

Myrmica ants host highly diverse parasitic communities: from social parasites to microbes

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Abstract *Myrmica* ants have been model species for studies in a variety of disciplines, including insect physiology, chemical communication, ant social dynamics, ant population, community ecology, and ant interactions with other organisms. Species belonging to the genus *Myrmica* can be found in virtually every habitat within the temperate regions of the northern hemisphere and their biology and systematics have been thoroughly studied. These ants serve as hosts to highly diverse parasitic organisms from socially parasitic butterfly caterpillars to microbes, and many *Myrmica* species even evolved into parasitizing species of their own genus. These parasites have various impacts both on the individuals and on the social structure of their hosts, ranging from morphological malformations to reduction in colony fitness. A comprehensive review of the parasitic organisms supported by *Myrmica* and the effects of these organisms on individuals and on whole ant colonies has not yet been compiled. Here, we provide a review of the interactions of these organisms with *Myrmica* ants by discussing host and parasite functional, behavioral or physiological adaptations. In addition, for all “symbiont groups” of *Myrmica* ants described in this paper, we examine the

present limitations of the knowledge at present of their impact on individuals and host colony fitness. In conclusion, we argue that *Myrmica* ants serve as remarkable resource for the evolution of a wide variety of associated organisms.

Keywords Host–parasite interaction · *Maculinea* · *Microdon* · Myrmecophily · Nematodes · *Rickia wasmannii*

The Red Ants of the genus *Myrmica*

In the temperate zone of North America, Asia and Europe one of the most common insect groups is the Red Ants of the genus *Myrmica* (Radchenko and Elmes, 2010). There are about 180 described species belonging to the genus *Myrmica* in the Holarctic. Most of the species, however, are found in Europe and Asia, while a smaller proportion occurs in North America (Radchenko and Elmes, 2010). They occur in virtually every terrestrial habitat, including meadows, forests, steppes and mountains (Radchenko and Elmes, 2010). The variations in the habitats occupied across the range are likely to result in different diets, habits, and ant or non-ant associations. *Myrmica* colonies contain on average 200–500 workers and usually one, but sometimes a few functional queens (Elmes and Petal, 1990; Wardlaw and Elmes, 1996). New nests can be founded by a single newly mated queen or, quite often, through the process known as colony budding (Elmes et al., 1998). Oviposition starts in early spring and lasts through the summer until autumn (Radchenko and Elmes, 2010). Parts of the larvae develop rapidly, but others enter diapause and overwinter (Fig. 1). The latter group includes both workers and all the gyne-presumptive larvae (Brian and Kelly, 1967).

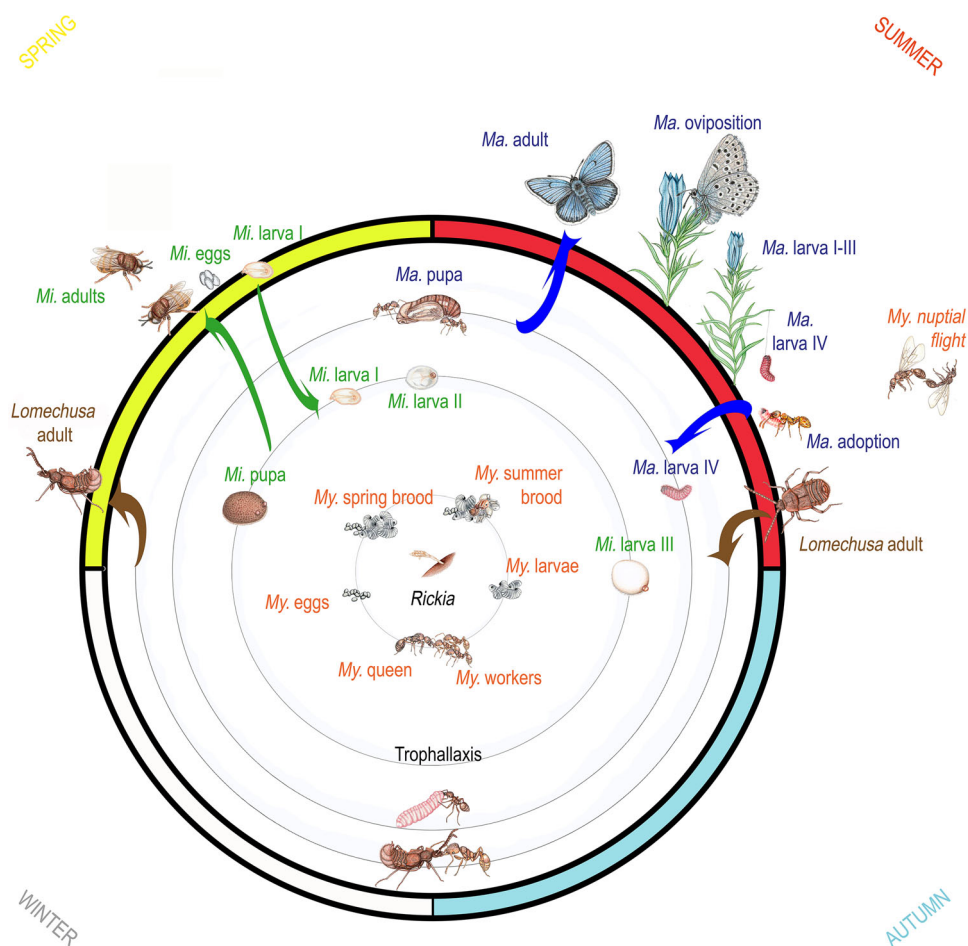
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Fig. 1 The life cycle of *Myrmica* ants (My.) and some of their frequent social parasites: *Microdon myrmicae* (Mi.), *Maculinea alcon pneumonanthe* ecotype (Ma.) and *Lomechusa pubicollis*. The fungal ectoparasite *Rickia wasmannii* is located inside the nest as it infects both workers and queens. *Arrows* reflect moments of entering and leaving host colony by social parasites. Numbers I, II, III, IV refer to particular larval instars



Myrmica ants have been model species for studies in a variety of disciplines, including insect physiology, chemical communication, social dynamics, ant population and community ecology, phylogeography and speciation (Radchenko and Elmes, 2010). There are slightly more than 700 scientific publications on *Myrmica* ants recorded on the WoS (as of 12/05/2014), although most concentrate on a handful of species. In addition, a comprehensive monograph on the biology and systematics of *Myrmica* ants in the Palearctic has been recently published by Radchenko and Elmes (2010).

Myrmica ants support a highly diverse array of parasitic organisms, many of which also have conservation value (see Thomas and Settele, 2004). The considerable amount of published data on these parasitic species notwithstanding, a comprehensive review treating these organisms and their known or probable effects on *Myrmica* ants has not been published yet. In our paper, we focus on *Myrmica* ants as hosts of many parasitic organisms belonging to various taxonomic groups, including social parasites, ecto- and endoparasitic species, such as fungi and nematodes, and microbial pathogens. Our aim is to review host and parasite functional, behavioral or physiological adaptations as well

as the current knowledge on the impact of these organisms on the individuals, and on the colony structure of their *Myrmica* hosts.

Exploitation of an ant society: social parasites

There are many definitions of social parasitism in ants (see Buschinger, 2009). In our review we present organisms that fit (i) the strict definition of social parasites, implying interaction between two social species, and (ii) the more broad definition that applies to other insects exploiting the resources of a single ant colony for a long period of time (see also Nash and Boomsma, 2008).

Ants parasitizing ants

Most ant social parasites of *Myrmica* species are members of the same genus (Radchenko and Elmes, 2003), with the exception of *Formicoxenus provancheri* and *F. quebecensis*. These two latter species are xenobiotic ants, i.e., they are able to build their own nest and take care of their brood, but they depend on their host for nutrition (Buschinger,

Table 1 Records of association between *Myrmica* ant species and the wide spectrum of their parasites

Taxonomic group of parasite	Parasite species	Type of association	<i>Myrmica</i> host species	References
Ants	<i>Formicoxenus provancheri</i>	xenobiosis	<i>M. incompleta</i>	Francoeur et al., 1985
	<i>Formicoxenus quebecensis</i>	xenobiosis	<i>M. ataskensis</i>	Francoeur et al., 1985
	<i>Myrmica arnoldii</i>	temporal inquilinism (?)	<i>Myrmica</i> sp.	Radchenko and Elmes, 2010
	<i>Myrmica bibikoffi</i>	temporal inquilinism	<i>M. sabuleti</i> , <i>M. spinosior</i>	Radchenko and Elmes, 2010
	<i>Myrmica luteola</i>	temporal inquilinism	<i>Myrmica</i> sp.	Radchenko and Elmes, 2010
	<i>Myrmica semiparasitica</i>	temporal inquilinism	<i>M. punctiventris</i>	Francoeur, 2007
	<i>Myrmica vandeli</i>	temporal inquilinism	<i>M. scabrinodis</i>	Radchenko and Elmes, 2010
	<i>Myrmica nefaria</i>	not clear; workers present	<i>M. rubestris</i>	Bharti, 2012
	<i>Myrmica colax</i>	inquilinism	<i>M. striologaster</i>	Cole, 1957
	<i>Myrmica ereptrix</i>	inquilinism	<i>M. aimonissabaudiae</i>	Radchenko and Elmes, 2001
	<i>Myrmica hirsuta</i>	inquilinism	<i>M. sabuleti</i> , <i>M. lonae</i>	Radchenko and Elmes, 2010
	<i>Myrmica kabylica</i>	inquilinism	<i>M. cognianti</i>	Radchenko and Elmes, 2010
	<i>Myrmica karavajevi</i>	inquilinism	<i>M. scabrinodis</i> , <i>M. sabuleti</i> , <i>M. lonae</i> , <i>M. rugulosa</i> , <i>M. gallieni</i>	Radchenko and Elmes, 2010; Witek et al., 2013a
	<i>Myrmica lampra</i>	inquilinism	<i>M. ataskensis</i>	Francoeur, 2002
	<i>Myrmica laurae</i>	inquilinism	<i>M. scabrinodis</i> , <i>M. spinosior</i>	Radchenko and Elmes, 2010
<i>Myrmica lemasnei</i>	inquilinism	<i>M. sabuleti</i> or <i>M. spinosior</i>	Radchenko and Elmes, 2010	
microgynae of <i>M. rubra</i>	inquilinism	<i>M. rubra</i>	Radchenko and Elmes, 2010	
<i>Myrmica myrmicoxena</i>	inquilinism	<i>M. lobulicornis</i>	Radchenko and Elmes, 2010	
<i>Lomechusa pubicollis</i>	predatory/ cuckoo	<i>Myrmica</i> sp.	Hölldobler and Wilson, 1990	
Beetle				

Table 1 continued

Taxonomic group of parasite	Parasite species	Type of association	<i>Myrmica</i> host species	References
Butterflies	<i>Maculinea alcon</i> <i>pneumonanthe</i> ecotype	cuckoo	<i>M. ruginodis</i>	Thomas et al., 1989; Elmes et al., 1994; Als et al., 2004
			<i>M. rubra</i>	Thomas et al., 1989; Elmes et al., 1994; Als et al., 2004
			<i>M. scabrinodis</i>	Höttinger et al., 2003; Elmes et al., 2003; Sielezniew and Stankiewicz, 2004; Tartally et al., 2008a; Witek et al., 2008
			<i>M. vandeli</i>	Sielezniew and Stankiewicz, 2004; Tartally et al., 2008a
			<i>M. salina</i>	Tartally et al., 2008a
			<i>M. aloba</i>	Arnaldo et al., 2011; Tartally et al., 2013
			<i>M. schencki</i>	Thomas et al., 1989; Steiner et al., 2003; Stankiewicz et al., 2005a; Tartally et al., 2008a, Sielezniew and Dziekanska, 2009
			<i>M. sabuleti</i>	Thomas et al., 1989; Steiner et al., 2003; Tartally et al., 2008a
			<i>M. scabrinodis</i>	Thomas et al., 1989;
			<i>M. speciooides</i>	Steiner et al., 2003; Tartally et al., 2008a
			<i>M. sulcinodis</i>	Steiner et al., 2003; Tartally et al., 2008a
			<i>M. lonae</i>	Steiner et al., 2003
			<i>M. ruginodis</i>	Tartally et al., 2008a
			<i>M. rugulosa</i>	Steiner et al., 2003
			<i>M. rugulosa</i>	Stankiewicz et al., 2005b
<i>Maculinea arion</i>	<i>M. sabuleti</i> , <i>M. scabrinodis</i>	predatory	Thomas et al., 1989; Sielezniew et al., 2010a	
	<i>M. schencki</i> , <i>M. lobicornis</i> , <i>M. hellenica</i> , <i>M. rugulosa</i>		Sielezniew and Stankiewicz, 2008; Sielezniew et al., 2010	
	<i>M. lonae</i> , <i>M. sulcinodis</i>	cuckoo/ predatory	Sielezniew et al., 2010b; Casacci et al., 2011	
<i>Maculinea teleius</i>	<i>M. rubra</i>		Thomas et al., 1989; Stankiewicz and Sielezniew, 2002; Tartally and Varga, 2005; Witek et al., 2008	
	<i>M. ruginodis</i>		Witek et al., 2008	
	<i>M. scabrinodis</i>		Tartally et al., 2008b; Witek et al., 2008	
	<i>M. scabrinodis</i> , <i>M. rubra</i>	predatory	Thomas et al., 1989; Stankiewicz and Sielezniew, 2002; Tartally and Varga, 2008; Witek et al., 2008	
	<i>M. gallieni</i>		Stankiewicz and Sielezniew, 2002; Tartally and Varga, 2008	
	<i>M. ruginodis</i>		Yamaguchi, 1988; Witek et al., 2008, 2010	
	<i>M. vandeli</i>		Thomas et al., 1989; Tartally and Varga, 2008	
	<i>M. rugulosa</i>		Witek et al., 2008, 2010	
	<i>M. slovaca</i>		Tartally and Varga, 2008	
	<i>M. speciooides</i>		Tartally and Varga, 2008	
	<i>M. sabuleti</i>		Thomas et al., 1989	
	<i>M. lobicornis</i>		Yamaguchi, 1988	
	<i>M. kamishattica</i> , <i>M. forcipata</i> , <i>M. angulinodis</i>		Woyciechowski et al., 2006	
	<i>M. kurokii</i>		Yamaguchi, 1988	

Table 1 continued

Taxonomic group of parasite	Parasite species	Type of association	Myrmica host species	References
Hoverflies	<i>Microdon albicomnatus</i>	predatory	<i>M. incompleta</i>	Akre et al., 1990; Howard et al., 1990
	<i>Microdon myrmicae</i>	predatory	<i>M. scabrinodis</i>	Schönroge et al., 2002; Speight, 2003; Stankiewicz, 2003; Beuker, 2004; Gammelmo and Aarvik, 2007; Bonelli et al., 2011
Ensifera	<i>Myrmecophilus acervorum</i>	predatory	<i>M. rubra</i> , <i>M. gallienii</i>	Stankiewicz, 2003; Bonelli et al., 2011
			<i>M. vandeli</i> , <i>M. sabuleti</i>	Bonelli et al., 2011
			<i>M. aloba</i>	Tartally et al., 2013
			<i>M. ruginodis</i> , <i>M. rubra</i> , <i>M. sabuleti</i>	Bezdečka et al., 2000
Collembola	<i>Cyphoderus albinus</i>	unknown	<i>M. rubra</i> , <i>M. ruginodis</i> , <i>M. scabrinodis</i>	Dekoneck et al., 2007
	<i>Platyarthrus schoblii</i>	unknown	<i>Myrmica</i> sp.	Homung et al., 2005
Acari	<i>Laelaspis myrmicae</i>	unknown	<i>M. rubra</i>	Constantinescu et al., 2011
	<i>Gymnolaelaps prestoni</i>	unknown	<i>Myrmica</i> sp.	Joharchi et al., 2011
Nematodes	<i>Dyplioscapter lycostoma</i> (Rhabditidae)	endoparasite	<i>M. rugulosa</i>	Poinar, 2012
	Member of Mermithidae family	endoparasite	<i>M. gallienii</i> , <i>M. rubra</i> , <i>M. ruginodis</i> , <i>M. sabuleti</i> , <i>M. scabrinodis</i> , <i>M. schencki</i> , <i>M. sulcinodis</i>	Czechowski et al., 2007a, b; Csósz and Majoros, 2009; Csósz, 2012
Fungi	<i>Hirsutella stibelliformis</i> var. <i>myrmicarum</i>	endoparasite	<i>M. rubra</i>	Evans et al., 2010
	<i>H. subramanianii</i> var. <i>myrmicarum</i>	endoparasite	<i>M. rubra</i>	Evans et al., 2010
Isopoda	<i>Hormiscium myrmecophilum</i>	endoparasite	<i>M. sabuleti</i> , <i>Myrmica</i> sp.	Espadaler and Santamaria, 2012
	<i>Paraisaria myrmicarum</i>	endoparasite	<i>M. rubra</i>	Evans et al., 2010
Microbes	<i>Rickettsia wasmannii</i>	ectoparasite	<i>M. scabrinodis</i> , <i>M. gallienii</i> , <i>M. rubra</i> , <i>M. ruginodis</i> , <i>M. sabuleti</i> , <i>M. slovaca</i> , <i>M. speciooides</i> , <i>M. spinosior</i> , <i>M. vandeli</i>	Espadaler and Santamaria, 2012; Csata et al., 2013
		pathogens	<i>M. rubra</i>	Espadaler and Santamaria, 2012; Csata et al., 2013
				Pearson and Raybould, 1998

2009). Both species are found in North America; *F. provancheri* is a parasite of *Myrmica incompleta* and *F. quebecensis* is associated with *M. alaskensis*. Nests of *Formicoxenus* ants are usually established at the edge of the nest of their host and the parasites always rear their brood separately from host brood chambers (Errard et al., 1997). The majority of parasitic individuals reside in the host nest and they are engaged in licking *Myrmica* workers to obtain regurgitations (Errard et al., 1997). Both *Formicoxenus* species use chemical mimicry, which is acquired during the first days of their adult life and is then maintained by the ants by frequently licking off cuticular hydrocarbon compounds from the hosts (Lenoir et al., 1997).

All other socially parasitic ant species of *Myrmica* belong to genus *Myrmica* itself (Radchenko and Elmes, 2003, 2010). These species are either (i) temporary social parasites, where the parasite queen depends on the host only during the founding stage of the colony or (ii) inquiline, where parasite queen(s) coexist(s) with host queen(s) and invest her (their) energy only in the production of sexual forms. Five *Myrmica* species are considered temporary social parasites: *M. arnoldii*, *M. bibikoffi*, *M. luteola*, *M. semiparasitica* and *M. vandeli* (Table 1) (see Radchenko and Elmes, 2003). The most commonly found is *M. vandeli*, which, as suggested by Radchenko and Elmes, (2003), is also a free-living competitor of *M. scabrinodis* in the center of its range, whereas in marginal populations it could become a temporal parasite of *M. scabrinodis*. The considerable frequency of mixed nests of both species could be seen as evidence of this strategy (Elmes et al., 2003). The biology of other temporary parasitic *Myrmica* species is not well known and in some cases only very few data are available, an indication that this kind of parasitism in genus *Myrmica* is still very much understudied (Buschinger, 2009).

Inquilinism has evolved several times within the genus *Myrmica* and some of the parasite-host pairs strongly support Emery's rule, which states that social parasites are closely related to their hosts (Emery, 1909; Jansen et al., 2010). This is indeed true for some parasitic ant species, which already share similar life history traits with their host ants, thus allowing them to enter and exploit the host resources more easily. Currently, 12 permanent ant social parasites are recognized in the genus *Myrmica* (Radchenko and Elmes, 2010; Jansen et al., 2010; Bharti, 2012) (Table 1). These social parasites show a set of characteristics called "inquiline syndrome" (Wilson, 1971) which include, among others, the reduced size of the queens, a lack of the worker caste, broadened postpetioles, hairiness and the reduction of the spurs on the middle and hind tibiae (Radchenko and Elmes, 2003). Data on host specificity of *Myrmica* inquilines are quite scarce, since in the case of some species only single specimen was collected, e.g. *M. myrmicoxena*

which was found only once in 1869 inside the nest of *M. lobicornis*. In contrast, *M. karavajevi* seems to be one of the most widespread *Myrmica* inquiline exploiting nests of several host species (Radchenko and Elmes, 2010; Witek et al., 2013a), but even for this species there are only about 30 records originating from different parts of Europe (Czechowski et al., 2012; Czekes et al., 2012; Witek et al., 2013a).

The most spectacular example of ongoing parasitic speciation processes within the genus *Myrmica* is that of *M. rubra* and its microgyne form, the so-called *M. microrubra* (Savolainen and Vepsäläinen, 2003). The small queens of *M. rubra* are results of an isometric reduction in normalized queens called macrogynes and they have the same negative queen effect on the development of overwintering larvae as 'normal' queens have (Elmes, 1976). Owing to their well-defined morphological character set, Seifert (1993) described this microgyne morph as a separate species under the name *M. microrubra*. Later, studies based on molecular evidence demonstrated that *M. microrubra* has not evolved separately to *M. rubra* and although they are locally separated, they do not differentiate on the regional level and they share a common gene pool (Steiner et al., 2006; Vepsäläinen et al., 2009; Leppänen et al., 2011). Therefore, the microgyne can be more readily considered an intraspecific parasitic morph of *M. rubra* (Steiner et al., 2006; Jansen et al., 2010). Some studies suggest, due to its distinctive morphological and behavioral features, that it is an intriguing example of ongoing sympatric speciation (Vepsäläinen et al., 2009; Jansen et al., 2010; Leppänen et al., 2011). The microgyne forms occur also in *M. ruginodis*, but in contrast to *M. microrubra* they are free living and produce normal workers (Brian and Brian, 1955).

Generally, low local density of *Myrmica* social parasites makes studies on adaptation and co-evolution between social parasites and their hosts very difficult (Radchenko and Elmes, 2010). We still do not know how host colonies are chosen and then infested, and which mechanisms allow *Myrmica* parasitic queens to survive and reproduce inside host colonies. Evidence that orphaned *Myrmica* colonies accept more readily foreign queens (Radchenko and Elmes, 2010) might suggest that they are generally more prone for ant social parasitism. Nevertheless, there is a need to refine our knowledge of associations between *Myrmica* ants and their inquilines through increasing the number of records both at local and at wider geographical range.

Protected butterfly caterpillars as social parasites

About 5,000 butterfly species belong to Lycaenidae family and most of these species are myrmecophilous (Pierce et al., 2002). As pointed out by Fiedler (2006), in the Palearctic region obligate ant-butterfly associations are rare and they

are biased towards the genus *Myrmica*, which are mainly hosts for obligate socially parasitic *Maculinea* butterflies (Thomas, 1980), but they can be also used by many other Lycaenids as facultative hosts (Fiedler, 2006). Over the course of the last decade, more than 100 scientific articles have been published on this butterfly genus (WoS), many of them focusing on host specificity and parasites' adaptations to successfully exploit ant colonies. There are four *Maculinea* (abbreviated as "Ma." below) species living in Europe: *Ma. teleius*, *Ma. nausithous*, *Ma. arion* and two ecotypes of *Ma. alcon* according to their foodplants, the *pneumonanthe* ecotype (former *Ma. alcon*) and the *cruciata* ecotype (former *Ma. rebeli*) (Als et al., 2004; Bereczki et al., 2005; Tartally et al., 2014). All of them have a peculiar life cycle (Fig. 1) and they require two different resources for larval development; namely, specific food plant species and *Myrmica* ant hosts (Thomas, 1980). After 2 weeks of feeding on the food plant, the 4th instar larva falls onto the ground and it has to be taken and adopted by *Myrmica* workers in order to continue its development (Thomas, 1984). Once inside the host nest, caterpillars such as *Maculinea teleius* and *Ma. arion* actively prey on *Myrmica* brood (Thomas and Wardlaw, 1992), or, in the case of both *Ma. alcon* ecotypes, which apply a so-called cuckoo strategy, larvae are mostly fed by ant workers and rarely prey on ant brood (Elmes et al., 1991). They can also use both strategies, as for instance *Ma. nausithous* does (Thomas and Elmes, 1998; Patricelli et al., 2010). From adoption till pupation *Maculinea* larvae spend 11 or 23 months inside *Myrmica* colonies (Thomas et al., 1998; Schönrogge et al., 2000; Witek et al., 2006).

Females' choices for the oviposition site play a key role in the survival of their offspring and therefore in the persistence of butterfly populations (Renwick and Chew, 1994). Studies dealing with the oviposition behavior of *Maculinea* butterflies have yielded contrasting results (e.g. Van Dyck et al., 2000; Thomas and Elmes, 2001). Some authors argue that during oviposition, *Ma. alcon* (*pneumonanthe* ecotype) and *Ma. nausithous* are unable to detect the presence of the host ants and females choose the larval host plant solely on the basis of phenological stage (Thomas and Elmes, 2001; Nowicki et al., 2005; Musche et al., 2006; Fürst and Nash, 2010; Czekes et al., 2014). However, other field studies suggest that the presence or absence of host ants influences females as they select oviposition sites (Scheper et al., 1995; Van Dyck et al., 2000; Wynhoff et al., 2008; Van Dyck and Regniers, 2010). All the aforementioned studies accounted for the role of single host ant species in the butterfly's oviposition choices and did not take into consideration all the potential *Myrmica* species present at the sites (Van Dyck et al., 2000; Thomas and Elmes, 2001; Wynhoff et al., 2008; Fürst and Nash, 2010). On the other hand, recently a correlation was found

between *Maculinea arion* oviposition choices and the presence of any *Myrmica* species in the surroundings of the host plant (Patricelli et al., 2011). How the female's selection of a valuable oviposition site is influenced by the closeness of *Myrmica* nests is still unclear. Irrespective of the mechanism, the female's ability to locate a suitable plant for oviposition, both with regards to host plant quality and *Myrmica* spp. presence/abundance, is of crucial importance for the butterfly brood in sites where there is a limited overlap between larval food plants and the foraging range of their host ants.

The next decisive point is the infiltration of the butterfly larvae in the host ant nest. The adoption of the caterpillars by ants is mediated by chemical deception (Akino et al., 1999; Schönrogge et al., 2004; Nash et al., 2008; Fürst et al., 2012). As it has been demonstrated in the case of the cuckoo butterflies, *Maculinea alcon* (*cruciata* ecotype) pre-adoption caterpillars synthesize a simple mixture of cuticular hydrocarbons (CHC) that weakly mimic those of *Myrmica* species in general, but that have the closest match to the hydrocarbon signature of their local host ant *M. schencki* (Akino et al., 1999; Elmes et al., 2002). Yet the low level of chemical similarity means that pre-adoption butterfly caterpillars could be retrieved by any foraging *Myrmica* species that happen to encounter it, and not just by *M. schencki* (Akino et al., 1999; Elmes et al., 2002; Schönrogge et al., 2004; Thomas et al., 2013) although in the laboratory adoption appears to be the most rapid with this local, main host ant species. Nash et al. (2008) found that the greater the match between the CHC-profile of *Ma. alcon* (*pneumonanthe* ecotype) and two of its host *Myrmica* species, the more easily ant colonies were exploited. They also demonstrated an ongoing 'arms race' between the *Maculinea* parasite and its primary host *Myrmica rubra*, which has significant genetic differentiation between populations. On the other hand, they did not find evidence of co-evolution between the butterfly and its second, sympatric host *M. ruginodis*, which in turn has panmictic populations with higher gene flow rate and thus has genetically more homogeneous populations. Thus, authors reach the conclusion that 'secondary' hosts may provide an evolutionary refuge for a parasite during periods of maladaptation with their preferred hosts and this would lead to dynamic shifts in host use over time. Studies on post-adoption changes in the chemical signatures of *Maculinea* larvae and *Myrmica* hosts are scarce (e.g. Witek et al., 2013b), but we may assume that selection on hosts to avoid being parasitized fuels the co-evolutionary arms races, in which parasites evolve better mimicry and hosts improve their recognition of parasites (Foitzik et al., 2003).

The communication in ants is mainly based on chemical cues (Hölldobler and Wilson, 1990), but the acoustic channel is also used, thus parasites are able to manipulate

their hosts by mimicking sound signals as well. After the seminal study by Devries et al. (1993), Barbero et al., (2009a) reported the first case of acoustic mimicry in an ant social parasite. Authors demonstrated that *Ma. alcon* (*cruciata* ecotype) larvae and pupae are able to mimic the sounds produced by *Myrmica schencki* queens, thus eliciting benevolent responses in worker ants, and, consequently, obtaining a high status in the host colony hierarchy. Up till now, chemical signals have failed to explain why butterfly larvae are treated preferentially to host ant worker brood, while acoustics now sheds light on the background of this behavior (Barbero et al., 2012). Differences in the sound emission of queens and worker ants have been demonstrated to occur in various *Myrmica* species, and the ability to mimic the highest social cast is also present in *Maculinea* predatory species (Barbero et al., 2009b, 2012; Thomas et al., 2010; Settele et al., 2011, Sala et al., 2014). Performing behavioral experiments to compare the role of acoustics in a predatory (*Ma. teleius*) vs. a cuckoo species (*Ma. alcon pneumonanthe* ecotype) in two different moments of the parasite life cycle, Sala et al. (2014) showed that ant workers responded preferentially to the sounds emitted by the predatory species recorded before any contact with the host ants (i.e. preadoption), as well as by the integrated (i.e. postadoption) larvae of the cuckoo forms; thereby, revealing a role of acoustic signals both in the adoption ritual and in postadoption treatment of the parasites.

Variations in chemical and acoustical adaptations applied by different *Maculinea* species are likely to depend on different feeding strategies and niches occupied by butterfly larvae inside an ant colony. Thomas et al. (2005) suggested that penetration of the most protected niches within a host colony and the stage of the social parasites at the time of entry into the ant nest influence the host specificity patterns. In the case of *Maculinea* butterflies, both cuckoo ecotypes are those that occupy central ant brood chambers and they are expected to be more host specific than predatory species (Thomas et al., 2005). The main cost of the cuckoo lifestyle is that increased specialization restricts each social parasite to a smaller regional part of its host range, as local adaptations seem to exist (Thomas et al., 2013). Recent studies carried out across Europe reveal complicated patterns of local host ant specificity where more than one *Myrmica* species is successfully exploited by the same *Maculinea* butterfly species (e.g., Elmes et al., 1994; Pech et al., 2007; Tartally et al., 2008; Witek et al., 2008; Sielezniew et al., 2010) (Table 1). Multiple host ant exploitation can depend e.g. on the localization of population with respect to the species range, the existence of cryptic species, and particular ecological conditions, which can influence the life history traits of *Myrmica* colonies within particular sites (Thomas et al.,

2005; Jansen et al., 2011). Further surveys including crossover, starvation or rescue experiments are; therefore, necessary for a better understanding of host ant specificity patterns in *Maculinea* butterflies.

The presence of *Maculinea* larvae inside *Myrmica* nests brings to their hosts other uninvited guests. Larvae and pupae of the *Maculinea* butterfly are known to host parasitoids of Ichneumonidae family: *Ichneumon* spp. in the case of both *Maculinea* cuckoo ecotypes, and *Neotypus* spp. that infest *Maculinea* predatory species (Thomas and Elmes, 1993; Munguira and Martín, 1999). These two parasitoids apply different strategies as *Ichneumon* wasp is attacking *Maculinea* larvae in the *Myrmica* nest, while *Neotypus* wasp attacks butterfly larvae when they are still living inside buds of their food plant (Thomas and Elmes, 1993; Tartally, 2005). The best studied strategy is that of *I. eumerus*, which reaches its *Ma. alcon* (*cruciata* ecotype) host inside the brood chambers of *Myrmica* nests, by releasing semiochemicals to induce fight among workers (Thomas et al., 2002). The secretion of one wasp is able to immobilize up to 80 % of an ant colony so the visit of *Ichneumon* female can be considered as an extremely stressful event for the host colony.

Socially parasitic syrphids

Myrmica ants also host larvae of *Microdon* (abbreviated as “Mi.” below) syrphid flies. There are two known *Microdon* species associated with *Myrmica* ants: the European *Microdon myrmicae* (Schönrogge et al., 2006; Bonelli et al., 2011) and the North American *Mi. albicomnatus* (Akre et al., 1990). *Microdon albicomnatus* can be found in colonies of *Myrmica incompleta* (Akre et al., 1990; Howard et al., 1990), however, it does not seem to be very genus specific, as its larvae were also found in nests of different *Formica* species and *Camponotus modoc* (Akre et al., 1990). Cryptic speciation could be a common process in social parasites, as already demonstrated in studies on *Microdon myrmicae* and *Mi. mutabilis* (Schönrogge et al., 2002), thus it is fair to assume that *Mi. albicomnatus* found in *Formica* spp. could be a different species than the one exploiting *Myrmica incompleta*. *Microdon myrmicae* is much more host specific, as in most European populations it uses *Myrmica scabrinodis*, although there are some places where other *Myrmica* species are also locally exploited (Bonelli et al., 2011) (Table 1).

Both *Microdon myrmicae* and *Mi. albicomnatus* are obligate predators of ant brood (Howard et al., 1990; Witek et al., 2012). It is known that females of *Mi. myrmicae* lay eggs directly on the surface of *Myrmica* nests and larvae actively move into the chambers to prey on small ant brood, growing the most during the 4 months of their life spent inside the host colony and using the *Myrmica* nest

primarily as shelter during winter time (Witek et al., 2012; Fig. 1). There is no information available about the specific mechanisms that allow *Microdon* larvae to enter and survive inside the *Myrmica* host nests, but as in the case of many other social parasites, e.g., the related *Microdon mutabilis*, different chemical signals seem to play an important role (Schönrogge et al., 2008).

A comparison of the CHC profiles of *Microdon albicomnatus* and its host *Myrmica incompleta* showed that, qualitatively, the parasite's profile is almost identical to its host ant brood (Howard et al., 1990). Moreover, these authors strongly suggest that the chemical mimicry of syrphid fly larvae is mediated by the biosynthesis of particular hydrocarbons (normal alkanes from C₂₂ to C₂₉, a few methylalkanes and two alkenes, among others). In contrast, the chemical profile of *Mi. myrmicae* larvae is very poor, with an average of eight hydrocarbon peaks (Witek et al., 2013b). This low number of compounds, together with their low concentration, indicates that *Mi. myrmicae* might use the 'chemical insignificance' strategy (sensu Lenoir et al., 2001) to penetrate the host colony.

Beetles as social parasites

In addition to butterflies and syrphid flies, beetles also exploit *Myrmica* colonies as shelter and food resources. One such European beetle is *Lomechusa pubicollis*, which, unlike the previously described social parasites, uses *Myrmica* colonies during its adult stage (Hölldobler, 1970). It is known that *L. pubicollis* larvae live inside nests of red wood ants and they emerge as adults in the late summer (Parmentier et al., 2014). Then they leave the nest and look for *Myrmica* colonies using the specific odor of their host ants as a cue. They do not enter the nest actively but wait to be carried in by host workers, and very elaborate adoption behavior is used during this process (Hölldobler, 1970). After spending the winter in *Myrmica* colonies, where they get food and protection (Fig. 1), in the spring adult beetles return to *Formica* nests to mate and lay their eggs. As suggested by Hölldobler and Wilson (1990), a shift in the presence of ant brood (brood is present in *Myrmica* colonies during the whole year unlike in *Formica*) is the reason for seasonal host change in *L. pubicollis*.

Other myrmecophilous arthropods

There are a number of other myrmecophilous arthropods known to live together with *Myrmica* species (Table 1), as woodlice from the genus *Platyarthus* (Berg, 1995; Hornung et al., 2005), mites (Constantinescu et al., 2011; Joharchi et al., 2011), the springtail *Cyphoderus albinus* (Dekoninck et al., 2007), and crickets of the genus *Myrmecophilus* (Bezdečka et al., 2000; Schlick-Steiner et al., 2003). All

these myrmecophilous arthropods have quite wide host range including other ant genera, but usually data on their distribution is very scarce (see e.g. Schlick-Steiner et al., 2003). With the exception of the cricket *M. acervorum*, which is known to steal food from ants and, occasionally, consume ant brood, no specific effect on host colony fitness is known for any of these species.

Exploitation of ant individuals: ectoparasites, endoparasites and microbe pathogens

Nematodes, the parasites that give rise to taxonomical confusions

There is a wide range of soil-inhabiting or epigeal nematodes that are endoparasites of several insect groups, including ants. Nevertheless, only a handful of ant-parasitic nematodes are known and there is a considerable lack of information concerning their life cycle (Poinar et al., 2006; Poinar and Yanoviak, 2008; Poinar, 2012). The morphological effects of nematodes on ants are particularly conspicuous in hosts, which were attacked in the early phase of larval development and parasitized individuals often display various degrees of modifications. Physogastry seems to be a general feature since the parasites usually reside in the gaster of the host (Kaiser, 1986; Czechowski et al., 2007a, b; Csősz and Majoros, 2009; Csősz, 2012; Poinar, 2012). In addition, nematodes can also manipulate host behavior to aid their transmission to the next host or to the habitat where egg-laying occurs (Kaiser, 1986; Oi and Pereira, 1993; Yanoviak et al., 2008; Poinar, 2012).

In the case of genus *Myrmica* most of the parasitic nematodes belong to the Mermithidae family and they parasitize quite a wide range of hosts (Table 1). In addition to gynes and workers, males can also serve as hosts at least in *M. scabrinodis* and *M. rugulosa* (Czechowski et al., 2007a). *Myrmica* hosts also present the so-called mermithogenic morphological syndromes, which are a combination of both worker-like and gyne-like structures and a few typically intermorphic features, such as oval head, more or less developed ocelli, reduced but visible thoracic sclerites, reduced or completely missing wings and swollen gaster (Czechowski et al., 2007a; Csősz and Majoros, 2009; Csősz, 2012). It seems that the female parasitogenic morphs emerge from queen-presumptive larvae, while probably worker larvae, if infected, die (Csősz and Majoros, 2009).

Owing to the conspicuous morphological modifications induced by nematodes, mermithized *Myrmica* individuals are often misidentified or even described as a new species, believed to be social parasites due to reduction of gyne characters (Csősz, 2012). This was the case of *M.*

myrmecophila and *M. symbiotica*, which are mermithogenic forms of *M. sulcinodis* and *M. scabrinodis*, respectively (Csősz, 2012). The prevalence of mermithid nematodes can be quite high: e.g. Czechowski et al. (2007b) reported a 25 % prevalence of infected individuals in a sample from a single *M. rubra* nest. In addition, the number of parasites varies in infected individuals: generally one worm is found inside one individual ant, but in rare instances even four nematodes have been present together in an infected individual (Csősz and Majoros, 2009).

There are two *Myrmica* parasitic nematode species known from other nematode families. *Dyploscapter lycostoma* (Rhabditidae) parasitizes *M. rugulosa*, and it occurs in the postpharyngeal gland, but no data is available on its effect on the host (Poinar, 2012). A generalist entomopathogen species, *Steinernema carpocapsae* (Steinernematidae) is known from *Myrmica*, but infection was observed only under laboratory conditions (Poinar, 2012). This nematode is known to carry symbiotic bacteria (e.g. *Xenorhabdus* spp.) that kill the insect host when released in its haemocoel, after which the bacteria and the insect are consumed by the worm (Zhou et al., 2002; Poinar, 2012). The same bacteria also produce the so-called ant deterrent factors in attacked insects that keep away other ants from the cadaver, thereby allowing the nematodes to develop (Zhou et al., 2002).

Clearly, there is much to discover in the relationship between nematode parasites and *Myrmica* ants. In most cases a great deal of basic information is still missing: the exact taxonomic status of the parasites, their life cycle, the mechanisms of transmission to hosts and, ultimately, the physiological changes they cause in the host that might trigger the development of morphological malformations in *Myrmica* specifically and ants generally.

The enigmatic associates of *Myrmica*: fungi

Various types of associations between ants and fungi exist: some fungi are known to harm and even kill the host, but in other cases they may benefit ants. Ant-associated fungi species can occur in the nest or as ectoparasites on the cuticle of the hosts, but also internally as endoparasites or endosymbionts (e.g. Schmid-Hempel, 1998; Little and Currie, 2007; Gibson and Hunter, 2010). Only sparse data are available on the relationships of *Myrmica* species with fungi. The negative effect of generalist entomopathogen fungi has been documented in their case (e.g. Graystock and Hughes, 2011), whereas ant specialist fungi species are scarcely known in this ant genus. Altogether, five fungal species are reported to be strictly associated with *Myrmica* ants. Evans et al. (2010) has recently described three pathogenic fungi belonging to the *Ophiocordyceps unilateralis* clade (Ascomycota: Sordariomycetes) from *Myrmica rubra*

in the UK: *Paraisaria myrmicarum*, *Hirsutella stilbelliformis* var. *myrmicarum*, and *H. subramanianii* var. *myrmicarum* (Table 1). All three fungi kill the host and produce fruiting bodies on corpses gathered in cemeteries far from the nest several days after the death of the individuals. Infection is revealed by extended gaster of the living workers due to presence of internal fungal mycelium. In addition, in both *Hirsutella* fungi, dead infected individuals display everted mouthparts. Nothing is known regarding the real prevalence of these fungi, but Evans et al. (2010) formulates the presumption that it could be quite low due to predation on corpses or detrimental field conditions for fungal development. The fourth fungal species, *Hormiscium myrmecophilum* (Ascomycota: Pezizomycotina) was recorded in *Myrmica* ants (Table 1) in Portugal and Spain (Espadaler and Santamaria, 2012), but there is no other information available regarding the phenology or behavior of this species.

The most well-known *Myrmica* associated fungus is *Rickia wasmannii* (Ascomycota: Laboulbeniales) found in Europe (Fig. 1). It exclusively exploits ants of the genus *Myrmica* (Espadaler and Santamaria, 2012; Csata et al., 2013), the most frequent being *M. scabrinodis*, while there are several less common hosts (Table 1) (see Espadaler and Santamaria, 2012; Csata et al., 2013). The fungus gives a conspicuous look to the host: fungal thalli appear on the surface of the hosts as clubbed setae-like structures under the stereoscope. Thus, highly infected ants appear unusually hairy.

Little is known about the effects of Laboulbeniales fungus species on their hosts; they are usually regarded as neutral (see Espadaler and Santamaria, 2012), despite the fact that they penetrate at least the outer layer of the cuticle. In the case of *R. wasmannii* its prevalence could reach extreme values either within population or within colony (authors, unpubl. data), which would also support its neutrality. However, recent laboratory experiments conducted on parasitized *M. scabrinodis* ants suggest that the fungus reduces significantly the lifespan of infected individuals (Csata et al., 2014).

To reduce virulence and transmission of entomopathogenic agents, such as fungi a number of hygienic behaviors have evolved in ants as e.g. auto- and allogrooming, allo- or self-exclusion of infected individuals, corpse disposal and/or cemetery formation (Oi and Pereira, 1993; Schmid-Hempel, 1998; Heinze and Walter, 2010). However, increasing frequency of allogrooming, while reducing the amount of spores on individual level, may assist the spread of pathogens among nest-mates (Oi and Pereira, 1993; Reber et al., 2011; Konrad et al., 2012). This mechanism might eventually aid the transmission of *R. wasmannii* among *Myrmica* nest-mates and it may explain its high prevalence as suggested by Csata et al. (2014). Active

disposal of corpses could limit or hinder *P. myrmicarum*, *H. stilbelliformis* and *H. subramanianii* infection in *M. rubra*, as it has been suggested by Evans et al. (2010), probably assisted by exposure to sunlight, which could significantly reduce fungal growth. The scientific puzzle of how *M. rubra* manages to avoid these deadly parasites is even more intriguing, since the control of the European fire ant, as *M. rubra* is called in the US, is quite a challenge and fungal pest control might be a solution (Evans et al., 2010).

Microbial pathogens of *Myrmica* ants

Most studies on symbiosis between microbes and social insects concentrated on ants and termites in tropical and subtropical regions. Various symbiotic bacterial communities have been described for several ant groups (e.g. Russell et al., 2009; Funaro et al., 2011). Symbiotic bacteria are mainly found in the guts that provide a suitable habitat for a wide range of microbes (Li et al., 2005; Stoll et al., 2007) and play essential roles in the success of herbivorous and fungivorous ants (Davidson et al., 2003; Pinto-Tomas et al., 2009; Russell et al., 2009). The worker ant surface can also provide a separate microbial niche, which for some ant species has a crucial role in providing antibiotics and fungicides (Little and Currie, 2007) or could generally contribute to protection against disease (Mueller, 2012). While such functional relationships are known for some bacterial groups, the function of many other groups is still poorly understood (Russell et al., 2009; Funaro et al., 2011) and virtually unknown in *Myrmica* ants.

Unfortunately, there appears to be only one study, by Pearson and Raybould (1998) that has considered the role of *Myrmica rubra* associated microbes as parasites or mutualists. The authors suggested that the internal microflora is essentially “parasitic” when gut microbes consume at least some of the resources ingested by the host (Pearson and Raybould, 1998). Based on the results of antibiotic treatments, the authors suggest that a heavy bacterial load overwhelms larval growth and results in small larvae, whereas large larvae have lighter loads. Because the larval developmental pathway (worker-determined or queen-potential) is linked to size, they conclude that the bacterial load also affects caste determination in *M. rubra*. With the experimental design used by Pearson and Raybould (1998), however, it is impossible to determine whether the antibiotic treatment affected workers or larvae or both, and technologies with which to document changes effectively in the microbial community under treatment were not available at that time. Therefore, more detailed surveys are claimed to provide concluding insights on the role of gut surface bacteria in *Myrmica* ants.

Prerequisites for the evolution of different parasites of *Myrmica* ants

In our review we focused on the wide spectrum of *Myrmica* ant associations with other organisms that negatively influence their ant hosts. Based on the data presented here we could formulate the hypothesis that genus *Myrmica* is particularly susceptible to exploitation both by social parasites and by ecto- and endoparasites. Hölldobler and Wilson (1990) recognized a few important features that predispose ant societies to ant–ant social parasitism: living in cool or arid climates, having polydomous-polygynous population structure and thus obtaining high nest densities. In our opinion this list can be completed with the existence of morphologically different gynes, like micro- and macrogynes, which vary in their behavior as e.g. apply alternative reproductive strategies. As suggested by Rüppele and Heinze (1999) microgynes can be very efficient in infiltrating in unrelated colonies and represent a potential for the evolution of social parasitism. All these, above mentioned, traits are characteristic of many *Myrmica* ant species, and some of them suggest that *Myrmica* colonies can be prone also to non-ant social parasites or fungi, such as *Rickia wasmannii*. When compared with monogynous ants, polydomous-polygynous colonies are loose, flexible and dynamic and could lead to the development of supercolonies occupying a huge area (Thomas et al., 2005). Colonies of some *Myrmica* species contain relatively high numbers of individuals and usually a few functional queens (Radchenko and Elmes, 2010), which in turn can result in lower relatedness among worker nest-mates (Elmes and Petal, 1990; Seppä and Walin, 1996). High genetic variability can be beneficial for social insect colonies (Sundström, 1995; Baer and Schmid-Hempel, 1999; Hughes and Boomsma, 2004), but it may increase the likelihood of being infested by social parasites due to the effect of consequently higher variability in nest-mate recognition cues (Gardner et al., 2007; Nash et al., 2008). In such cases polygyny can be costly, as communication signals, both chemical and acoustical, exchanged among colony members can be more variable than in monogynous species. Therefore, they can be more easily mimicked by intruders, both by other ant species and other arthropods. On average, polygyny can also increase the chance of infection by *R. wasmannii* as colonies could be more open for adoption of new, unrelated queens (Elmes, 1987), which could be originally infected by this fungus. In addition, the life cycle of *Myrmica* ants, different from that of Formicine ants, could also be a driving force for the emergence of specific parasites; namely, the existence of overwintered ant larvae makes *Myrmica* ants worthy targets for specific “predators”. The presence of an essential food resource throughout the

year is especially important for the predatory social parasites (Fig. 1).

Considerations for future studies

Different selective pressures coming from both pathogens infecting ant individuals as well as from social parasites exploiting the host colony resources can affect the evolution of life history traits of their *Myrmica* hosts. Unfortunately, data concerning the impact of parasites on the host fitness is available only for a few cases, which makes difficult to compare the strength of such pressures and their outcomes. Even in the case of the most thoroughly studied parasitic system concerning *Maculinea* butterflies our knowledge is limited. We know that *Maculinea* predatory species prefer to feed mostly on the largest available ant larvae (Thomas and Wardlaw, 1992), whereas cuckoo strategists reduce “attendance (nurse)” worker fitness by decreasing their survival and weight (Wardlaw et al., 2000). Cuckoo caterpillars also compete with *Myrmica* brood for worker attention and sometimes they eat ant larvae (Wardlaw et al., 2000). *Microdon myrmicae* larvae feed on ant brood as well, but unlike predatory *Maculinea* they eat mostly eggs and small ant larvae (Witek et al., 2012). In all cases, the reduction of the number of ant larvae decreases the total colony production, but it is not known if and how these parasitic loads influence the production of sexual forms, which is one of the most important component of colony fitness. Some information can be inferred from data collected on *Microdon mutabilis*, that has similar feeding strategy to *Mi. myrmicae*. *Microdon mutabilis* larvae, by eating ant brood, increase the food supply per ant larva thus allowing the surviving ant larvae to develop into gynes (Schönrogge et al., 2006; Hovestadt et al., 2012).

There is also few data available on the effects of parasitic *Myrmica* species on their host colony production, how they compete with the host queen or change the division of labor inside host nest. There is some information showing that the microgynes of *M. rubra* may produce almost 40 times as many queens as do macrogyne queens, but their worker production is highly reduced (Elmes and Brian, 1991). Moreover, it was shown that microgynes attract workers like macrogyne queens do, thus they compete for worker attention and for food supplements (Cammaerts et al., 1987). It is interesting, but still unresolved whether similar effects can be found in the case of other parasitic *Myrmica* species, particularly inquiline social parasites.

Nematodes could significantly reduce the fitness of colonies due to their castration effect on young gynes and males. However, no specifically designed studies on this question have been carried out. Also the effect of the

pressure that fungi and microbes exert on *Myrmica* colonies, e.g. on colony structure or production, should be the subject of further inquiry.

At the moment we have very little knowledge of the socially parasitic communities of ants, whether we are speaking of the interactions among different parasite species or the interactions between them and their ant hosts. The fact that there are some *Myrmica* populations, such as the one in Luna de Jos in Romania, which are parasitized by several *Maculinea* species, *Microdon myrmicae* and the fungus *Rickia wasmannii* (Tartally et al., 2008a; Csata et al., 2013; Czekes et al., 2014) or in Krakow in Poland, where many *Myrmica scabrinodis* colonies are infested by four species of social parasites as well as by *R. wasmannii* (Witek et al., 2013a, b) suggests that *Myrmica* can endure high parasitic pressures of different natures. Additionally, co-occurrence of these different parasites can also change the trajectories of interactions among them and their *Myrmica* hosts. It is possible that *R. wasmannii* might change the chemical profile of ant workers and influence communications between social parasites and their hosts. Similarly, we can imagine that microbes associated with *Myrmica* not only affect ant colony dynamics, but may also have significant impacts on their social parasites because the tight interaction between *Myrmica* ants and their social parasites should, at least in part, imply an exchange of microbes and subsequently a role of the latter in the co-evolution of the host and parasite system. All the hypotheses presented above need to be tested, and given the high diversity of different parasites to which they play the role of host, *Myrmica* ants offer an excellent opportunity for further study.

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