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ZIKIC, Vladimir; LAZAREVIC, Maja; TOMANOVIC, Zeljko; ILIC MILOSEVIC, Marijana; STANKOVIC, Sasa S.; MILENKOVIC, Darija; PETROVIC-OBRADOVIC, Olivera

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Artículos

Mutualistic associations between aphids and aphid-attending ants registered in Serbia

Asociaciones mutualistas entre pulgones y las hormigas que los atienden registradas en Serbia

Vladimir ZIKIC
University of Niš, Department of Biology and Ecology, Faculty of Sciences and Mathematic, Serbia
Maja LAZAREVIC
University of Niš, Department of Biology and Ecology, Faculty of Sciences and Mathematic, Serbia
Zeljko TOMANOVIC
University of Belgrade, Institute of Zoology, Faculty of Biology, Serbia
Marijana ILIC MILOSEVIC
University of Niš, Department of Biology and Ecology, Faculty of Sciences and Mathematics, Serbia
Sasa S. STANKOVIC sasasta@gmail.com
University of Niš, Department of Biology and Ecology, Faculty of Sciences and Mathematics, Serbia
Darija MILENKOVIC
University of Niš, Department of Biology and Ecology, Faculty of Sciences and Mathematics, Serbia
Olivera PETROVIC-OBRADOVIC
University of Belgrade, Institute of phytomedicine, Faculty of Agriculture, Serbia

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Abstract: Aphids and ants are relatively well faunistically studied in Serbia. However, there is a need to present the mutualistic associations between these two groups of insects, since there is not sufficient information on this topic for the territory under investigation. In total, 220 samples of plant-aphid-ant associations were included in this study. In 59 localities from all parts of Serbia, 32 ant taxa were registered and connected with 74 identified aphid taxa. The most frequently collected ant species found attending various aphid species were *Lasius niger* (L.), *L. alienus* (Foerster) and*Prenolepis nitens* (Mayr). The most common aphid species was *Aphis fabae* Scopoli collected on 27 plant species. The trophic associations are presented as a list of ant taxa followed with aphids and their host plants.

Keywords: Aphididae, Formicidae, Hemiptera, Hymenoptera, Myrmecophily.

Resumen: Los pulgones y las hormigas están relativamente bien estudiados faunísticamente en Serbia. Sin embargo, es necesario presentar las asociaciones mutualistas entre estos dos grupos de insectos, ya que no existe suficiente información sobre este tema para el territorio investigado. En total, se incluyeron en este estudio 220 muestras de asociaciones planta-áfido-hormiga. En 59 localidades de todas las partes de Serbia, se registraron 32 taxones de hormigas y se relacionaron con 74 taxones de áfidos identificados. Las especies de hormigas recogidas con mayor frecuencia que asistían a varias especies de áfidos fueron *Lasius niger* (L.), *L. alienus* (Foerster) y *Prenolepis nitens*

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(Mayr). La especie de pulgón más común fue *Aphis fabae* Scopoli, recogida en 27 especies de plantas. Las asociaciones tróficas se presentan como una lista de taxones de hormigas seguida de los áfidos y sus plantas hospedadoras.
Palabras clave: Aphididae, Formicidae, Hemiptera, Hymenoptera, Myrmecophilia.

INTRODUCTION

More than 5,000 species of aphids (Hemiptera: Aphididae) are described worldwide (Favret, 2020), with 384 species registered in Serbia. Yet, the expected number is about 550 (Petrović-Obradović et al., 2021). Aphids are small insects that produce honeydew (sugar-rich liquid), which is a result of excessive suction of plant sap from the phloem. Honeydew of aphids contains melesitosis (trisaccharide), which plays an important role in the interactions between aphids and ants (Yao, 2014). Certain species of ants collect, or "milk", honeydew from aphids, providing the aphid colony protection from predators, such as ladybirds or lacewings and hymenopterous parasitoids such as Aphelinidae, Figitidae or Braconidae, exclusively the subfamily Aphidiinae (Way, 1963; Novgorodova & Gavrilyuk, 2012). Aphids derive many other benefits from ants; ants clean them of honeydew thus retaining the energy that aphids can use to feed and reproduce undisturbed. Ants promote apterous aphid forms, which again results in aphids saving their energy for other purposes. Ants build galleries in the earth around the aphid colonies providing them with both better protection and a microclimate.

Mutual relations between ants and other organisms are known as myrmecophily (Stadler & Dixon, 1999; Parker & Grimaldi, 2014; Saha et al., 2018). Homopterans are certainly the largest target group for aphid-associated ants (Way, 1963). The most researched is the cooperation between ants, aphids, and their relations with the aphids' enemies; from the evolutionary and ecological aspect (Stadler & Dixon, 2005) or from the aspect of biological control application (Starý, 1966). Starý (1966) recognized three types of aphid-ant relationships: (1) constant, which is continuous, implying morphological adaptations in members of this mutualistic relationship; (2) temporary, occurring throughout all or almost all time in the season; (3) facultative, a most common situation, implying the accidental presence of ants in the colony and the lack of a serious mutualistic relationship with the aphids.

An interesting fact is that the number of recorded ant-aphid associations is relatively small. Ho#lldobler & Wilson (1990) explain this through the disproportionate number of species of both actors of the association in the northern and southern hemispheres; the highest diversity of ants in tropical regions, unlike aphids which are certainly more diverse in temperate regions. Siddiqui et al. (2019) suggest that the transition zones in which the two groups meet could be subtropical regions, and the diversity of ant-aphid associations may be the greatest. Although the exact number of ant-aphid associations is not known, Stadler & Dixon (1998) note that only one third to a quarter of all aphid species are ant attended, and among them, a small number are

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obligatory myrmecophiles. Some of the subterranean aphids, like many Pemphiginae, and many Lachninae, for example species from the genus *Protrama* Baker, are in an obligatory relationship with ants. Obligate myrmecophiles aphids are morphologically "modified" and prepared to live with ants. They usually have small cauda and small siphunculi. Around the dorsally placed anus there are many hairs, where droplets are kept until taken by ants. Ants promote production of apterae and in the genera *Stomaphis* Walker, they even make dispersal of aphids to other trees. A very common aphid, such as *Aphis fabae* Scopoli, is a facultative myrmecophile. However, ants do not visit aphids which produce plentiful wax, or have long siphunculi and cauda, or live in more or less closed galls, for example: *Eriosoma lanigerum* (Hausmann), *Uroleucon* Mordvilko, *Prociphilus* Koch, and others (Heie, 1980).

There are 17 ant subfamilies with about 13,500 described species worldwide (Bolton, 2018). The exact number of species that connect aphids is not known. The species from the subfamily Formicinae are the most numerous in mutual relations with their "protégés", especially those included in the genera, *Formica* L. and *Lasius* Fabricius (Starý, 1966). Among Myrmicinae, *Myrmica* Latreille and *Tetramorium* Mayr also feed on aphid honeydew. The myrmecofauna of Serbia is composed of 141 species (Petrov, 2004). So far, there have been no published works on ants that attend aphid colonies for the territory of Serbia, and ex-Yugoslavia. The greatest contribution to the ant fauna on the territory of Serbia was by the myrmecologist Dr. Ivan Petrov (e.g., Petrov, 2000; 2004).

As aforementioned, both aphid and ant fauna have been well researched in Serbia. However, information on their interrelationships and trophic patterns, including aphids' host plants is lacking. The primary goal of the current study is to present aphid-ant associations in Serbia during a period of almost 30 years of research on the ecology and diversity of aphids. Secondly, we expect this paper will provide a better insight into the faunistic complexes of the examined groups and serve as a platform in further research of ant and aphid interactions.

MATERIAL AND METHODS

Study area

Samples of ant-attended aphids were collected on the entire territory of Serbia, although predominantly in the north and southeastern parts (Fig. 1). Most of the samples were collected from lowland areas, both rural and urban, but also from higher altitudes such as Rajac mt at about 800 m above sea level (a.s.l.), Crna Trava at about 900 m a.s.l., Radan mt at about 1,000 m a.s.l. and Vlasinsko jezero (lake) at 1,250 m a.s.l. A detailed list of exploration sites with coordinates is provided in Table I. The collection within the research was conducted during two periods, from 1990 to 1997, and from 2016 to 2017.

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Fig 1. Map of Serbia with researched localities marked with numbers. In the two boxes, the overlapping localities are given in better resolution. Additional data on localities are presented in Table I.

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No.	Name	Coordinates
1	Kikinda	N 45°50'15'', E 20°28'04''
2	Ada, Mol	N 45°46'09'', E 20°07'02''
3	Nova Crnja	N 45°39'56'', E 20°35'45''
4	Novi Bečej, Kumane	N 45°32'37'', E 20°13'16''
5	Žitište	N 45°29'01'', E 20°33'16''
6	Zrenjanin	N 45°22'11'', E 20°23'07''
7	Žabalj	N 45°22'59'', E 20°04'49''
8	Titel, Vilovo	N 45°14'56'', E 20°08'53''
9	Zrenjanin, Perlez	N 45°12'45'', E 20°22'08''
10	Kovačica, Uzdin	N 45°11'55'', E 20°37'22''
11	Sremski Karlovci	N 45°12'21'', E 19°56'08''
12	Kovačica	N 45°06'34'', E 20°37'50''
13	Zrenjanin, Čenta	N 45°06'59'', E 20°23'33''
14	Opovo	N 45°03'29'', E 20°25'47''
15	Indija	N 45°03'25'', E 20°05'19''
16	Opovo, Sefkerin	N 45°03'16'', E 20°25'03''
17	Stara Pazova	N 44°58'26'', E 20°09'40''
18	Kovilovo	N 44°54'33'', E 20°25'19''
19	Pančevo	N 44°52'03'', E 20°40'19''
20	Pančevo, Starčevo	N 44°48'26'', E 20°43'09''
21	Beograd, Surčin	N 44°47'56'', E 20°15'59''
22	Beograd, Bečmen	N 44°46'51'', E 20°12'52''
23	Beograd, Karaburma	N 44°48'16'', E 20°31'37''
24	Beograd, Bot. bašta	N 44°48'54'', E 20°28'26''
25	Zemun	N 44°50'24'', E 20°24'33''
26	Beograd, Višnjica	N 44°49'50'', E 20°32'48''
27	Beograd	N 44°48'04'', E 20°28'16''
28	Beograd, Ada Ciganlija	N 44°47'24'', E 20°24'06''
29	Beograd, Dušanovac	N 44°46'50'', E 20°29'01''
30	Beograd, Topčider	N 44°46'52'', E 20°26'21''
31	Pančevo, Omoljica	N 44°45'36'', E 20°44'35''
32	Pećinci, Ašanja	N 44°45'19'', E 20°05'12''
33	Obedska bara	N 44°44'09'', E 19°59'07''
34	Obrenovac, Mladost	N 44°41'54'', E 20°06'27''
35	Smederevo, Lugavčina	N 44°11'18'', E 21°04'07''
36	Majdanpek, Debeli lug	N 44°21'52'', E 21°54'41''
37	Smederevska palanka	N 44°21'53'', E 20°56'47''
38	Bor, Gornjane	N 44°14'31'', E 22°03'41''
39	Suvobor, Rajac mt.	N 44°08'06'', E 20°15'04''
40	Tara mt, Derventa	N 43°57'23'', E 19°21'19''
41	Perućac	N 43°57'21'', E 19°25'35''
42	Kraljevo, Maglič	N 43°36'42'', E 20°32'20''
43	Kruševac, Donji Stepoš	N 43°31'17'', E 21°18'29''
44	Niš, Banja Topilo	N 43°26'53'', E 21°52'40''
45	Sićevačka klis, Sićevo	N 43°19'54'', E 22°03'50''
46	Niš, Deveti Maj	N 43°19'09'', E 21°49'08''
47	Niš, Kamenički vis	N 43°24'03'', E 21°57'01''
48	Niš, Gornji Matejevac	N 43°22'13'', E 21°57'46''
49	Niš, Pantelej	N 43°19'58'', E 21°55'03''
50	Niš, Trošarina	N 43°18'38'', E 21°55'27''
51	Niš, Palilula	N 43°18'33'', E 21°54'20''
52	Niška banja	N 43°17'30'', E 22°00'25''
53	Prokuplje, G. Konjuša	N 43°11'53'', E 21°25'03''
54	Gadžin Han, Ovsinjinac	N 43°08'23'', E 22°08'55''
55	Radan mt.	N 42°58'03'', E 21°33'58''
56	Leskovac	N 42°59'32'', E 21°56'14''
57	Lebane, Konjino	N 42°56'07'', E 21°45'50''
58	Crna Trava	N 42°48'30'', E 22°18'06''
59	Vlasinsko jezero (lake)	N 42°44'13'', E 22°19'52''

Table I. Location data on the investigated localities

Material collection

Specimens of aphids were collected by cutting infected parts of the plants, mainly leaves and twigs, and placing them in plastic boxes of 0.5 litre volume. The boxes, filled with sampled material, were then covered with a mesh cloth to prevent insects from escaping and to allow the boxes to be ventilated. Before covering the boxes, we picked up 10-20 adult specimens of aphids, both winged and wingless for later identification. Thus, collected aphid specimens were placed in 1.5 ml plastic tubes and conserved in 96% ethyl alcohol. Aphids were identified using identification keys (Blackman & Eastop, 2021). Worker ants were collected along with aphids in the field and placed in the same boxes with aphids. Once the ants were dead, by the same procedure as for aphids, they were preserved in 96% ethyl alcohol in 2 ml plastic microtubes. The ants were identified by Dr. Marko Karaman (Natural History Museum

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of Montenegro). The taxa names of aphids and ants have been adopted according to the Fauna Europaea online database (van Achterberg, 2013).

RESULTS

In the present study, 220 samples of 32 ant taxa and 74 aphid taxa were collected from 59 localities across Serbia. The results were presented in alphabetical order following ant scientific names; subfamily, genus, and species, respectively. The same was done for aphids and plants, while data on date of sampling are given chronologically.

Abbreviations for legators: [AS] A. Stojiljković, [MIM] M. Ilić Milošević, [ML] M. Lazarević, [MR] M. Ristić, [NM] N. Mladenović, [OPO] O. Petrović-Obradović, [SS] S. Stanković, [VŽ] V. Žikić and [ŽT] Ž. Tomanović.

Subfamily Dolichoderinae

Tapinoma **sp. 1** – *Aphis umbrella* (Borner) on *Malva sylvestris* L., Niš, Deveti Maj, 18.05.2016, MR.

Tapinoma **sp. 2** – *Aphis umbrella* on *Malva sylvestris*, Niš, Deveti Maj, 18.05.2016, MR.

Subfamily Formicinae

Camponotus (Myrmentoma) tergestinus **Muller** – *Callaphis juglandis* (Goeze) on *Juglans regia* L., Obedska bara, 07.06.1997, ŽT; Opovo, 23.06.1997, ŽT.

Camponotus (Colobopsis) truncatus **(Spinola)** – *Brachycaudus cardui* (L.) on *Prunus domestica* L., Prokuplje, Gornja Konjuša, 23.04.2016, MR.

Camponotus (Myrmentoma) piceus **(Leach)** – *Aphis ruborum* (Borner) on *Rubus fruticosus* L., Prokuplje, Gornja Konjuša, 29.05.2016, MR; – *Brachycaudus cardui* on *Prunus avium* L., Kruševac, Donji Stepoš, 01.05.2016, ML; – *B. cardui* on *Prunus domestica*, Prokuplje, Gornja Konjuša, 23.04.2013, MR.

Camponotus (Tanaemyrmex) aethiops **(Latreille)** – *Lachnus* sp. on *Quercus cerris* L., Prokuplje, Gornja Konjuša, 15.06.2016, MR.

Formica (Serviformica) balcanina **Petrov & Collingwood** – *Aphis fabae* Scopoli on *Cirsium arvense* (L.) Scop., Vlasinsko jezero (lake), 30.06.2016, SS; – *Aphis* sp. on *Anthriscus* sp., Vlasinsko jezero (lake), 30.06.2016, SS; – *Chaetosiphon fragaefolii* (Cockerell) on *Fragaria vesca* L., Kruševac, Donji Stepoš, 17.04.2016, ML; – *Cavariella aegopodii* (Scopoli) on *Peucedanum officinalis* L., Vlasinsko jezero (lake), 30.06.2016, SS; – *Ctenocallis dobrovljanskyi* Klodnitsky on *Chamaecytisus heuffelii* (Wierzb.), Vlasinsko jezero (lake), 28.07.2017,

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VŽ; – *Dysaphis sorbi* (Kaltenbach) on *Sorbus aucuparia* L., Sićevačka klisura, Sićevo, 11.06.2017, VŽ.

Formica (Serviformica) cinerea **Mayr** – *Aphis fabae* on *Cirsium arvense*, Niš, Pantelej, 28.07.2017, VŽ; – *Brachycaudus* sp. on *Echium vulgare* L., Majdanpek, Debeli Lug, 09.06.1990, OPO; – *Symydobius oblongus* (von Heyden) on *Betula pendula* Roth var. pendula, Vlasinsko jezero (lake), 21.07.1990, OPO.

Formica (Serviformica) cunicularia **Latreille** – *Aphis fabae* on *Rumex patientia* L., Niš, Deveti Maj, 15.04.2016, MR; – *A. fabae* on *Bifora radians* Bieb., Prokuplje, Gornja Konjuša, 29.05.2016, MR; – *Aphis ruborum* on *Rubus fruticosus*, Prokuplje, Gornja Konjuša, 29.05.2016, MR; – *Brachycaudus cardui* on *Prunus cerasifera* Ehrh., Vlasinsko jezero (lake), 22.05.2016, VŽ; – *Cavariella aegopodii* on *Pastinaca hirsuta* Pančić, Vlasinsko jezero (lake), 30.06.2016, SS; – *Dysaphis plantaginea* (Passerini) on *Malus pumila* Mill., Obedska bara, 07.06.1997, ŽT; Beograd, 01.08.1997, ŽT.

Formica (Serviformica) fusca **L.** – *Cavariella aegopodii* on *Smyrnium perfoliatum* L., Niš, Niška banja, 24.05.2016, VŽ.

Formica (Serviformica) gagates **Latreille** – *Aphis fabae* on *Anthriscus sylvestris* (L.) Hoffm., Niš, Niška banja, 14.05.2017, VŽ; – *A. fabae* on *Rumex* sp., Niš, Kamenički vis, 04.06.2017, NM; – *Periphyllus* sp. on *Acer monspessulanum* L., Niš, Gornji Matejevac, 21.05.2017, SS.

Formica (Serviformica) glauca **Ruzsky** – *Aphis fabae* on *Hedera helix* L., Prokuplje, Gornja Konjuša, 29.05.2016, MR.

Formica (Formica) pratensis **Retzius** – *Aphis fabae* on *Anthriscus sylvaticus* (L.) Hoffm., Prokuplje, Gornja Konjuša, 01.05.2016, MR; – *A. fabae* on *Arctium lappa* L., Pećinci, Ašanja, 15.06.1996, ŽT; – *A. fabae* on *Galium mollugo* L., Prokuplje, Gornja Konjuša, 23.04.2016, MR; – *Brachycaudus cardui* on *Prunus cerasifera*, Vlasinsko jezero (lake), 22.05.2016, VŽ; – *Chaitophorus nigricantis* Pintera, on *Salix alba* L., Majdanpek, Debeli Lug, 09.06.1990, OPO; – *Chaitophorus vitellinae* (Schrank) on *S. alba*, Majdanpek, Debeli Lug, 09.06.1990, OPO; – *Ctenocallis dobrovljanskyi* Klodnitsky on *Chamaecytisus heuffelii*, Vlasinsko jezero (lake), 28.07.2017, VŽ; – *Myzus cerasi* (Fabricius) on *Prunus cerasus* L., Prokuplje, Gornja Konjuša, 23.04.2016, MR; – *Pterocomma* sp. on *Salix alba*, Majdanpek, Debeli Lug, 09.06.1990, OPO; – *Sipha maydis* Passerini on *Triticum aestivum* L. subsp. aestivum, Suvobor, Rajac mt., 18.05.1990, OPO.

Formica (Raptiformica) sanguinea **Latreille** – *Acaudinum centaureae* (Koch) on *Centaurea scabiosa* L., Majdanpek, Debeli Lug, 09.06.1990, OPO.

Formica (Serviformica) rufibarbis **Fabricius** – *Aphis baloticolla* Szelegiewicz on *Ballota nigra* L., Beograd, 29.06.1996, ŽT; Stara Pazova, 10.06.1997, ŽT; – *Aphis ulmariae* Schrank on *Filipendula ulmaria* (L.) Maxim., Vlasinsko jezero (lake), 23.07.1990, OPO; – *Macrosiphum rosae* (L.) on *Rosa* sp., Beograd, 09.06.1997, ŽT; – *Metopeurum fuscoviride* Stroyan on *Tanacetum vulgare* L., Vlasinsko jezero (lake), 30.06.2016,

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VŽ; – *Myzus cerasi* on *Prunus cerasus,* Prokuplje, Gornja Konjuša, 23.04.2016, MR.

Lasius (Cautolasius) flavus (**Fabricius**) – *Aphis serpylli* Koch on *Thymus praecox* Opiz, Vlasinsko jezero (lake), 25.08.2017, VŽ.

Lasius (Dendrolasius) fuliginosus (**Latreille**) – *Aphis vitalbae* Ferrari on *Clematis vitalba* L., Prokuplje, Gornja Konjuša, 03.04.2016, MR; Gadžin Han, Ovsinjinac, 13.04.2016, MR; – *Cavariella* sp. on *Salix* sp., Obedska bara, 07.05.1995, ŽT; – *Cavariella* sp. on *Salix* sp., Obedska bara, 07.06.1997, ŽT; – *Dysaphis reaumuri* (Mordvilko) on *Pyrus spinosa* Forssk., Radan mt., 10.06.2017, VŽ; – *Lachnus* sp. on *Quercus* sp., Bor, Gornjane, 06.07.1990, OPO; – *Pterocomma pilosum* Buckton on *Salix* sp., Beograd, Ada Ciganlija, 23.03.1990, OPO.

Lasius (Lasius) alienus (**Foerster**) – *Aphis crepidis* (Börner) on *Crepis biennis* L., Ada, Mol, 23.06.1997, ŽT; – *Aphis fabae* on *Papaver somniferum* L., Obedska bara, 07.06.1997, ŽT; – *A. fabae* on unidentified plant, Titel, Vilovo, 10.06.1997, ŽT; – *A. fabae* on *Rumex* sp., Beograd, 10.06.1995, ŽT; – *A. fabae* on *Tordylium maximum* L., Niš, Pantelej, 20.05.2016, VŽ; – *Aphis farinosa* Gmelin on *Salix* sp., Majdanpek, Debeli Lug, 31.03.1990, OPO; – *Aphis rumicis* L. on *Rumex* sp., Smederevo, Lugavčina, 15.04.1990, OPO; – *Aphis forbesi* Weed on *Fragaria vesca*, Beograd, Višnjica, 12.08.1997, ŽT; – *Aphis salviae* Walker on *Salvia nemorosa* L., Kovačica, Uzdin, 22.06.2017, ŽT; – *Aphis urticata* Gmelin on *Urtica dioica* L., Beograd, Surčin, 01.05.1993, ŽT; Kovilovo, 15.06.1993, ŽT; Beograd, Dušanovac, 06.06.1995, ŽT; Pančevo, Omoljica, 13.06.1996, ŽT; Čenta, 20.06.1996, ŽT; Obedska bara, 07.06.1997, ŽT; Stara Pazova, 10.06.1997, ŽT; Opovo, Sefkerin, 23.06.1997, ŽT; – *Aphis violae* Schouteden on *Viola tricolor* L., Vlasinsko jezero (lake), 23.07.1990, OPO; – *Brachycaudus cardui* on *Carduus acanthoides* L., Zrenjanin, 20.06.1996, ŽT; Zrenjanin, Perlez, 13.06.1997, ŽT; Nova Crnja, 23.06.1997, ŽT; – *Brachycaudus* sp. on *Stachys* sp., Bor, Gornjane, 05.07.1990, OPO; – *Chaitophorus nigricantis* on *Salix* sp., Smederevo, Lugavčina, 31.03.1990, OPO; – *Dysaphis plantaginea* on *Malus pumila*, Obedska bara, 07.06.1997, ŽT; Beograd, 01.08.1997, ŽT; – *Macrosiphum* sp. on *Tanacetum* sp., Bor, Gornjane, 06.07.1990, OPO; – *Phorodon humuli* (Schrank) on *Prunus cerasifera*, Pančevo, Starčevo, 17.07.1996, ŽT; Beograd, Bečmen, 07.06.1997, ŽT; Stara Pazova, 10.06.1997, ŽT; Kovačica, 22.06.1997, ŽT; Beograd, 16.08.1997, ŽT; Prokuplje, Gornja Konjuša, 01.05.2016, MR; – *Tetraneura* sp. on *Setaria verticillata* (L.) P. Beauv., Beograd, 12.08.1997, ŽT.

Lasius (Lasius) brunneus (**Latreille**) – *Aphis ruborum* on *Rubus caesius* L., Beograd, Karaburma, 21.05.1990, OPO; – *Aphis violae* on *Viola tricolor*, Vlasinsko jezero (lake), 23.07.1990, OPO.

Lasius (Austrolasius) carniolicus **Mayr** – *Geoica urticularia* Passerini on *Triticum aestivum* subsp. aestivum (root), Inđija, 10.06.1997, ŽT.

Lasius (Lasius) emarginatus (**Olivier**) – *Aphis fabae* on *Carduus acanthoides*, Prokuplje, Gornja Konjuša, 29.05.2016, MR; – *A. fabae* on *Digitalis grandiflora* Miller, Tara, Derventa, 23.06.2016, SS; –

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A. fabae on *Galium aparine* L., Niš, Gornji Matejevac, 09.06.2016, VŽ; – *Aphis podagrariae* Schrank on *Aegopodium podagraria* L., Niš, Trošarina, 01.06.2016, SS; – *Aphis pomi* De Geer on *Malus pumila*., Prokuplje, Gornja Konjuša, 23.04.2016, MR; – *Brachycaudus cardui* on *Prunus cerasifera*, Kruševac, Donji Stepoš, 08.05.2016, ML; – *Cavariella aegopodii* on *Smyrnium perfoliatum*, Niš, Niška banja, 24.05.2016, VŽ; – *Tetraneura* sp. on *Setaria verticillata* (root), Beograd, 12.08.1997, ŽT.

Lasius (Lasius) niger **(L.)** – *Aphis baloticolla* on *Ballota nigra*, Beograd, 29.06.1996, ŽT; Stara Pazova, 10.06.1997, ŽT; – *Aphis craccivora* Koch on *Medicago sativa* L., Kovilovo, 10.05.1992, ŽT; Beograd, Surčin, 20.06.1995, ŽT; Žabalj, 20.06.1996, ŽT; – *A. fabae* on *Althaea officinalis* L., Sremski Karlovci, 10.06.1997, ŽT; – *A. fabae* on *Malus pumila,* Prokuplje, Gornja Konjuša, 29.05.2016, MR; – *A. fabae* on *Rumex patientia*, Niš, Deveti Maj, 15.04.2016, MR; Kraljevo, Maglič, 08.05.2016, ML; – *A. fabae* on *Urtica urens* L., Novi Bečej, Kumane, 20.06.1996, ŽT; – *Aphis gossypii* Glover on *Althaea officinalis*, Niš, Banja Topilo, 08.07.2017, VŽ; – *Aphis lambersi* (Börner) on *Daucus carota* L. (root), Tara, Derventa, 23.06.2016, VŽ; – *Aphis pomi* on *Mespilus germanica* L., Lebane, Konjino, 24.04.2016, SS; – *Aphis spiraephaga* Müller on *Spirea media* Fr. Schm., Beograd, Bečmen, 15.06.1996, ŽT; – *Aphis umbrella* on *Althaea officinalis,* Obrenovac, Mladost, 20.05.1990, OPO; – *A. umbrella* on *Malva* sp., Beograd, 17.04.1990, OPO; – *Aphis urticata* on *Urtica dioica*, Beograd, Surčin, 01.05.1993, ŽT; Kovilovo, 31.07.1993, ŽT; Beograd, Dušanovac, 13.06.1995, ŽT; Čenta, 20.06.1996, ŽT; Kikinda, 23.06.1997, ŽT; Prokuplje, Gornja Konjuša, 01.05.2016, MR; – *Aphis vitalbae* on *Clematis vitalba,* Niš, Deveti Maj, 06.04.2016, MR; – *Brachycaudus* sp. on *Prunus persica* (L.) Batsch, Žabalj 20.06.1996, ŽT; – *Brachycaudus cardui* on *Carduus acanthoides,* Zrenjanin, 20.06.1996, ŽT; Obedska bara, 07.06.1997, ŽT; Čenta, 10.06.1997, ŽT; Pančevo, 22.06.1997, ŽT; – *B. cardui* on *Prunus cerasifera*, Niš, Deveti Maj, 06.04.2016, MR; Kruševac, Donji Stepoš, 01.05.2016, ML; – *Brachycaudus persicae* Passerini, on *Prunus persica*, Beograd, 05.04.1990, OPO; – *Cavariella aegopodii* on *Chaerophyllum hirsutum* L., Perućac, 22.06.2016, VŽ; – *Dysaphis ranunculi* (Kaltenbach) on *Ranunculus arvensis* L., Čenta, 10.06.1997, ŽT; – *Macrosiphum rosae* on *Rosa* sp., Kruševac, Donji Stepoš, 11.04.2016, ML; – *Microlophium carnosum* (Buckton) on *Urtica dioica*, Niš, Deveti Maj, 18.05.2016, MR; – *Myzus cerasi* on *Chrysanthemum* sp. Beograd, 07.05.1996, ŽT; – *M. cerasi* on *Prunus avium*, Beograd, Dušanovac, 06.06.1995, ŽT; Beograd, Višnjica, 24.05.1997, ŽT; Obedska bara, 07.06.1997, ŽT; – *M. cerasi* on *Prunus cerasifera*, Kruševac, Donji Stepoš, 17.04.2016, ML; Kruševac, Donji Stepoš, 08.05.2016, ML; – *Myzus persicae* (Sulzer) on *Capsicum annuum* L., Smederevska Palanka, 09.05.1996, OPO; Čenta, 13.06.1997, ŽT; – *M. persicae* on *Prunus persica*, Beograd, 05.04.1990, OPO; Lebane, Konjino, 24.04.2016, SS; – *Phorodon humuli* on *Prunus spinosa* L., Niš, Deveti Maj, 17.04.2016, MR.

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Lasius (Lasius) **cf.** *niger* (**Linnaeus**) – *Brachycaudus cardui* on *Carduus acanthoides*, Niš, Deveti Maj, 18.05.2016, MR.

Lasius (Lasius) paralienus **Seifert** – *Aphis fabae* on *Agrostemma githago* L., Prokuplje, Gornja Konjuša, 29.05.2016, MR; – *A. fabae* on *Bifora radians*, Prokuplje, Gornja Konjuša, 29.05.2016, MR; – *A. fabae* on *Carduus acanthoides*, Leskovac, 12.06.2017, AS; – *A. fabae* on *Cirsium arvense*, Leskovac, 19.07.2017, AS; – *A. fabae* on *Matricaria chamomilla* L.,Prokuplje, Gornja Konjuša, 29.05.2016, MR; – *A. fabae* on *Xeranthemum annuum* L., Prokuplje, Gornja Konjuša, 29.05.2016, MR; – *Aphis gossypii* on *Ballota nigra* , Niš, Deveti Maj, 18.05.2016, MR; – *Aphis intybi* Koch on *Cichorium intybus* L., Niš, Deveti Maj, 23.06.2016, MR; – *Aphis ruborum* on *Rubus fruticosus*, Prokuplje, Gornja Konjuša, 29.05.2016, MR; – *Dysaphis pyri* (Boyer de Fonscolombe) on *Pyrus eleagnifolia* Pallas, Radan mt., 10.06.2017, SS.

Lasius (Lasius) psammophilus **Seifert** – *Aphis craccivora* on *Medicago sativa*, Niš, Deveti Maj, 17.04.2016, MR; – *Aphis fabae* on *Matricaria chamomilla*, Prokuplje, Gornja Konjuša, 13.05.2016, MR; – *A. fabae* on *Rubus* sp., Kruševac, Donji Stepoš, 01.05.2016, ML; – *A. fabae* on *Rumex patientia*, Niš, Palilula, 28.04.2016, ML; – *Aphis gossypii* on *Ballota nigra*, Prokuplje, Gornja Konjuša, 23.04.2016, MR; – *Aphis passeriniana* (Del Guercio) on *Salvia officinalis* L., Niš, Deveti Maj, 06.04.2016, MR; – *Aphis sambuci* L. on *Sambucus nigra* L., Prokuplje, Gornja Konjuša, 23.04.2016, MR; – *Myzus cerasi* on *Prunus avium*, Kruševac, Donji Stepoš, 01.05.2016, ML; – *M. cerasi* on *Prunus cerasus*, Prokuplje, Gornja Konjuša, 23.04.2016, MR.

Lasius **sp. 1** – *Aphis fabae* on *Chenopodium album* L., Prokuplje, Gornja Konjuša, 29.05.2016, MR.

Lasius **sp. 2** – *Aphis urticata* on *Urtica dioica*, Prokuplje, Gornja Konjuša, 01.05.2016, MR.

Prenolepis nitens (**Mayr**) – *Anoecia corni* (Fabricius) on *Cornus* sp., Beograd, 12.04.1990, OPO; Zemun, 09.04.1990, OPO; – *Aphis fabae* on *Anthriscus sylvestris*, Niš, Niška banja, 14.05.2017, VŽ; – *A. fabae* on *Euonymus europaeus* L., Beograd, Topčider, 13.05.1993, 03.05.1997, ŽT; Prokuplje, Gornja Konjuša, 02.04.2016, MR; – *A. fabae* on *Galium mollugo*, Prokuplje, Gornja Konjuša, 29.05.2016, MR; – *A. fabae* on *Philadelphus coronarius* L., Kruševac, Donji Stepoš, 16.04.2016, ML; – *A. fabae* on *Rumex patientia*, Kruševac, Donji Stepoš, 01.05.2016, ML; – *Aphis hederae* Kaltenbach on *Hedera helix*, Kruševac, Donji Stepoš, 11.04.2016, ML; Kruševac, Donji Stepoš, 01.05.2016, ML; Niš, Pantelej, 01.05.2016, VŽ; – *Aphis pomi* on *Chaenomeles japonica* (Thunb.) Lindley ex Spach, Kruševac, Donji Stepoš, 01.05.2016, ML; Kruševac, Donji Stepoš, 08.05.2016, ML; – *Aphis ruborum* on *Rubus* sp., Kruševac, Donji Stepoš, 01.05.2016, ML; – *Aphis sambuci* on *Sambucus nigra*, Niš, Deveti Maj, 17.04.2016, MR; Kruševac, Donji Stepoš, 01.05.2016, ML; – *Aphis urticata* on *Urtica dioica*, Žitište, 22.07.1997, ŽT; Kruševac, Donji Stepoš, 07.04.2016, ML; Gadžin Han, Ovsinjinac, 13.04.2016, MR; Kruševac, Donji Stepoš, 01.05.2016, ML; Prokuplje, Gornja Konjuša, 01.05.2016, MR; – *A. urticata* on *Urtica* sp., Smederevo,

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Lugavčina, 15.04.1990, OPO; – *Aphis viburni* Scopoli on *Viburnum opulus* L., Gadžin Han, Ovsinjinac, 13.04.2016, MR; – *Aphis vitalbae* on *Clematis vitalba*, Niš, Niška banja, 11.04.2016, MR; – *Brachycaudus persicae* on *Prunus domestica*, Smederevo, Lugavčina, 04.05.1990, OPO; – *Chaetosiphon* sp. on *Lamium maculatum* L., Beograd, Botanička bašta, 17.06.1997, ŽT; – *Dysaphis* sp. on *Pyrus communis* L., Beograd, Višnjica, 24.05.1997, ŽT; – *Dysaphis* sp. on *P. communis*, Obedska bara, 07.06.1997, ŽT; – *Hyalopterus pruni* (Geoffroy) on *Prunus spinosa*, Niš, Palilula, 28.04.2016, ML; – *Lipaphis alliariae* Müller on *Alliaria petiolata* (Bieb.) Cavara & Grande, Gadžin Han, Ovsinjinac, 13.04.2016, MR; – *Macrosiphum rosae* on *Rosa canina* L., Kruševac, Donji Stepoš, 08.05.2016, ML; – *M. rosae* on *Rosa* sp., Kruševac, Donji Stepoš, 01.05.2016, ML; – *Periphyllus* sp. on *Acer campestre* L., Gadžin Han, Ovsinjinac, 13.04.2016, MR; *Periphyllus* sp. on *Acer monspessulanum*, Niš, Niška Banja, 11.05.2016, MIM; – *Phorodon humuli* on *Prunus cerasifera* Niš, Deveti Maj, 17.04.2016, MR; Prokuplje, Gornja Konjuša, 01.05.2016, MR; – *Thelaxes* sp. on Quercus robur L., Radan mt. (1000 m a.s.l.), 12.06.2016, SS.

Subfamily Myrmicinae

Crematogaster schmidti (**Mayr**) – *Aphis sambuci* on *Sambucus nigra*, Prokuplje, Gornja Konjuša, 02.04.2016, 23.04.2016, MR; – *Periphyllus* sp. on *Acer monspessulanum*, Niš, Niška banja, 24.05.2016, VŽ; – *Phorodon humuli* on *Prunus cerasifera* Prokuplje, Gornja Konjuša, 01.05.2016, MR; – *P. humuli* on *Prunus mahaleb* L., Niš, Gornji Matejevac, 21.05.2017, SS.

Messor structor (**Latreille**) – *Aphis umbrella* on *Malva neglecta* Wallr., Crna Trava, 23.07.1990, OPO; – *Myzus persicae* on *M. neglecta,* Crna Trava, 23.07.1990, OPO.

Myrmica rubra (**Linnaeus**) – *Cavariella aegopodii* on *Chaerophyllum hirsutum*, Perućac, 22.06.2016, VŽ; – *Pterocomma salicis* (Linnaeus) on *Salix* sp., Vlasinsko jezero (lake), 24.07.1990, OPO.

Tetramorium caespitum (**Linnaeus**) – *Aphis fabae* on *Beta vulgaris* L. var. cicla, Leskovac, 26.05.2017, AS; – *A. fabae* on *Cirsium arvense*, Beograd, Surčin, 15.06.1993, ŽT; 21.07.1993, ŽT; Smederevska Palanka, 13.06.1997, ŽT; Opovo, 23.06.1997, ŽT; – *Aphis taraxacicola* (Börner) on *Taraxacum* sp., Beograd, Surčin, 03.04.1990, OPO.

In this survey, we counted 167 ant-aphid associations. Three species stand out as participants of most associations. *Lasius niger* forms 28 associations, almost 17% of the total number. This species is followed by *Prenolepis nitens* with 26 associations (15.57%) and its congener *L. alienus*, which makes 18 associations (10.78%). The percentage of ant-aphid associations is presented in Fig. 2, where only half of the ant species is presented because the other 16 species forming 1-2 associations with values less than 1.8% are not presented.

Ants were collected in 74 colonies of aphid species out of a total of 384 species registered in Serbia, which means that some aphid associations

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have not yet been documented. As a facultative myrmecophilous species, *Aphis fabae* was present in 43 samples in our study, this species is most frequently found in the present survey and makes up 38 associations. The second most frequent species in this research was *Aphis urticata*. It was collected 21 times forming only five associations. This is followed by *Brachycaudus cardui* (16 samples and 10 associations), *Phorodon humuli* (11 samples and 5 associations) and *Myzus cerasi* (10 samples and 7 associations). Other aphid species were sampled less than ten times.

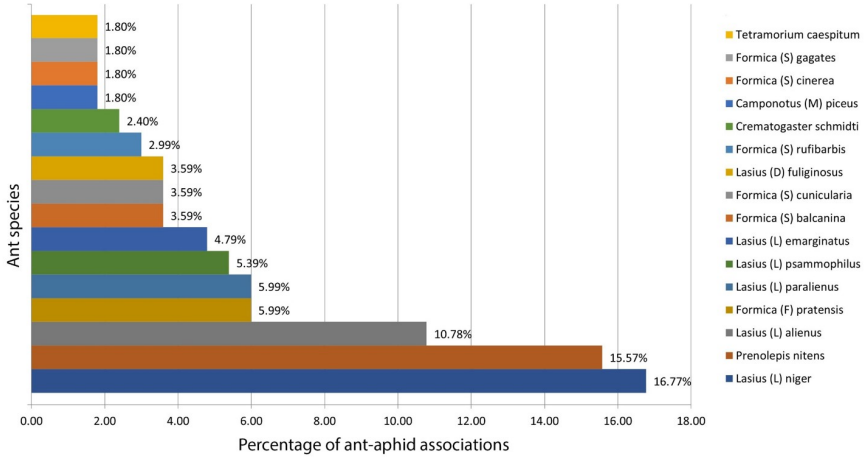

Fig. 2. Percentage of ant-aphid associations in the whole sample.
Species forming 1-2 associations. Values less than 1.8% are not presented.

DISCUSSION

This paper presents the first surveys of aphid-tending ants on the territory of Serbia, where their mutualistic relationships are presented through a complete association, plant-aphid-ant. The majority of the ants have been identified at the species level, except the four taxa belonging to the genera *Lasius* Fabricius and *Tapinoma* Förster. Of the three subfamilies presented here, Formicinae and Myrmicinae are listed with four genera each, while the subfamily Dolichoderinae is represented only by the genus *Tapinoma*.

The review of the literature has shown that there is no exact number of aphid species that are attended by each ant species. As already mentioned, some of the ant-aphid relationships are facultative, and therefore cannot always be registered (Starý, 1966). It is not entirely clear why this happens, but it is known that some species of ants show opportunistic behaviour in search of food and aphids. For example, it is shown that *Lasius niger* exhibits collective exploration of new territories and thus establishes relationships with various aphid species along the way (Devigne & Detrain, 2002). Usually, this species establishes the most numerous ant-aphid associations. For example, in a similar study, Novgorodova and Ryabinin, (2018) showed that *L. niger* was registered in associations with 103 species of aphids out of a total of 198 registered within the subfamily Aphidinae in the same survey. *Lasius niger* is one of the most common

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ants in Europe and the Balkans, often found as synanthropic species. This species has been observed in many countries and apparently has almost Holarctic distribution (AntWeb. Version 8.54.9. 2021). It is the most widespread species in Serbia (Petrov, 2002). On the other hand, *Prenolepis nitens*has a somewhat narrower area and is mainly distributed in the Mediterranean region, although it is often found throughout the Balkan Peninsula (Seifert, 2007; Vesnić & Lelo, 2010). This species is also known as the European false honey ant and feeds mainly on sweet fruits, nectar and elaiosomes. In addition, *P. nitens* also obtains a substantial amount of sugar from different aphid species (Bregant, 1998). *Prenolepis nitens* often forms numerous associations with aphids. For example, in a similar survey conducted in Turkey, Akyürek *et al*. (2016) report *L. alienus* as one of the most common species forms associations with aphids along its two congeners (*L. brunneus* and *L. turcicus* Santschi). In the same survey, the most common aphid species attended by ants were *Aphis fabae, A. spiraecola* Patch, and *Brachycaudus cardui*. We have assumed that the reason for the abundance of *A. fabae* is that it is a polyphagous species (Petrović-Obradović, 2003; Blackman & Eastop, 2021) that is present everywhere, thus very often collected.

It was unexpected that some aphid taxa, such as *Pterocomma* Buckton, *Geoica* Hart, *Tetraneura* Hartig or *Symidobius oblongus* Von Heyden, were not abundant in the sampled material. These taxa are known as regularly visited by ants (Molnár et al., 2000), especially the species from the genera *Geoica* and *Tetraneura*that are in permanent relationships with aphid tending ants (Pontin, 1978; Depa et al., 2020). Having in mind that species from the genera *Geoica* and *Tetraneura* live hidden, in the underground, or form galls, their concealment often led to them rarely being collected in the whole sample.

The coaction between ants and aphids is recognized as mutualism and is defined as an interaction between two species that is beneficial for both species (Bronstein, 2015). One might expect that aphid species attended by ants are thriving in comparison to others, however in some cases, for example between *L. niger* and *A. fabae*, when a different food is abundant ants often prey on aphids (Offenberg, 2001). A similar behaviour has been observed also in other aphid tending ant species, for example *Formica rufa* L. (Skinner, 1980). Nevertheless, the relationship between aphids and ants is widely present in nature and is one of the classic examples of mutualistic behaviour that often involves various adaptations driven by coevolution between the two groups.

Since this paper represents one of the first works on ant-aphid associations in Serbia, this is certainly not the definite number of aphids tended ants on the list. On the contrary, we assume that the number of ant and aphid species in associations is many times higher, primarily due to the lack of data, but also due to the flexible nature of mutual relations. Further research will greatly contribute to discovering the number of these interrelationships between the two groups of insects.

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