus* Nicolet, 1842 was used as the shared prey of the three myrmecophilous predators (Fig. 1). The increase of aggressive events caused by increased worker densities will likely change the behavior of persecuted myrmecophilous predators, whereas the behavior of myrmecophilous predators that provoke little or no aggression is expected not to alter (Fig. 1). Therefore, we hypothesized that increasing worker densities would have the strongest negative effect on the prey capture rate of the myrmecophilous predator that provoked the highest degree of aggression.

Materials and methods

Study system and sampling

Myrmecophiles, ant workers, and organic nest material were repeatedly collected in a colony of the red wood ant *Formica rufa* Linnaeus, 1761 in Boeschepe, France, from June until September 2017. This supercolony was headed by many queens (polygynous) and consisted of multiple mounds which constantly exchanged workers and resources (polydomous). Myrmecophiles were collected by spreading out nest material into a large plastic tray. The white springtail *C. albinus* is an obligate ant symbiont that may reach high densities in ant nests (Parmentier et al. 2015). Ant workers pay little or no attention to its presence (Parmentier et al. 2016b). This springtail is likely to be the principal prey for many myrmecophilous predators and was, therefore, used as the myrmecophilous prey in the experiment (Parmentier et al. 2016a). We selected three predators which were obligate ant symbionts as well. *Stenus aterrimus* is a

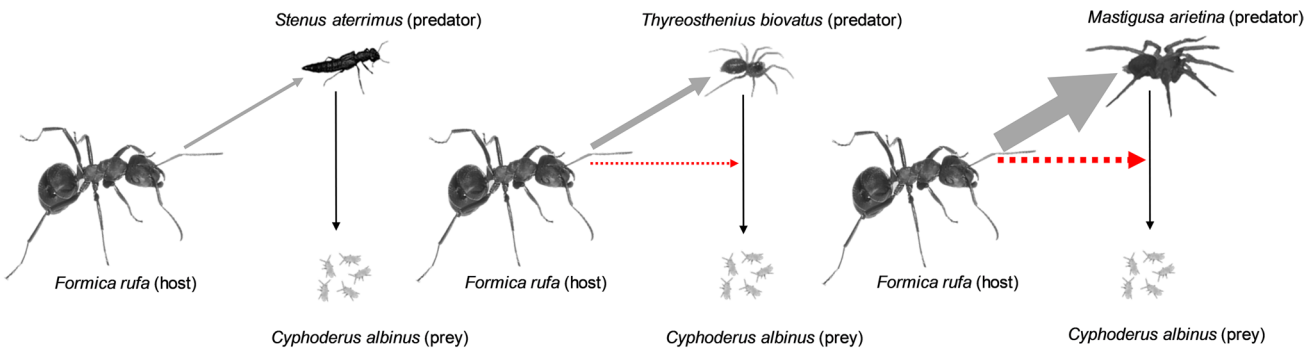

Fig. 1 Overview of the ant–symbiont and symbiont–symbiont interactions in the red wood ant microcosm. Black arrows depict prey–predator interactions between myrmecophiles; gray arrows denote aggressive interactions between ant and myrmecophiles. The thickness of the lines corresponds with the provoked 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) (color figure online)

rove beetle specialized to capture springtails (Koerner et al. 2012). Ants show weak rates of aggression (aggression in 13% of encounters; see Parmentier et al. 2016a) towards this species and are distributed throughout the nest (Parmentier et al. 2016b). The two other selected predators were the spiders *T. biovatus* and *M. arietina*. The former can be found throughout the nest and is occasionally attacked (aggression in 24% of encounters), whereas the latter is strongly persecuted (aggression in 73% of encounters) and is restricted to the sparsely occupied periphery of the nest (Parmentier et al. 2016b). The three tested myrmecophilous predators predate on the springtail and interact with their host by kleptoparasitism and brood predation (so far only recorded for *T. biovatus* and *M. arietina*, Parmentier et al. 2016a). The ants do not predate on the myrmecophilous predators and prey, but only negatively interact with them by an aggression response.

Ant workers were kept in a container with a plaster-filled bottom and given access to water and sugar water ad libitum prior to the experiment. The myrmecophilous prey *C. albinus* was cultured in a container with organic nest material and some hundreds of workers of the supercolony. Myrmecophilous predators were individually placed in small snap-lid containers (diameter 4.5 cm) filled with moistened plaster in the lab. Next, we offered to all predators three *C. albinus* prey to level out differences in feeding status. Subsequently, the beetle *S. aterrimus* and the spider *M. arietina* were starved for a period of 4 days and the spider *T. biovatus* for 10 days. We opted for a longer starvation period in *T. biovatus,* as the proportion of surviving prey in presence of *T. biovatus* starved for 4 days (mean = 0.92, N = 10) was close to prey survival without predators. Starving *T. biovatus* for a period of 10 days considerably increased its prey capture rate. Nest material was stored in a freezer (− 21 °C) to kill tiny and hidden organisms such as mites, and which could potentially serve as additional prey for the myrmecophilous predators. We reconciled the extensive search effort to find the relatively rare predators with the need for a high number of replicates, by reusing the predators in subsequent trials. Before using a predator again, it was first re-isolated, fed with three individuals of *C. albinus* prey and starved as before. All spider individuals were female.

Experiment: prey–predator interactions under different worker densities

We aimed with this experiment to test the effect of increasing density of ant workers on the prey capture success of symbiotic predators (Fig. 1). The experiment was done in plastic containers (diameter 5 cm, height = 5.5 cm) with a 1-cm bottom of plaster of Paris. The side of the container was coated with fluon to prevent ants and myrmecophiles to climb on. The container was closed with a lid in which there was a hole (diameter 2 cm) covered with fine mesh. This prevented myrmecophiles from escaping by rare flying (*S. aterrimus*) or jumping events (*C. albinus*). Approximately 5 mL of the defrosted organic material was then added to the container together with five fully grown individuals of *C. albinus* collected in the stock colony. The nest material and plaster were moistened. As we wanted to test prey–predation under differing worker densities, we assigned 0 (0 W: control), 5 (5 W: low density), 15 (15 W: medium density) or 45 (45 W: high density) ant workers to a container. Finally, one starved predator individual of *S. aterrimus*, *T. biovatus* or *M. arietina* was introduced (Fig. 2). The introduction of the predator in the container was approximately 30 min later than the prey giving the latter time to hide. After 48 h, the number of surviving prey individuals out of five was recorded. To test the effect of predation, we need to control for natural mortality of the prey. Therefore, we counted the number of prey out

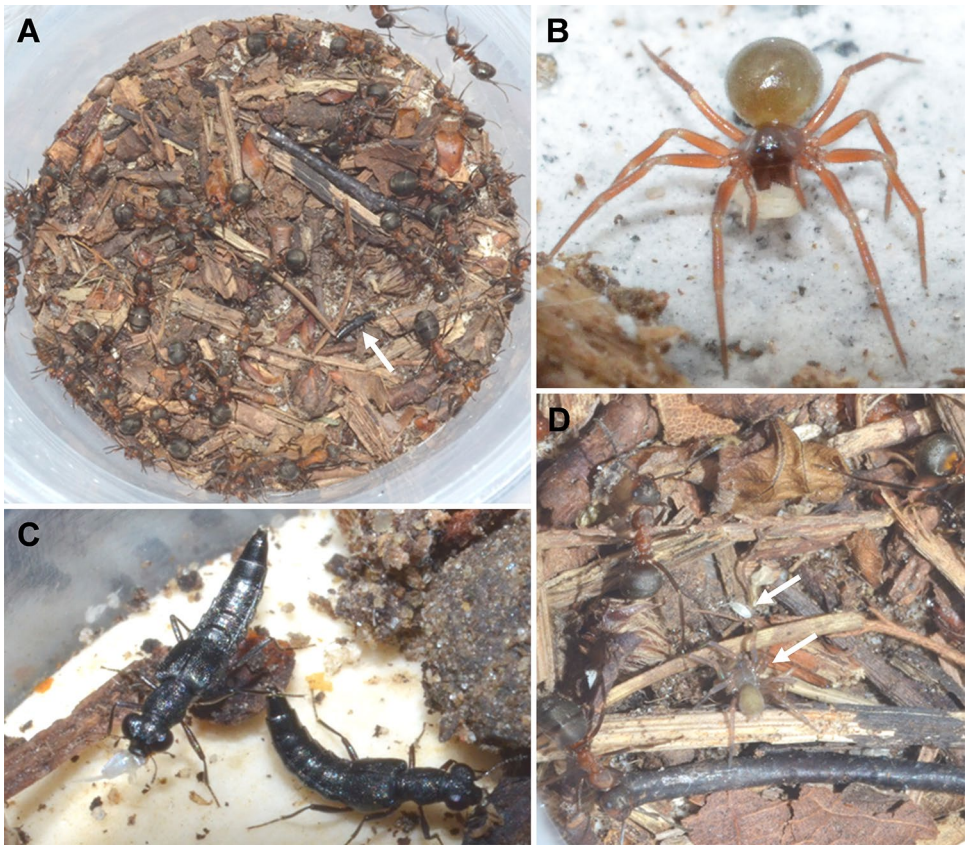

Fig. 2 **a** Top view of a container used in the experiments. In this trial, the rove beetle *Stenus aterrimus* (indicated by arrow) is introduced in a container with 45 red wood ant workers. **b** The springtail *Cyphoderus albinus* captured by *Thyreosthenius biovatus*. **c** The springtail *C. albinus*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

of five that survived without predators under the four levels of worker density (number of replicates: 0 W = 37, 5 W = 39, 15 W = 37, 45 W = 40). All containers were kept at 20–22 °C in complete darkness. The experiment was conducted from July until October 2017. The number of trials for each treatment is summarized in Table 1. We did not test the effect of 45 workers on the prey capture rate and survival of *M. arietina*. In four preliminary tests with this species, all individuals died within a couple of hours. The spider is expected not to survive these stressful conditions, which was already suggested by another lab experiment (Parmentier et al. 2016b). As it was difficult to obtain large numbers of *M. arietina*, we chose to allocate the spiders only to 0 W, 5 W and 15 W to assess their prey capture rate.

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)		

Statistical analyses

Myrmecophile survival under different levels of worker density

In some trials, predators were dead before the end of the 48 h test period. This could be explained by natural mortality, starvation, through increased stress or inflicted injuries by the ants (Parmentier 2016). The effect of ant worker density on predator survival was compared by calculating the proportion of trials in which the predator survived. Here, we only based on trials in which the predator was used for the first time so that the exposure time to the ants was comparable. We compared pairwise the effect of different levels of ant density on predator survival by employing Fisher exact tests and subsequently controlled the false discovery rate of the corresponding *P* values using the Benjamini–Hochberg (BH) procedure (Benjamini and Hochberg 1995).

To test the effect of ant density on the proportion of surviving *C. albinus* in the absence of predators, a quasibinomial error distributed (to account for overdispersion) GLM was used with logit link function. We assessed the significance of these baseline data with a likelihood-ratio test using the 'Anova' function of the R-package car (Fox and Weisberg 2011).

Prey–predator interactions under different worker densities

Capture success under different worker densities was based on trials where the predators survived until the end. One trial was excluded, because the predator was visibly hurt at the end and which may have affected its prey capture success. In all other trials, predators showed normal behavior at the end. For each predator separately, we modeled the proportion of surviving prey under different densities of ant workers using a GLMM (generalized linear mixed model) with binomial error distribution and logit link function. Treatment (= different levels of worker ant density: 0 workers, 5 workers, 15 workers and 45 workers) was included as a fixed factor. To account for reusing predator individuals in subsequent trials (max. 4 trials per individual), we included predator identity as a random factor. This factor was nested in treatment as an individual was always exposed to the same treatment level (i.e., identical worker ant density) in all of its replicates. We also added an observation level random factor to correct for overdispersion (Browne et al. 2005). The GLMMs were run using the 'glmer' function in R-package lme4 (Bates et al. 2015) and significance was tested using a likelihood-ratio test implemented in the 'Anova' function of the R-package car (Fox and Weisberg 2011). Subsequently, the different levels of ant density in these GLMM-models were pairwise compared with the glht function of the 'multcomp' package (Hothorn et al. 2008). Within each series of pairwise tests, we controlled the false discovery rate using the BH-procedure.

Results

Myrmecophile survival under different levels of worker density

The prey *C. albinus* was rarely noticed by the host ant and freely foraged in the nest material. Survival of this species was correspondingly very high after 48 h across all treatments. It was seemingly not affected by the presence of ants, ranging from low to high density of ant workers (quasibinomial GLM, $\chi^2 = 3.60$, $P = 0.31$; Fig. 3). Survival rate of the predator *S. aterrimus* was high and equal across the 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 *T. biovatus* declined with increasing worker density (Table 1, Fig. 3), but the six pairwise BH-corrected Fisher Exact tests were not significantly different. Survival of the spider *M. 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 (48 h-period) (Table 1). Natural mortality was very low and constant across all four 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 the absence of ants. Indeed, the proportion of surviving prey *C. albinus* in the 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 the presence of *S. aterrimus*, *T. biovatus,* and *M. arietina,* resp. Survival of *C. albinus* in the presence of the spiders *T. biovatus* and *M. arietina* was significantly higher with increasing ant density ($GLMM_{T.\ biovatus}$: $\chi^2 = 28.27$, $P < 0.001$; $GLMM_{M.\ arietina}$: $\chi^2 = 31.61$, $P < 0.001$), indicating a lower capture rate of both spiders in higher ant densities. BH controlled post hoc tests on the survival of *C. albinus* with *T. biovatus* indicated that *C. albinus* survival without ants and with low ant density was significantly higher than in the treatments with medium and high ant densities (Table 2). Higher worker density thus negatively affected prey capture success of the two spiders (Fig. 3). In contrast, survival of *C. albinus* with *S. aterrimus* was significantly higher in

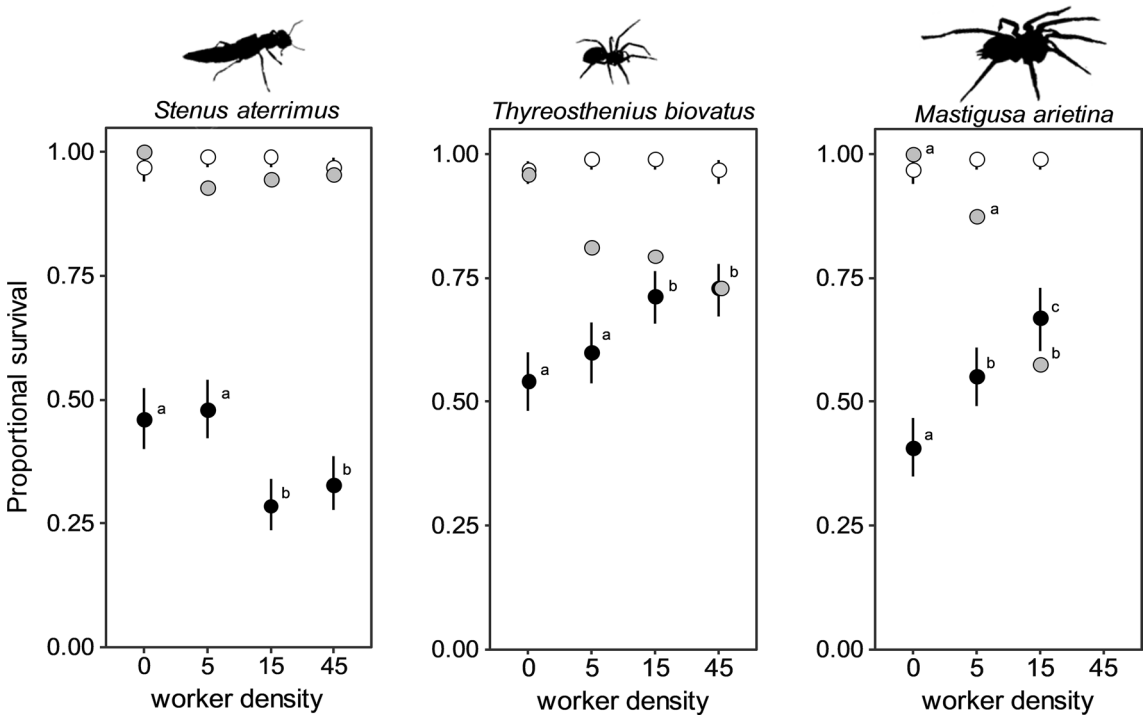

Fig. 3 Multipanel displaying at 4 densities (0, 5, 15 and 45) of host ant workers: (i) proportional survival of *Cyphoderus albinus* in absence of a myrmecophilous predator (white points) (ii) proportional survival of a myrmecophilous predator (gray points) and (iii) proportional survival of *C. albinus* 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) labeled with different letters are significantly different at the $\alpha = 0.05$ level (corrected for multiple testing using Benjamini–Hochberg procedure)

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 *Mastigusa 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	–	–	–	–	–	–	–	–

Significant values ($P < 0.05$) are displayed in bold.

the absence and low densities of ants compared to medium and high worker densities (GLMM: $\chi^2 = 31.96$, $P < 0.001$, Table 2), reflecting a higher prey capture rate of the beetle in medium and high worker densities.

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 Blumstein 2015, see for myrmecophilous beetles in von Beeren et al. 2010), and will eventually decrease their prey capture rate (Abrams et al. 1996; Preisser 2005; Cooper and Blumstein 2015). In line with the prediction that the defense behavior of animals will increase with higher levels of risk (Lima and Bednekoff 1999), we found that the negative effect of increasing worker density was more pronounced in the spider *M. arietina*. As this species provokes aggression much more frequently and severely than *T. biovatus*, it is expected to show a stronger defense response and its foraging behavior will consequently be more affected. The reduced prey capture rate observed in the spiders could also result from a more timid prey instead of a more timid predator in presence of more ants. But this mechanism is unlikely because the prey's foraging behavior and survival seemed not to be affected by ant density (pers. observations TP). *Stenus aterrimus* is hardly noticed by the ants and could freely forage in the crowded nest chambers. We did a priori not expect a change in its predation rate (Fig. 1), but our results surprisingly showed that the beetle captured more prey in denser nest chambers. No convincing explanation has yet been found to explain this pattern. It is possible that the increased prey capture rate of *S. aterrimus* in densely populated chambers could be driven by a higher encounter rate between prey and predator. Higher ant densities may stimulate either the activity of the predator, prey or even both leading to more prey captures.

While trait-mediated effects were omniprevalent, we also found evidence of density-mediated indirect effects, which are caused by a lethal effect of increasing ant density on two predators. Survival of *M. arietina* was significantly lower in chambers with higher worker densities. A negative, yet non-significant, trend in survival was detected in *T. biovatus*. As in many other networks, trait-mediated and density-mediated indirect effects act thus simultaneously in our study system (Abrams et al. 1996; Banerji et al. 2015). Reduced survival of the spiders with increasing ant density could be caused by starvation or higher levels of stress. Additionally, crowded nest chambers offer fewer hiding places and could make the spiders more vulnerable to lethal ant attacks. We found no evidence of reduced survival of the beetle *S. aterrimus* in denser nest chambers. It should be noted that the 48 h test period was relatively short and we cannot exclude long-term detrimental effects of high worker densities on beetle fitness. Nevertheless, aggression towards the beetles is extremely low, which hints that the long-term impact of living in high worker densities is low for this species.

Indirect effects can have a major effect on competitive interactions. Plants are well known to mediate competitive interactions between herbivores (Inbar and Gerling 2008; Utsumi et al. 2010). Typically, a herbivore induces morphological or chemical defences in the host plant which in turn will hamper the fitness of a competing herbivore (Inbar and Gerling 2008). Likewise, host-mediated interspecific competition in parasite communities has been reported in multiple studies focusing both on micro- and macroparasites (Waage and Davies 1986; Chilcutt and Tabashnik 1997; Bush and Malenke 2008; Lebrun et al. 2009; Ulrich and Schmid-Hempel 2012). Both theoretical (Levine et al. 2017) and empirical work (van Veen et al. 2005) underline the role of indirect effects in host–symbiont network stability and shaping species coexistence. Multiple studies already reported niche partitioning in host–symbiont networks (Proffit et al. 2007; Hechinger et al. 2009; von Beeren et al. 2010), but did not report indirect effects as a mechanism of the symbiont community assembly so far. We suggest that indirect effects may shape the competitive interactions between the three symbiotic predators in our study system. The host ant differently affected the prey capture rate of competing predators, resulting in a competitive advantage for predators that induce lower aggression by the host than their competitors. The springtail *C. albinus* is generally the most abundant myrmecophilous prey in red wood ant nests. It can be found throughout the nest, but it reaches its highest densities in the center of the nest (Parmentier et al. 2016a, pers. observations TP). Densities of other prey species are low in the core of the nest, but a group of facultative symbionts can be found at the periphery of the nest (unpublished results). These species (mites, flies, spiders …) mostly live away from ant nests (Robinson and Robinson 2013; Parmentier et al. 2014), but

may occupy the nest periphery in high numbers. The spider *M. arietina* cannot compete with the other predators in the core of the nest. It strictly lives at the periphery of the nest and it is readily killed in dense nest chambers (Parmentier et al. 2016b). *Mastigusa arietina* is likely to have a broader dietary niche than the two other predators as it may feed on the diverse community of facultative symbionts as well. The predators *S. aterrimus* and *T. biovatus*, in contrast to *M. arietina*, can be found throughout the nest (Parmentier et al. 2016b). Based on our results, the beetle *S. aterrimus* will have a strong competitive advantage to *T. biovatus* in the more crowded parts of the nest, because of higher tolerance to high worker densities and an increased predation response.

Our results contribute to a deeper understanding of the dynamics occurring in host–symbiont networks. We showed that variable conditions in a host environment determine interaction strength of associated symbionts by inducing density- and trait-mediated indirect effects. Fitness balances of the symbionts may shift with the variation in host conditions. Further research is needed to understand whether the interplay of indirect effects facilitates species coexistence and explains the spatial niche partitioning of the myrmecophile symbiont community.

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Author contribution statement TP conceived, designed and performed the experiments. TP, FL, TW and DB analyzed the data. TP wrote the manuscript; other authors provided editorial advice.

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