



# Do mutualistic associations have broader host ranges than neutral or antagonistic associations? A test using myrmecophiles as model organisms

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## Abstract

Symbiotic associations are found across all kingdoms of life and are integral to ecosystem structure and function. Central to understanding the ecology and evolution of symbiotic relationships is an understanding of what influences host range; the number of host species that a symbiont can utilize. Despite the importance of host breadth among symbionts, relatively little is known about how the relationship that a symbiont has with its host influences its host range. Additionally, contrasts among interaction types often involve diverse groups of unrelated host species. To test how host range varied with interaction type, we used a global synthesis of over 1600 species of myrmecophiles, those organisms that have symbiotic associations with ants. We used an indexed literature search to collate known myrmecophile species and their hosts, and to determine how two degrees of dependence (facultative, obligate) and four types of relationships (mutualism, commensalism, kleptoparasitism, and parasitism) among myrmecophiles and their hosts influence host range. Our synthesis showed that, overall, myrmecophiles exhibited a high degree of host specialization, and facultatively dependent myrmecophiles had broader host ranges than those with obligate interactions. Myrmecophiles with mutualistic relationships had broader host ranges than neutral or antagonistic relationships. Additionally, lepidopteran myrmecophiles exhibited broader host range patterns than other taxa. Our results have important implications for how symbiotic associations are understood, with positive relationships (mutualisms) associated with broader host range, and antagonistic relationships (parasitism) associated with narrow host range.

**Keywords** Symbiotic associations · Myrmecophiles · Host range · Symbionts

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## Introduction

Symbiotic associations have an important influence on ecosystem structure and function, and have been credited with driving global diversity (Thompson 1994; Poulin 2004). These close associations between organisms are found in all kingdoms of life, at differing degrees of dependence, with species facultatively associated with or obligatory dependent on their hosts, and involving a wide range of relationship types (mutualisms, commensalisms, and parasitism). Associations can be mutually beneficial to both symbiont and host (mutualisms), beneficial to the symbiont with no effects on host (commensalisms), or antagonistic to the host while benefiting the symbiont (parasitism) (Boucher et al. 1982).

Central to understanding the ecology and evolution of symbiotic interactions is predicting what factors promote or constrain the number of host species used by a symbiont. Understanding the costs and benefits of host breadth in species interactions has been a major aim of research into

plant-herbivore, plant-pollinator, host-parasite, and other symbiotic interactions (Futuyma and Moreno 1988; Poulin et al. 2011; Kamiya et al. 2014). Symbionts associated with fewer hosts are often more morphologically or behaviourally specialized, and better able to utilize host resources than those with multiple hosts, but potentially have reduced availability of hosts in space and time (Thompson 1994; Thomas and Elmes 2004). A reduced host availability becomes more common with coevolution of symbionts and their hosts, leading to highly specialized traits for the exploitation of particular host resources (Proctor and Owens 2000; Krasnov et al. 2001). Consequently, facultative symbionts tend to have broader host ranges than obligates, which rely on their associations to survive.

The type of relationship between an organism and its hosts may also affect host range. Contrasts of positive (mutualistic) and antagonistic (parasitic) relationships, however, have often involved comparisons among taxonomically dissimilar hosts, making it difficult to test the role of relationship type. Many mutualistic relationships such as pollination or seed dispersal, show a low degree of host specialization for the pollinator or disperser (Thompson 1994). However, other interactions have shown that coevolution of mutualist symbionts and hosts can result in highly specific and narrow host ranges (Boucher et al. 1982; Kawakita et al. 2010). For example, the pollinating fig wasps have a narrow host range of trees in the genus *Ficus* (Ramirez 1970; Machado et al. 2005), and specialist anemone fish may also exhibit a narrow host range of their mutualist sea anemones (Ollerton et al. 2007). Parasitic associations often favour narrow host ranges, along with morphological and/or behavioural specialisation, as adaptations to overcome host defenses are needed (Price 1980; Schär and Voburger 2013). However, broad host ranges can also be found in a wide range of free-living parasitic associations such as avian brood parasites (Davies and Brooker 1989), kleptoparasitic birds (Brockmann and Barnard 1979; Thompson 1994), cookie cutter sharks (Papstamatiou et al. 2010), and vampire bats (Voigt and Kelm 2006). Comparisons of wide ranging associations between different organisms and unrelated hosts make it difficult to determine how relationship type may be influencing host range.

Myrmecophiles, those organisms associated with ants (Hymenoptera: Formicidae) (Kistner 1982; Kronauer and Pierce 2011), provide an excellent model to examine how host range varies among a wide range of symbiotic associations within a single group of hosts. Myrmecophiles exhibit a wide spectrum of association types, are taxonomically diverse, and all use similar hosts (ants) (Kistner 1982; Hölldobler and Wilson 1990). Ants are abundant, ubiquitous and ecologically dominant in most terrestrial ecosystems, and provide a wide set of resources for myrmecophiles such as homeostatic colonies, protection from predators, stored food,

and potential prey items (brood and workers). Ants aggressively defend their colonies and resources, and myrmecophiles must use a variety of tactics to evade, avoid, or placate their hosts (Hughes et al. 2008). In simple terms, myrmecophiles either have to attract ants or overcome ant defences to associate with their hosts. Attracting ants for many mutualistic myrmecophiles involves providing honeydew (sugary secretions) in exchange for protection (Kaminski et al. 2010; Tegelaar et al. 2012). This relationship involves a cost of honeydew production but may not limit the number of ant hosts that can utilize this widely acceptable carbohydrate resource (Kindlmann et al. 2007). Conversely, overcoming ant defences through mimicking chemical cues (Akino et al. 1999; Elgar and Allan 2006; Witte et al. 2009), tactile communications (Hölldobler 1971) and/or audio cues (Sala et al. 2014) is often much more specific to particular ant taxa. The cost of overcoming ant defences, therefore, may limit the number of potential hosts (von Beeren et al. 2011). Using myrmecophiles as a model allows us the opportunity to examine symbiotic associations on a broader scale and determine how dependence and relationships may drive host range.

Here we report a global synthesis of the host range of myrmecophiles of all symbiotic relationship types. We compiled a database of 350 published studies on 1605 myrmecophile species and quantified how dependence, type of relationship, and taxonomic group vary with host range. We test the predictions that (1) facultative myrmecophiles would have broader host range (number of associated ant species) compared to obligates, as they do not require ants to survive, but would be expected to opportunistically associate with numerous ant species; and (2) beneficial associations would have broader host ranges than antagonistic ones, as hosts would have more defences against negative relationships. For each dependence and relationship type, we tested whether patterns were consistent across the major taxonomic groups of myrmecophiles.

## Methods

### Data compilation

We searched for publications indexed in the ISI Web of Science using the terms: myrmecophil\* or “ant associat\*” or “ant inquiline” or “synechtran\*” or “synoekete\*” or “symphile\*” or “trophobiont\*”. Searched words are all associated with myrmecophiles and their relationships with ants (Hölldobler and Wilson 1990). This method of accumulating references follows methods used by other meta-analyses and data-syntheses which used literature databases to compile data (Chamberlain and Holland 2009; Kamiya et al. 2014). Of a total of 787 results,

we selected those involving only invertebrate myrmecophiles; excluding fungi, microbes, and plants. Mites (Subclass Acari), nematodes (Phylum Nematoda) and collembola (Subclass Collembola) were also excluded from the study as while many species of these three invertebrate groups have been reported from ant nests, and may be true myrmecophiles (Rettenmeyer et al. 2011), many published studies do not allow us to conclusively determine their relationship with ants (Parker 2016; Glasier and Acorn 2013). Additionally, both mites and collembola were rarely identified to species in the available literature (Campbell et al. 2013).

With problems of identification in references and the need to exclude certain taxonomic groups for our research, we felt it necessary to provide a definition that we used for the word myrmecophile. Myrmecophile is derived from the Greek word ‘myrmex’ (ant) and ‘philos’ (loving), so in simple terms, myrmecophile means “ant-lover” (Kronauer and Pierce 2011). Other definitions that are frequently quoted are “an organism found in association with ants” (Kistner 1982) and “any organism that is dependent on ants at least during part of its lifecycle” (Hölldobler and Wilson 1990). To test our hypotheses, however, we followed Parker’s (2016) definition of myrmecophiles which is “species that capitalize on the social fabric of ant biology”.

Studies we included in our analysis were restricted to our definition of a myrmecophile, and those that reported a unique host name for each myrmecophile, the type of relationship, the degree of association, sample location, and host ant species. Further studies were added by examining the reference lists from each paper found. Under these search criteria, we compiled a data set derived from 350 published studies (Appendix A in ESM). Additionally, we made the effort to correct for nomenclature synonyms for both ants and myrmecophiles to the best of our ability.

We defined host range as: “all the ant species which a myrmecophile utilizes as a host” (modified from Van Klinken 2000). Host range is different from host specificity, which is “how acceptable and/or suitable hosts are relative to each other” and can be a “continuum from extreme specialists with a host range restricted to a single host species, to so-called generalists which have a broad host range” (Van Klinken 2000). We used host range in our analysis because it is a species-scale variable while host-specificity is more important at the community and population level. Moreover, for many myrmecophile species, suitability of hosts has not been extensively studied and therefore would have been an unreliable variable to test (Mynhardt 2013). Information on host range however accumulates incidentally and incrementally over time while research is occurring and therefore is more reliable.

## Contrasts in host range among myrmecophile taxa, reliance and relationship types

To test the hypothesis that host range (sum of all ants) varied among myrmecophile taxa, we contrasted the number of ant species associated with each myrmecophile species among orders. Host number for each species was determined by summing all host records from the examined literature. Host range was contrasted among orders using a generalized linear model, with a Poisson error structure and the number of references per myrmecophile species as a statistical offset. The number of references was used as a statistical offset, instead of a covariate, to account for the observation that highly studied taxa tended to have more host species. Statistical offsets control for sample bias, reduce the influence that the number of references surveyed have on our myrmecophile species richness, and help to better model the effects of other variables (Werner and Guven 2007). The significance of the predictor variable in the generalized linear model was determined using an analysis of deviance, contrasting the two models with and without the predictor variable. Maximum likelihood estimates for each level of the predictor variable and 95% confidence intervals obtained from bootstrapping were obtained for visualizing variation among and within orders. All analyses were conducted with the R package lme4 (Bates et al. 2014). To control for some species being over-studied (such as species in the genus *Phengaris*, Order Lepidoptera: Family Lycaenidae), every myrmecophile with five or more studies (a total of eight species) was designated to have only five studies (the asymptote of the sigmoidal relationship of the number of studies in relation to number of hosts).

Each myrmecophile species was categorized by their dependence: facultative or obligate, based on information in relevant studies. A facultative dependent was defined as an invertebrate that may associate with ants, but does not need to, to survive [for example: the aphid *Aphis fabae cirsiacanthoides* Scopoli, 1763 (Stadler and Dixon 1999) or the caterpillar *Parrhasius polibetes* (Stoll, 1781) (Kaminski and Rodrigues 2011) that may be tended by ants, but are able survive without ant association; or many beetles of the family Latridiidae that may seek refuge in ant nests, but do not have to, to survive (Lapeva-Gjonova and Rucker 2011)]. An obligate dependent was defined as an invertebrate that required an association with ants to survive [for example: the highly co-evolved obligate mutualisms between mealy-bugs and *Acropyga* ants, where both need one another to survive (Smith et al. 2007); or the spider *Cosmophasis bitaeniata* (Keyserling 1882), that has evolved to almost exclusively eat the larva of weaver ants, *Oecophylla smaragdina* Fabricius, 1775 (Edgar and Allen 2006)]. To test the hypothesis that obligate myrmecophiles are involved in more specialized interactions, we contrasted host range between facultative

and obligate myrmecophiles using generalized linear models (as above). This was done for all myrmecophile species and also within the five most speciose orders of myrmecophiles (Diptera, Coleoptera, Hemiptera, Hymenoptera and Lepidoptera).

Myrmecophiles were placed along a gradient ranging from positive to negative association using four relationship types: mutualist, commensal, kleptoparasite, or parasite. Mutualists were defined as having an association that benefited both myrmecophile and ant host [for example, aphids farmed/protected by ants (Stadler and Dixon 1999), or bees co-habiting with ants in a nest for mutual protection (Sakagami et al. 1989)]. Commensal relationships were defined as associations where myrmecophiles benefited, but there were no benefits or detriments to the ant host [for example, moth larva living in middens of an ant colony (Sanchez-Pena et al. 2003) or crickets living within a colony, but not using ant resources (Komatsu et al. 2009)]. For this study, kleptoparasites were associations where myrmecophiles stole food and/or resources from their ant hosts, but did not prey upon them (for example, beetles that steal food from passing ants or are fed by ants, Lencina et al. 2011; von Beeren et al. 2011). Parasites were defined as myrmecophiles that harmed their hosts, by feeding directly on ants and/or their brood. They may also be organisms that steal food and predate on ants,

such as some lycaenid butterfly larva (Thomas and Elmes 2004; Witek et al. 2008). Associations were cross checked among different references and the most supported association was used. Similarly, if an association was deemed an error or a dead-end host (an association that does not allow for a myrmecophile to survive for long) within a reference, we corrected the database with the best supported information.

## Results

### The distribution of myrmecophiles among invertebrate taxa and relationship types

Our literature review identified 1605 myrmecophile species from 127 families and 20 orders of invertebrates, derived from 4399 records in 350 publications (Table 1). Species from the Order Coleoptera comprised ~64% of reported species associated with ants (Table 1). Other speciose orders with 50 or more species of myrmecophiles were the Diptera, Hemiptera, Hymenoptera and Lepidoptera (Table 1). The majority of species (~90%) were only reported from one study. The reported species were evenly distributed among facultative (47% of species) and obligate (53%)

**Table 1** The orders of invertebrates that are known myrmecophiles, with the number of species and families of myrmecophiles per order, the number of species for each type of interaction, and the number of references per order

Order	Species	Families	Dependence		Relationship type				References	
			Facultative	Obligate	Mutualist	Commensal	Kleptoparasite	Parasite		
Coleoptera	1028	35	483	545	2	396	538	92	112	
Hemiptera	289	25	189	100	282	0	0	7	78	
Lepidoptera	70	5	20	50	39	4	17	10	82	
Diptera	57	6	2	55	0	4	5	48	30	
Hymenoptera	51	16	4	47	5	3	1	42	21	
Isopoda	23	8	12	11	0	23	0	0	12	
Orthoptera	16	2	1	15	0	6	10	0	21	
Polydesmida	14	4	14	0	0	14	0	0	4	
Araneae	9	7	1	8	1	6	0	2	16	
Blattodea	9	4	4	5	0	6	3	0	8	
Geophilomorpha	9	3	9	0	0	9	0	0	1	
Thysanura	9	3	1	8	0	5	4	0	11	
Lithobiomorpha	6	1	6	0	0	6	0	0	1	
Julida	4	1	4	0	0	4	0	0	2	
Pseudoscorpionida	4	2	1	3	0	4	0	0	3	
Isoptera	3	1	3	0	0	3	0	0	2	
Dermaptera	1	1	1	0	0	1	0	0	1	
Neuroptera	1	1	1	0	0	1	0	0	1	
Polyxenida	1	1	1	0	0	1	0	0	1	
Thysanoptera	1	1	1	0	0	1	0	0	1	
Total	20	1605	127	762	845	331	497	578	201	350

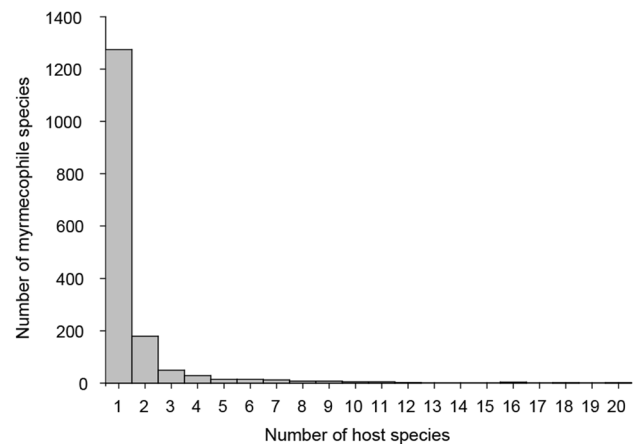
myrmecophiles (Fig. 1). Kleptoparasitic relationships were most commonly reported (36% of species), while parasitic relationships were least reported (12.5%, Fig. 1).

### Contrasts of host range among myrmecophile taxa, dependence, and relationship types

Most myrmecophiles were reported from only one ant host (~80% of species), but the number of host species ranged from 1 to 20 (Fig. 2) and myrmecophiles, on average, were associated with  $1.55 \pm 0.04$  (mean  $\pm$  SE) host ant species. The number of ant hosts per myrmecophile species varied significantly among orders (Fig. 3,  $\chi^2 = 212.76$ ,  $df = 19$ ,  $P < 0.001$ ). Within the five most speciose (> 50 species of myrmecophiles) orders Lepidoptera and Hemiptera had ~54% more hosts compared to the other three orders ( $\chi^2 = 177.19$ ,  $df = 4$ ,  $P < 0.001$ ). The host range of the Diptera, Coleoptera, and Hymenoptera did not differ (Fig. 3).

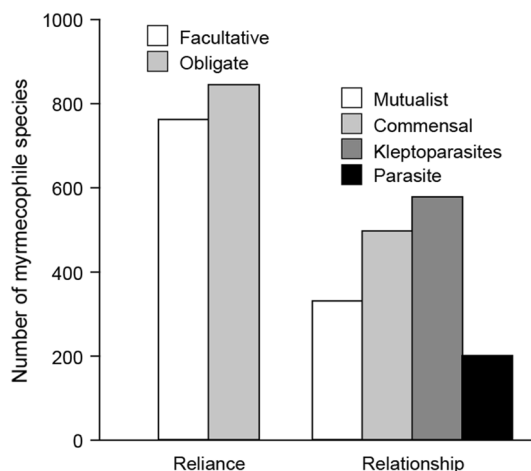
Across all species, facultative myrmecophiles were associated with ~75% more hosts than obligate myrmecophiles (Fig. 4,  $\chi^2 = 51.55$ ,  $df = 1$ ,  $P < 0.001$ ). Host range varied with dependence in the Lepidoptera, with facultative species using, on average, about two more host species than obligate species ( $\chi^2 = 35.81$ ,  $df = 1$ ,  $P < 0.001$ ). Within the Hemiptera, facultative hemipterans used a greater number of hosts than obligates ( $\chi^2 = 31.14$ ,  $df = 1$ ,  $P < 0.001$ ). Host range did not differ between facultative and obligate myrmecophiles in the Diptera ( $G2 = 0.03$ ,  $df = 1$ ,  $P = 0.853$ ), Coleoptera ( $\chi^2 = 1.71$ ,  $df = 1$ ,  $P = 0.191$ ), or Hymenoptera ( $\chi^2 = 0.07$ ,  $df = 1$ ,  $P = 0.788$ ).

The host range of myrmecophiles significantly varied with relationship type (Fig. 5,  $\chi^2 = 170.55$ ,  $df = 3$ ,  $P < 0.001$ ). Mutualists had at least ~61% more hosts than

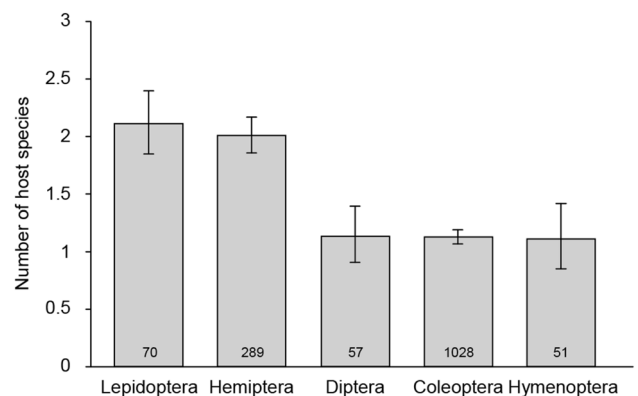


**Fig. 2** The distribution of host breadth (number of ant species) for all species of myrmecophile

all other relationship types and the host range of commensals, kleptoparasites and parasites did not differ from one another (Fig. 5). Host range also varied with the type of relationship in the Lepidoptera ( $\chi^2 = 44.20$ ,  $df = 3$ ,  $P < 0.001$ ). Mutual and commensal lepidopteran myrmecophiles had, on average, about two more host species than kleptoparasites and parasites (Fig. 5). Relationship type did not vary with host range within the Coleoptera ( $\chi^2 = 6.6$ ,  $df = 3$ ,  $P = 0.085$ ), Diptera ( $\chi^2 = 0.10$ ,  $df = 2$ ), Hemiptera ( $\chi^2 = 2.27$ ,  $df = 1$ ,  $P = 0.132$ ), or Hymenoptera ( $\chi^2 = 0.14$ ,  $df = 1$ ,  $P = 0.831$ ).

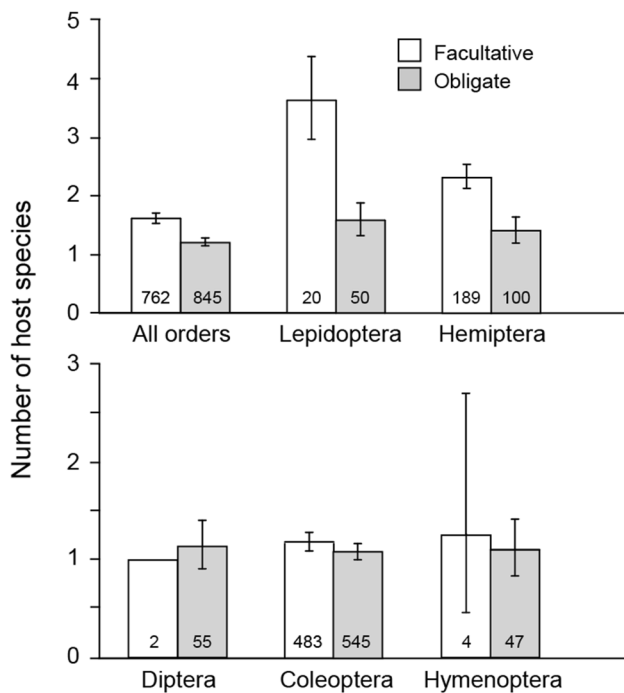


**Fig. 1** The number of myrmecophile species exhibiting different degrees of reliance on their ant hosts and type of relationships with ants



**Fig. 3** The number of host ant species per myrmecophile species for the five most speciose orders of myrmecophiles. Data are estimates and 95% confidence intervals from a generalized linear model contrasting host range across orders. Sample sizes (numbers of myrmecophile species) are given above the x axis





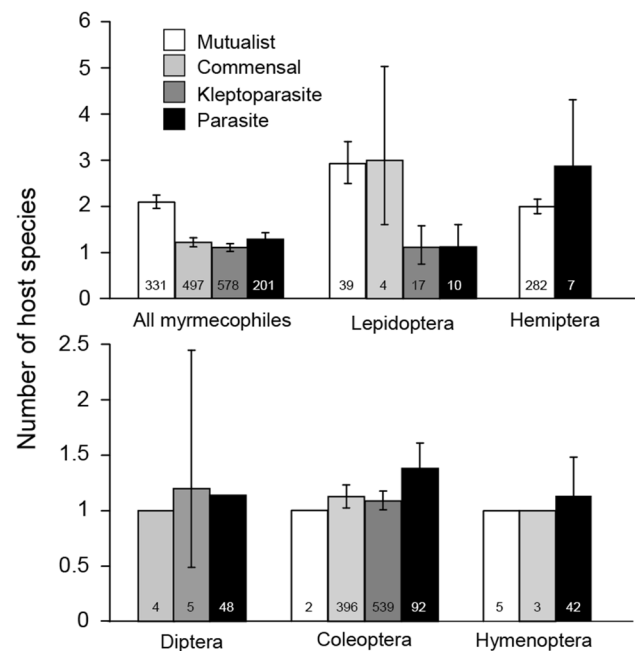
**Fig. 4** Differences in the number of host ant species per myrmecophile species between facultative and obligate interactions for all species and for each of the most five most speciose orders. Data are estimates and 95% confidence intervals from a generalized linear model contrasting host range between interaction types. Sample sizes (numbers of myrmecophile species) are given above the x axis

## Discussion

Our global analysis of the host use of myrmecophiles revealed four general conclusions. First, myrmecophiles are highly diverse, but exhibited narrow reported host ranges (Fig. 1). Second, facultative myrmecophiles had a broader host range than obligates. Third, mutualistic associations had a greater host breadth than other relationship types. Last, orders that had primarily mutualistic taxa (Lepidoptera and Hemiptera) exhibited broader host ranges than orders with taxa that did not.

### Host range of myrmecophilic orders

Our synthesis revealed a high diversity and wide range of invertebrate taxa closely associated with ants. Insects are the most speciose group of myrmecophiles, but there are also taxa from the Crustacea, Arachnida, Diplopoda and Chilopoda. These myrmecophiles have a wide range of associations with their ant hosts, from mutualisms where myrmecophiles provide honey dew in return for protection by their ant hosts, to parasites living within nest feeding on ant brood. Despite local diversity of ants being high in most environments, myrmecophiles in general have narrow host ranges, with the vast



**Fig. 5** Differences in the number of host ant species per myrmecophile species among mutualistic, commensal, kleptoparasitic and parasitic interaction types. Data are estimates and 95% confidence intervals from a generalized linear model contrasting host range between interaction types, for all species and for each of the most five most speciose orders. Sample sizes (numbers of myrmecophile species) are given above the x axis

majority of species having been reported to associate with only one ant species.

We found that lepidopterans had a broader host range, of about two ant species per lepidopteran species, than the other orders of myrmecophiles, except hemipterans. Differences in life history traits among orders might explain this difference. For example, lepidopterans associate with ants as caterpillars, and spend a large part of their larval stage feeding on host plants (Fielder 1996). As the food plant is a more important resource than protection from ants, the ability to associate with multiple host ant species across the geographic range of the host plant(s) would be more advantageous than specializing towards associations with only one ant species. Several studies indicate support for the notion that different lineages of the same species will utilize different host ants depending on locality (Witek et al. 2008; Eastwood et al. 2006). This localized specialization may be a major factor influencing broader host range of lepidopterans.

Similar to lepidopterans, most hemipteran myrmecophiles are mutualists, and they show a broader host range than the other orders of myrmecophiles, but on average, a narrower host range than lepidopterans. The difference between lepidopterans and hemipterans may be that aphids are “farmed” by ants, thus leading to potential coevolution between hemipteran myrmecophiles and ants (Ivens 2015).

Ants are able to control hemipteran myrmecophiles, resulting in specialization of not only the myrmecophile but also the host (Maschwitz and Hänel 1985; Schneider and LaPolla 2011). Additionally, certain species of ants may monopolize aphid resources, excluding other ants from hemipteran colonies and reducing potential host interactions (Delabie 2001; Blüthgen et al. 2006). Finally, many ant species are obligate hemipteran farmers (Maschwitz and Hänel 1985; Oliver et al. 2008; Schneider and LaPolla 2011). These specialized associations potentially drive speciation among both hemipterans myrmecophiles and ant hosts (Oliver et al. 2008).

The similar and narrow host ranges of myrmecophiles in the Diptera and Hymenoptera may have resulted from the fact that most are ant parasites. Moreover, they are parasitoids, laying their eggs either in adult workers or ant brood (Porter 1998; Loiacono et al. 2013). To penetrate a host ant colony, and/or host ant individual (when an organism is an internal parasite) requires a high degree of specialised adaptations (behavioural, chemical) to overcome ant defence systems, and therefore may limit host breadth of a species (Thompson 1994). A narrow host range was also observed in the Coleoptera, but this group had a diverse set of relationships with ants. Their use of a low number of host ant species may relate to abilities to better utilize particular host resources (Thompson 1994) or being limited by ant defensive mechanisms (von Beeren et al. 2011). Overall, taxa with narrow host ranges are likely more efficient at using their particular ant hosts as resources, and are most likely specialized, behaviourally or physically, to nullify their ant host's defences.

### Host range of dependence and relationship types

Consistent with our predictions, we found that facultative myrmecophiles have broader host ranges than obligates. Facultative associations are often opportunistic in nature, relying on chance encounters of symbionts interacting with a host (Rodrigues et al. 2010). The ability to interact with more ant species would increase the chance of encountering hosts and therefore benefit a facultative myrmecophile. The narrower host ranges observed in obligate myrmecophiles are likely to result from beneficial adaptations that allow better use of host resources. Coevolution among obligate symbionts is likely to increase the dependence on chosen hosts and lead to narrower host ranges (Fleming and Holland 1998; Machado et al. 2005; Campbell et al. 2013).

Our results are consistent with prediction that myrmecophiles involved in mutualistic interactions would have broader host ranges than those in antagonistic interactions (kleptoparasites and parasites). While some mutualistic interactions are highly specialised, broad host ranges among mutualists have been widely reported. For example, photosynthetic dinoflagellate symbionts often use a wide range of

host corals as structural hosts (Baker 2003) and hummingbirds can pollinate a wide range of flowers and in return, harvest nectar (Hoeksema and Brun 2000). As mutualists have ~61% broader host range than other relationships, it is apparent that they are able realize a wider potential niche than other myrmecophiles.

We predicted that parasitic myrmecophiles, the symbionts that are most antagonistic to ants, would have the narrowest host range. The basis of our prediction was that, as parasites feed directly on ants or ant brood, ants would likely evolve defensive mechanisms to prevent parasitic attacks, forcing the parasites to utilize a narrower range of host species so that resources were more readily available. However, we found that kleptoparasites and commensals had host ranges equally narrow as parasitic myrmecophiles. There are several explanations for this. Ants use a wide range of chemical, tactile, visual, and audio cues to recognize nest mates and larvae (Akino et al. 1999; Jackson and Ratnieks 2006). As different ant species use different cues, and cues within species can vary, adaptations to overcome these defenses may limit the number of host associations a myrmecophile is able to have. It may be most beneficial to allocate resources to overcome defensive cues of a limited number of ant species, rather than utilizing resources to associate with a multitude of hosts.

Interestingly, commensal myrmecophiles shared similar host ranges as kleptoparasites and parasites. This contrasted with our prediction that neutral associations would exhibit broader host ranges than antagonistic associations. Commensal myrmecophiles exhibit a wide range of life styles associated with ants. For example, they may overwinter in ant nests (Sanders 1964), live in waste middens of a colony (Rettenmeyer et al. 2011), or inhabit the galleries of a nest (Gray 1971). These differing life styles make it difficult to determine what unifying factor might be limiting the host range of commensals. It may also be that commensals are equally limited by ant defenses as kleptoparasites and parasites.

It should be noted that the number of associations and nature of interactions for many species of myrmecophiles have not been extensively studied (Mynhardt 2013). Consequently, variation in host range and patterns among interaction types is not fully understood and has the potential to change with further investigation of particular groups. Moreover, it has also been suggested that there could be over 80,000 extant myrmecophilous species (Schönrogge et al. 2000). The search parameters for our study were defined to retrieve references that provided direct evidence of relationships among myrmecophiles and their host ants. Thus, although the species richness of myrmecophiles considered here is high ( $n=1605$ ), it is still relatively small fraction of the potential diversity. The limited information on individual myrmecophile species (~90% with only one citation) indicates the need for more

research on these ant symbionts, specifically studies of biology and interactions with their ant hosts (Mynhardt 2013). Given that host range of invertebrates can be related to study effort (Poore et al. 2008), we used the number of publications per myrmecophile species as a statistical offset in our analyses to help account for the possible effects of variation in sampling effort (Werner and Guven 2007). While we are confident that using a statistical offset mitigated the influence of sampling effort on the patterns of host range across orders and interaction types, the low number of studies for most myrmecophile species indicates that our model estimates of host range are likely at a lower limit. Clearly more research is needed, not just for groups of myrmecophiles but also for particular species to increase our understanding of myrmecophilic associations.

To strengthen future myrmecophile research, a phylogenetic analysis of myrmecophile species, ant hosts, and host range would be beneficial, as accounting for relatedness of hosts and symbiont species can be influential in determining host range (Nunn et al. 2004; Poore et al. 2008; Poulin et al. 2011). Although ant phylogenetics (Rubin and Moreau 2016) and the phylogenies for many myrmecophile lineages such as lycaenid butterflies (Pellissier et al. 2017) or staphylinid beetles (Parker and Grimaldi 2014; Maruyama and Parker 2017) are improving, there is still not enough information at the species level to do a global analysis, as presented here.

## Conclusion

Our global synthesis indicates that facultative associations promote broader host ranges than obligate interactions, and that beneficial (mutualistic) associations promote broader host ranges than neutral (commensal) and antagonistic (kleptoparasitic and parasitic) associations. Our study has broad implications for the evolution of symbiotic associations. As ants live in highly guarded social societies, most myrmecophiles exhibit narrow host ranges to exploit the resources associated with those societies. By studying myrmecophiles, we have a better understanding of how differences in host dependence and relationship influences host range in symbiotic associations.

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