

# New association between red wood ant species (*Formica rufa* group) and the myrmecophilic spiders *Mastigusa arietina* and *Thyreosthenius biovatus*

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## Abstract

Ants belonging to the *Formica rufa* species group, counting 10 representatives in Europe, are often referred to as red wood ants (RWAs). These dominant, mound building species are known to host in their nests an extremely diverse fauna of associated myrmecophilic arthropods, among which are the two W-Palaeartic spider species *Mastigusa arietina* (Thorell 1871) and *Thyreosthenius biovatus* (O. Pickard-Cambridge 1875). The actual host range of these spiders within the *Formica rufa* group is little known, due to the taxonomic uncertainties that have characterized RWAs in the past. We conducted a large-scale survey for assessing the occurrence of both spider species in association with different RWAs, with a focus on an accurate identification of the ant species. We recorded co-occurrence data for 5 European representatives of the *Formica rufa* group, and we reported for the first time on the co-occurrence of *M. arietina* with *Formica aquilonia* Yarrow 1955, *Formica lugubris* Zetterstedt 1838 and *Formica paralugubris* Seifert 1996, and of *T. biovatus* with *F. aquilonia*. We found no association between the rate of presence/absence of the two spiders and host ant species or sampling localities, which suggests a non-selective exploitation of RWA hosts by the two myrmecophilic spiders.

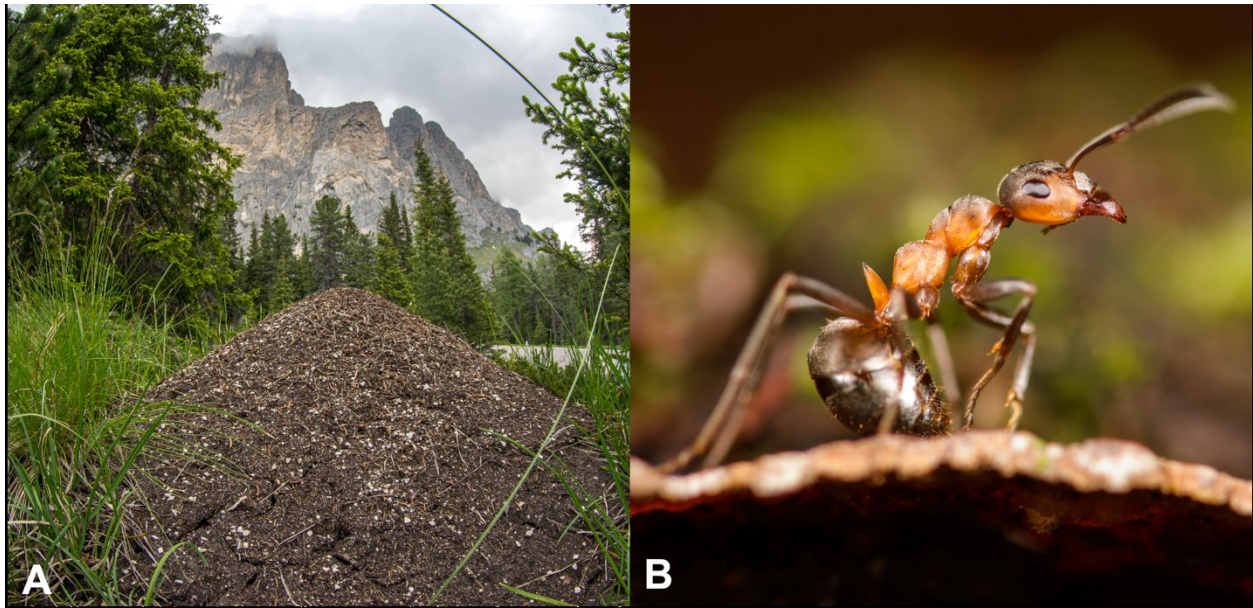
**Key words:** myrmecophily, RWA, host preference, ant association, Alps.

## Introduction

Ant nests represent a potentially advantageous microhabitat for other arthropods as they provide less microclimatic fluctuations if compared to the outside environment and abundant food from different sources. They also represent a well-protected environment for avoiding predator and parasitoids, with the tradeoff of having to co-exist with a great number of aggressive and territorial worker ants (Cushing, 1997; Parmentier, 2020). Arthropods showing some degree of association with ants can be divided into two groups: myrmecomorphs and myrmecophiles (Donisthorpe, 1927; Cushing, 1997). Myrmecomorphs may, in rare instances, mimic ants' morphology and/or behaviour as a form of Peckhamian (aggressive) mimicry, which involves a model being predated by the mimic (McIver and Stonedahl, 1993; Cushing, 1997). More often, they are believed to do so as a form of Batesian mimicry, playing the role of (relatively) harmless mimics imitating a harmful species to avoid attacks from visually hunting predators or parasitoids (McIver and Stonedahl, 1993; Cushing, 1997; Nelson and Jackson, 2006; 2012; Huang *et al.*, 2011). Ants are in fact often avoided by generalist predators due to their aggressiveness and frequent unpalatability, distastefulness or noxiousness to vertebrates and other invertebrates (Edmunds, 1978; Hölldobler and Wilson, 1990; Taniguchi *et al.*, 2005; Nelson and Jackson, 2006). Myrmecophilic arthropods live in close association with ants at varying degrees, from foraging alongside them in the periphery of the colonies up to spending their whole life cycle inside the nest (Wasmann, 1894; Donisthorpe, 1927; Hölldobler and Wilson, 1990). Myrmecophiles manage

to avoid ants' attacks by using different strategies, ranging from defensive anatomical modifications and behavioural responses to chemical adaptations with modifications of their cuticular hydrocarbon (CHC) profile (Hölldobler and Wilson, 1990; Lenoir *et al.*, 2001; Akino, 2002; von Beeren *et al.*, 2011; Parker, 2016). Myrmecophily in spiders was reviewed by Cushing (1997; 2012) who reports the phenomenon in 13 out of the 129 known spider families (WSC, 2022), and only in a minority of cases myrmecophilic spiders also happen to be myrmecomorphic (Cushing, 2012).

Red wood ants (*Formica rufa* group; henceforth referred to as RWAs) form a species group belonging to the genus *Formica* L. 1758 distributed across the Holarctic. The fourteen species found in the Palaeartic form a monophyletic clade (Trager, 2016; Borowiec *et al.*, 2021) and can, in some cases, hybridize, making the taxonomy of the group particularly challenging (Bernasconi *et al.*, 2011; Seifert, 2021). Ten species occur in Europe, namely *Formica aquilonia* Yarrow 1955, *Formica dusmeti* Emery 1909, *Formica frontalis* Santschi 1919, *Formica helvetica* Seifert 2021, *Formica lugubris* Zetterstedt 1838, *Formica paralugubris* Seifert 1996, *Formica polyctena* Foerster 1850, *Formica pratensis* Retzius 1783, *Formica rufa* L. 1761 and *Formica truncorum* F. 1804. These ants are ecologically dominant, mound-building species that constitute a key element for ecosystem functioning in temperate and boreal forests in which they live (figure 1) (Gosswald, 1989; Frouz *et al.*, 2005; 2016; Stockan *et al.*, 2016). Their mound nests support an impressive diversity of obligate and facultative guests, with 125 arthropod species reported as obligate myrmecophiles living inside or in the proximity of RWA mounds



**Figure 1.** *Formica rufa* group. **A)** *F. aquilonia* mound at Sella Pass (CZ), Italy; **B)** *F. polycytena* worker.

(Parmentier *et al.*, 2014). Parmentier *et al.* (2017) classify RWA-associated myrmecophiles on the degree of their host specificity, with values ranging from 0 to 4, with 4 being strict specialists (only recorded with RWAs), 3 being specialists (sometimes recorded with non-RWAs), 2 being characterized by moderate specificity (recorded with RWAs but distribution in non-RWAs probably equally important) and 1 being generalists (species with a broad host spectrum). Spider species that are known to occur inside Palearctic RWA mounds are *Mastigusa arietina* (Thorell 1871) from the family Hahniidae, *Acartauchenius scurrilis* (O. Pickard-Cambridge 1873) and *Thyreosthenius biovatus* (O. Pickard-Cambridge 1875) from the family Linyphiidae and *Phrurolithus festivus* (C. L. Koch 1835) from the family Phrurolithidae (Cushing, 1997; Parmentier *et al.*, 2014). The main ant host of *A. scurrilis* is a member of the *Tetramorium caespitum* complex, but in some instances this spider was also found in association with *Formica rufa* and *Lasius flavus* (F. 1782) (Donisthorpe, 1908; 1927). *P. festivus* is common both inside and outside of ant nests and is reported to occasionally prey on ants. This species was found in association with *F. rufa*, *Formica sanguinea* Latreille 1798, and different species belonging to the genus *Lasius* F. 1804 (Donisthorpe, 1927; Bristowe, 1941; Boevé, 1992).

*M. arietina* is one of the three currently recognized species belonging to the genus *Mastigusa* Menge 1854 (figure 2A). It is found in Europe, Algeria, Russia, and Iran (WSC, 2022). In Europe, it is recorded everywhere except for Ireland, the Balkans, Moldova, Belarus, Lithuania, and Latvia (Nentwig *et al.*, 2022). Given the small number of scattered records registered for all the countries where this species is present, it is often considered rare all over its known range, yet targeted efforts to monitor its abundance and distribution are lacking. This species was described from a specimen collected in a *Formica rufa* mound in Sweden (Westring, 1861) and was later mostly collected in association with ants, yet with some sporadic records of reproductive populations outside of

ant nests, specifically under rocks and bark or in caves (Simon, 1898; 1913; Donisthorpe, 1908; Jackson, 1913; Fage, 1931). Specimens have been observed mostly in ant nests of *F. rufa*, but also *F. polycytena*, the non-RWA *Formica fusca* L. 1758, *Lasius fuliginosus* (Latreille 1798), *Lasius alienus* (Foerster 1850), *Lasius brunneus* (Latreille 1798), *Messor muticus* (Nylander 1849) and *Tetramorium caespitum* L. 1758 (Westring, 1861; Pickard-Cambridge, 1900; Donisthorpe, 1908; Klausen, 1974; Palmgren, 1977; Roberts, 1995; Parmentier *et al.*, 2015; 2020; Franc and Hemala, 2020). Most of the ant-association data with RWAs, starting from Westring's original description, come from a time where the distinction of the different RWA species was not clear due to the taxonomic uncertainties regarding the *Formica rufa* group, something that first started to improve thanks to Yarrow's (1955) revision of the RWAs of the British Isles. However, the taxonomy of the RWAs in Europe has long remained unresolved, so that the actual host species is unknown for the majority of *M. arietina* records. Being recorded in association with RWAs, non-RWA *Formica* species and other ant genera, *M. arietina* could be considered as a 2 (moderate specificity) according to Parmentier's classification on host specificity. Parmentier *et al.* (2017) registered a low amount of cuticular hydrocarbons on the cuticle of these spiders, a trait that could help myrmecophilic arthropods in avoiding chemical detection by host ants by facilitating the integration into their colony with a strategy known as "chemical insignificance" (Leonir *et al.*, 2001; 2013; Witte *et al.*, 2008). In laboratory trials, *M. arietina* specimens were found to provoke strong aggressive responses in *Formica* ants, suggesting a somewhat low level of integration inside the colonies (Parmentier *et al.*, 2016; 2018).

*T. biovatus* is one of the two species belonging to the genus *Thyreosthenius* Simon 1884 (figure 2B). It is a widespread species in Europe and Russia (WSC, 2022). In Europe, the only areas where it has not been found yet are the Iberian Peninsula, southeast Europe (except for



**Figure 2.** Myrmecophilic spiders found in mounds of RWA. **A)** *M. arietina* female, from Corona (BZ), Italy; **B)** *T. biovatus* female, from Corona (BZ), Italy.

Bulgaria), Belarus and Lithuania (Nentwig *et al.*, 2022). Similar to *M. arietina*, the few specimens recorded from its distribution range lead it to be considered a rare species. It has been recorded from ant nests of the RWA species *F. lugubris*, *F. polychtena*, *F. pratensis* and *F. rufa*, and the non-RWA *Formica* species *F. fusca* and *F. sanguinea* (Bösenberg, 1899; Simon, 1926; Bristowe, 1939; Wiehle, 1960; Palmgren, 1976; Robinson, 1998; Parmentier *et al.*, 2014; 2015). Regarding its actual host range within the *Formica rufa* group, our knowledge suffers from the same taxonomic problems mentioned for *M. arietina*. Being recorded both with RWAs and non-RWAs, but not with species from other genera, *T. biovatus* host specificity can be classified as a 3 (specialist). As in *M. arietina*, Parmentier *et al.* (2017) registered a low amount of CHCs in *T. biovatus*, hypothesizing again chemical insignificance as an integration strategy. In laboratory trials, this species showed lower levels of aggression if compared to *M. arietina*, suggesting a higher level of integration in RWA colonies (Parmentier *et al.*, 2016; 2018). Records of adults outside ant nests are known but may be related to dispersal activity or temporary foraging away from the mounds rather than to true free-living habits, since reproduction outside of ant nests has never been ob-

served (Bristowe, 1939; Parmentier *et al.*, 2021). This species though shows a great mobility in the proximity of the nests, as observed by Parmentier *et al.* (2021) who collected great number of specimens in pitfall traps placed up to 25 meters away from the mounds.

In this study, a large-scale field survey was carried out within the Alpine regions of Northern Italy to assess the occurrence of *M. arietina* and *T. biovatus* inside nests of different RWA species, with the aim of better understanding their ecology and host preferences within the *Formica rufa* group.

## Materials and methods

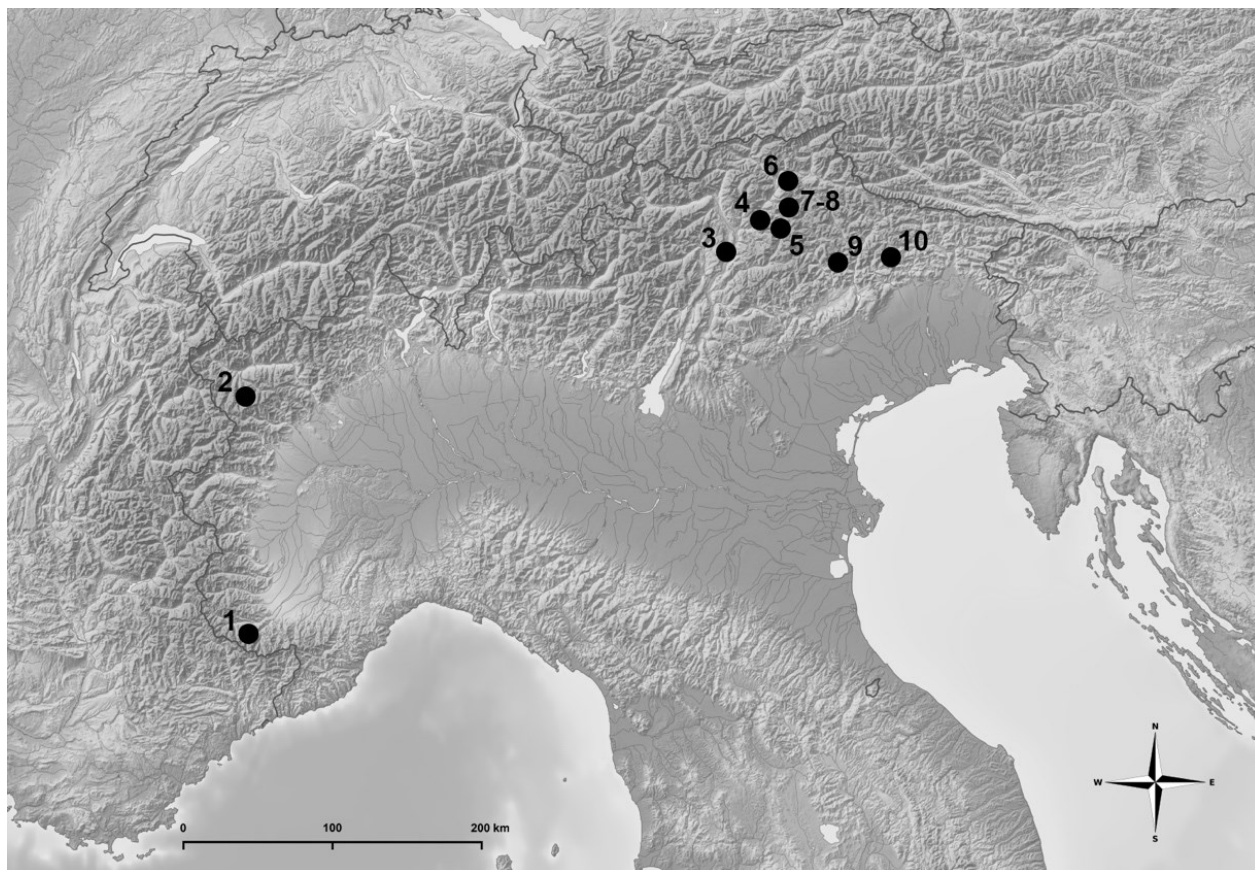
### Study area

Fieldwork was conducted between 2018 and 2020 in 10 localities in the Eastern and Western Italian Alps, based on previous records of the two spider species or given the known presence of RWAs in the area. A complete list of the sampling localities with elevation and habitat type is given in table 1. A map showing the investigated localities is given in figure 3.

**Table 1.** List of sampling sites with localities, altitudinal range covered, habitat type and RWA species observed.

Site	Locality	Elevation (m a.s.l.)	Habitat	RWA species
1	Gias delle Mosche, Valdieri (CN)	1703	European spruce forest with European larch and European beech	<i>F. lugubris</i>
2	Chabod trail, Valsavarenche (AO)	1890-2080	European larch forest with Swiss pine and European spruce	<i>F. paralugubris</i>
3	Corona, Cortaccia (BZ)	1195-1211	European spruce forest	<i>F. polychtena</i> ; <i>F. rufa</i>
4	Above Hofer Alpl, Fié allo Sciliar (BZ)	1533	Pine forest with European spruce	<i>F. aquilonia</i>
5	Sella Pass, Canazei (TN)	2040	Pine forest with European spruce	<i>F. aquilonia</i>
6	Around Roner Alm, Luson (BZ)	1777-1819	European spruce forest with Baltic pine	<i>F. aquilonia</i>
7	Val Chedul, Selva di Val Gardena (BZ)	1760-1781	Swiss pine forest with European spruce and European Larch	<i>F. aquilonia</i>
8	Col Raiser, Santa Cristina (BZ)	2058	Swiss pine forest with European spruce and European Larch	<i>F. aquilonia</i>
9	Val Pramper, Forni di Zoldo (BL)	1433-1477	European spruce and European larch forest	<i>F. aquilonia</i>
10	Casera Casavento, Claut (PN)	934-940	European spruce forest	<i>F. polychtena</i>





**Figure 3.** Map of the investigated localities in the Alps. Numbers refer to sites as reported in table 1.

### Sample collection

The search for myrmecophilic spiders inside RWA ant hills was carried out by digging carefully by hand inside the above ground mound and collecting a couple of litres of mound material. This was then sifted on a white fabric sheet for better spotting the spiders, using an entomological sieve with an  $8 \times 8$  mm mesh. After sifting, nest material, ants and brood were carefully returned to the nest to minimize disturbance. The presence of spiders in the nests was assessed by the collection of adult and juvenile specimens, yet for *M. arietina* also by the finding of its characteristic flat and discoidal egg-sacks, often laid on the surface of hard debris such as small logs, pinecones, or pieces of bark found inside the nest (Donisthorpe, 1927). Specimens were collected by the means of entomological forceps or pooters and stored in 70% or 96% ethanol, in order to allow for an ideal preservation for both morphological examination and molecular analyses. Ant worker specimens were collected with entomological forceps from the top of the nests and stored in 70% and 96% ethanol for the same reasons as above. For each of the investigated mounds, coordinates, elevation, and habitat type were recorded. Given the location of most of the sampling sites inside protected areas, permits were obtained for the collection of both spider and ant specimens.

### Morphological identification of spiders and ants

Spiders were examined and measured using a stereoscopic microscope equipped with a Leica DFC450C camera and Leica Application Suite v3.6 software and

photographed using a BK+ Imaging System from Visionary Digital equipped with a Canon EOS 7D camera. Identification was carried out with the keys of Roberts (1987) for *T. biovatus* and the redescrptions and keys provided by Wunderlich (1986) for *M. arietina*.

Ants were examined with a stereoscopic microscope. Measurements were taken on photos by using the software ImageJ (Schneider *et al.*, 2012) and pictures obtained with a Canon MP-E 65mm f/2.8 1-5 $\times$  macro lens mounted on a Canon 1300D camera. Identification was carried out with the key provided by Seifert (2021). *F. helvetica*, recently described based on only molecular data, was not taken into consideration due to the impossibility of identifying it morphologically and its geographic range being outside our study area.

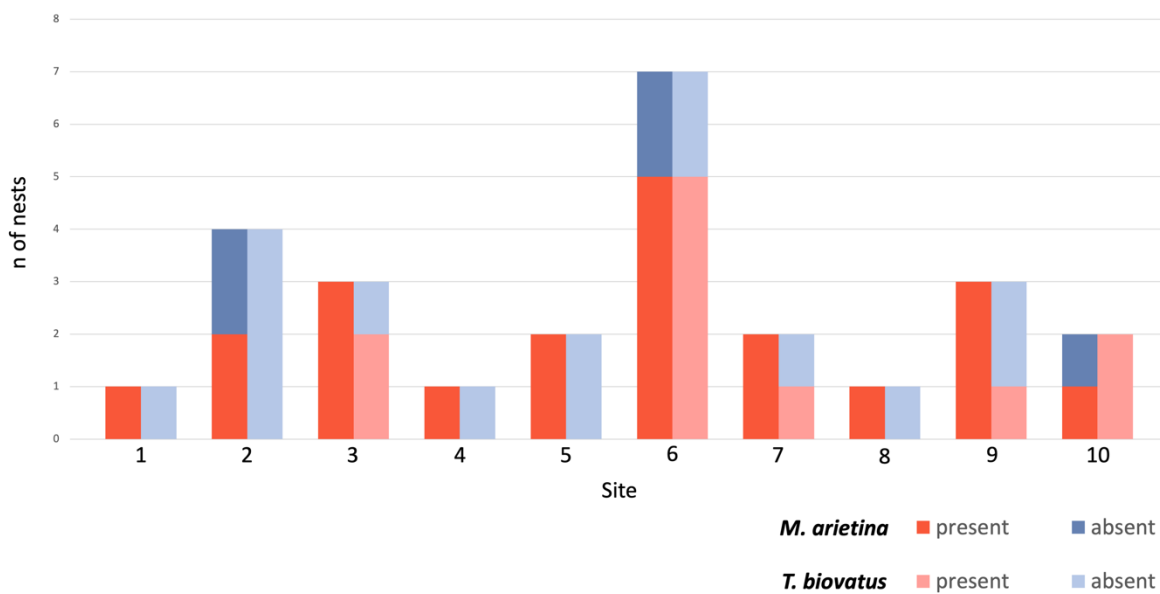
### Results

A total of 26 RWA mounds were investigated at the 10 sampling sites, details and coordinates for each of the nests are reported in supplemental material table S1. These belonged to 5 out of the 7 RWA species known to occur in the study area, namely *F. aquilonia*, *F. lugubris*, *F. paralugubris*, *F. polycytena* and *F. rufa*; no nests of *F. pratensis* and *F. truncorum* were found in the sampling sites. Only one RWA species was observed in each sampling site, except site 3, in which *F. polycytena* and *F. rufa* were found in sympatry. The majority of investigated nests (62%) belonged to

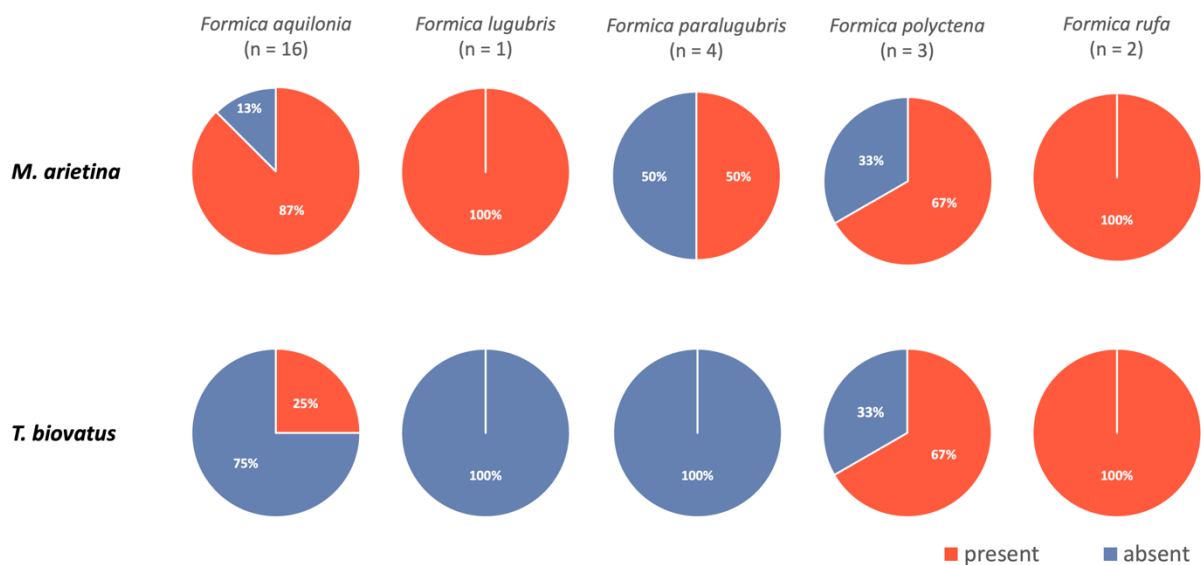
*F. aquilonia*, the other RWA species being present in a lower percentage of the nests: *F. paralugubris* = 15%, *F. polycтена* = 11%, *F. rufa* = 8%, *F. lugubris* = 4%. There was a clear geographic distinction regarding the RWA species found, with *F. aquilonia*, *F. polycтена* and *F. rufa* observed in the Eastern Alps sites and *F. lugubris* and *F. paralugubris* in the Western Alps sites. The presence of each RWA species in the 10 sampling sites is summarized in table 1. The spider *M. arietina* was present in 81% of the inspected mounds and at all sampling sites (figure 4). It was found in association with all the 5 RWA species investigated, although with different occurrence frequencies (figure 5). It was recorded between 934 and 2058 m a.s.l. in coniferous and mixed forests dominated by European spruce, larch,

or pine. Adult males were collected from June to July and in September, while adult females from July to September.

The occurrence of *T. biovatus* was lower, as it was recorded in only 31% of the inspected nests and only in the Eastern Alps sites (figure 4). This species was only recorded with 3 out of the 5 RWA species investigated, namely *F. aquilonia*, *F. polycтена* and *F. rufa* (figure 5). It was recorded in the same habitats as *M. arietina*, yet from a narrower altitudinal range (934-1837 m). Adult males were collected in June, and August to September, adult females in June and September. New distributional data generated for the two spider species in Italy can be found in supplemental material table S2.



**Figure 4.** Number of nests with presence/absence of the two spider species for each of the 10 sampling sites. Numbers refer to sites as reported in table 1.



**Figure 5.** Ratio of presence/absence of the two spider species in the investigated mounds for each RWA species.

## Discussion and conclusions

In the present work we report about updated co-occurrence data of RWA species and myrmecophilic spiders *M. arietina* and *T. biovatus*, expanding knowledge about their ecology, ant-association, and distribution in the Italian range.

### Host range and ecology

The geographical distribution of the different RWA species sampled was not random and reflected the actual distribution of the species over the Alpine arch area. *F. aquilonia* is known to be present in Eastern and Central Alps, with its westernmost limit being 9°E (Stockan *et al.*, 2016). Considering that both sites investigated in the Western Alps are located westward that distribution limit (7°E), the observed absence of this species in the area was expected. On the contrary, *F. paralugubris* is known to be present in Western and Central Alps, with its easternmost limit being 11°E (Stockan *et al.*, 2016). Being all sites investigated in Eastern Alps located eastward 11.2°E, again, the observed absence of this species in the area was expected. The other three species are more widely distributed over the Alpine arch, and their presence or absence may be related to ecological factors or local distribution patterns (Ronchetti, 1963; 1965; 1966; Seifert, 2021). The presence of both *F. polyctena* and *F. rufa* in site 3 agrees with known co-occurrence of the two species in Central Europe where they may form hybrid zones (Seifert, 1991; Czechowski, 1996; Gyllestrand *et al.*, 2004; Bernasconi *et al.*, 2011).

During the surveys, *M. arietina* was found in association with all the RWA species observed in the study area. This represents the first direct observation of the co-occurrence of *M. arietina* with *F. aquilonia*, *F. lugubris* and *F. paralugubris*. On the other hand, *T. biovatus* was found in association with only three RWA species, namely *F. rufa*, *F. polyctena* and *F. aquilonia*, without being observed with *F. paralugubris* and *F. lugubris*. As for the absence of observations of *T. biovatus* during our surveys in the Western Alps, this could likely be due to the smaller number of sampling localities and ant nests that were inspected as compared to those investigated in the Eastern Alps, especially when considering the known presence of this species in both Switzerland and France (Nentwig *et al.*, 2022) or its ability to live in *F. lugubris* nests (see a record from the United Kingdom - Robinson, 1998). This represents the first observation of co-occurrence of this species with *F. aquilonia*. As reported before, the lack of literature records of both species in association with *F. aquilonia*, and of records of *M. arietina* in association with *F. lugubris* and *F. paralugubris* is probably due to the taxonomic issues affecting the different RWA species in the past (Seifert, 2021), leading to RWAs being identified with a generic “*Formica rufa*”. These, together with the limited knowledge about the historical and present distribution of the different RWA species in most of the countries, makes it difficult to reconcile most of the historical records to actual RWA species.

This work represents the first attempt to search for these spiders in nests of as many different RWAs as possible and with a strong focus on an accurate species-level identification of the ants, according to the modern taxonomy of the group, to get detailed information about

the host preferences of these spiders. The wide range of host species that were found in association with *M. arietina* confirms the fact that this spider shows a low host specificity, having been also recorded with ants belonging to other genera in the subfamily Formicinae, such as *Lasius*, and even species from the subfamily Myrmicinae. The new records of co-occurrence with three RWA species expand our knowledge about the ecology of this spider and its myrmecophilic habits. The observations in site 3, where spiders were collected in sympatric nests of *F. rufa* and *F. polyctena* few hundred meters apart one from the other, suggests that *M. arietina* opportunistically occupies RWA mounds based on their local availability rather than exhibiting a preference for certain species. Something similar can be observed for *T. biovatus*. The new data concerning its co-occurrence with *F. aquilonia* add new information about the ecology and host preference of this species and points out to a non-selective exploitation of the different RWA species like in *M. arietina*. The wide host range of the two spiders is also compatible with the finding of reduced levels of CHCs on their cuticle (Parmentier *et al.*, 2017). Chemical insignificance would indeed allow both species to quickly adapt and move from one host to the other. In contrast to more complex strategies involving the imitation of the host's CHC profile, which require a high degree of specialization, chemical insignificance may facilitate dispersal and colonization of new areas.

### Presumed rarity of *M. arietina* and *T. biovatus*

According to literature data, both species can be considered rare in Italy, given the low number of collected specimens and the limited number of sites from which they have been recorded (Pantini and Isaia, 2019). Our findings show a different picture, as specimens were easily collected in all sampling sites for *M. arietina* and in all sampling sites in the Eastern Alps for *T. biovatus*. The suggested rarity of this species is probably an effect of biased sampling techniques, since the collection of myrmecophilic arthropods associated with RWAs requires access to the mound nest and subsequent extraction of specimens from the nest material, procedures not commonly performed during general biodiversity surveys, or the placement of pitfall traps in the proximity of the nests (Parmentier *et al.*, 2021). By selectively investigating RWA nests both spider species appear to be more widespread and common in the study area than previously thought, as also reported for other European countries like Denmark (Scharff and Gudik-Sørensen, 2006) and Britain (Donisthorpe, 1927). Given the almost continuous presence of RWAs over the Alps Mountain range it is likely that the distribution of the two species follows that of the hosts, something that could be tested also in other European countries where RWA occur.

### Concluding remarks

Ant nests are known to host a wide range of myrmecophilic arthropod taxa. These are though poorly studied, with some noticeable exceptions in Coleoptera (Parker, 2016) and Lycaenid butterflies (Fiedler, 1991; Pierce *et al.*, 2002; Casacci *et al.*, 2019). Moreover, little is still known about their distribution, ecology, and the nature of

their relationships with the host ants. A proper knowledge of myrmecophilic taxa is even more important as the great number of non-ant species living inside of RWA mound nests represent a component of biodiversity which is often overlooked and that, if not properly considered, can lead to an underestimation of the species richness of a given area. The new data produced here regarding the occurrence of *M. arietina* and *T. biovatus* in association with widely distributed RWA species and the ease with which the two species were collected in areas where their presence went unnoticed until now, clearly emphasize this. Our findings confirm how little research has been conducted on ant associates in Southern Europe, implying that the same patterns observed for the two spider species could easily apply to myrmecophilic species belonging to other arthropod taxa that await re-discovery.

## Acknowledgements

Authors are grateful to the directors and staff of the protected areas where fieldwork was carried out, namely the Alpi Marittime Nature Park, Gran Paradiso National Park, Dolomiti Bellunesi National Park, Dolomiti Friulane Nature Park and of the Ufficio Natura, Provincia autonoma di Bolzano, for authorizations and logistical support. Authors are also grateful to Carlo Maria Legittimo and Gabriele Greco from Aracnofilia - Associazione Italiana di Aracnologia, for support on the field and to Andrea Colla from the Natural History Museum of Trieste for fieldwork planning and logistical support in Friuli. This project was carried out as part of the project "All Taxa Biodiversity Inventory + Monitoring Mercantour / Alpi Marittime". This work was supported by Canziani funding to AL; the PhD grant to FC was co-funded by Canziani and by the Natural History Museum of Denmark.

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Received March 31, 2022. Accepted June 23, 2022.

(Supplemental material available at <http://www.bulletinofinsectology.org/Suppl/vol75-2022-231-238castellucci-suppl.pdf>)