

Ant (Hymenoptera: Formicidae) - aphid (Hemiptera: Aphididae) interactions in different habitats from Turkey with new mutualistic associations

Şahin Kök*, Nihat Aktaş† and Ismail Kasap‡

*Department of Plant and Animal Production, Lapseki Vocational School, Çanakkale Onsekiz Mart University, 17800, Çanakkale, Turkey, †Faculty of Science, Department of Biology, Trakya University, 22030, Edirne, Turkey and ‡Faculty of Agriculture, Department of Plant Protection, Çanakkale Onsekiz Mart University, 17020, Çanakkale, Turkey

- Abstract**
- 1 This study aimed to investigate the interactions between ants and aphids on host plants in different habitats located in the northwestern part of Turkey. A total of 26 ant species belonging to 13 genera and 3 subfamilies from the family Formicidae (Hymenoptera) were found associated with 52 aphid species belonging to 22 genera from the family Aphididae (Hemiptera: Aphidoidea) on 66 host plant species from 24 plant families.
 - 2 In total, 132 tritrophic ants–aphids–host plants interactions including new associations were revealed.
 - 3 Also, we present results on the interactions of ants–aphids–host plants in different habitats such as cultivated, uncultivated and urban areas. About 85 tritrophic interactions of ants–aphids–host plants were revealed in cultivated, 27 tritrophic interactions in uncultivated and 20 tritrophic interactions in urban areas. Tritrophic interactions were more diverse in cultivated areas than uncultivated and urban areas.
 - 4 Our results reveal that the interactions between ants and aphids are highly diverse and that they vary on host plants in different habitats. It may be thought that this is due to the specialization resulting from the high diversity of host plants of aphids in cultivated areas and increased the presence of ants.

Keywords Ant, aphid, host plant, mutualism, tritrophic interaction.

Introduction

The interactions between ants (Hymenoptera: Formicidae) and aphids (Hemiptera: Aphididae), an example of a successful mutualism among organisms, is one of the most researched topics by many researchers during the last century. Such relationships have aroused interest in different disciplines such as aphidology, myrmecology, pest management, biological control of pests, insect ecology and evolution. In this mutualistic association, honeydew secreted by some aphids feeding on the phloem of host plants is consumed by certain ants. This food source fulfills the carbohydrate requirements needed by ants and is used as an energy resource for their vital activities. In return for providing food, these aphids are protected by the ants from predation and parasitism (Way, 1963; Addicott, 1978). Naturally, the mutualism of aphids and ants has a much more complex and comprehensive content, especially in terms of evolutionary perspective.

Ant presence plays an important role in the morphological evolution of some organs, on biological features such as development, reproduction and host alternate, communication, presence of endosymbionts and their effects on some aphids. Contrary to obligatory and facultative, the interactions between aphids and ants occur with various degrees of involvement on both sides. Also, the evolution of parthenogenetic lineages in some aphid species can be evaluated as a result of ant attendance (Depa *et al.*, 2020).

Organisms in mutualistic interactions each gain benefits, but this situation may come at a cost to both partners. Although the interactions between ants and aphids are mostly based on mutualism, in some cases, these interactions between them are without significant cost for aphids; some ant species hunt non-myrmecophilous aphids (Novgorodova, 2005). For example, the presence of ants has significant impacts on the biological features such as developmental time, offspring production, development of embryos and mean relative growth rate of the aphid species, *Aphis fabae cirsiacanthoides* Smith & Parron, 1978 on

Correspondence: Şahin Kök. Tel.: +90 0541 746 37 66; e-mail: sahinkok@gmail.com

the host plant, *Cirsium arvense* (L.) Scop. (Asteraceae) (Stadler & Dixon, 1998). In the case of ants, there is an energy cost for collecting, transporting and storing honeydew and an increased dependence on aphids as a source of fuel for foraging (Stadler & Dixon, 2005). Also, the presence of ants plays an important role as a result of mutualistic adaptation on the morphological and life cycle features of myrmecophilous aphids on host plants. Morphologically, the interactions with ants can cause issues such as shortened or reduced siphunculi, reduced waxy covering on the body, shortened cauda and perianal ring of setae on aphids (Way, 1963; Heie, 1987). Besides, ants in these interactions can disrupt the seasonal migration of host-alternating aphids and can cause aphids to display only asexual reproductive behaviour on secondary host plants (Moran, 1992; Kindlmann *et al.*, 2007).

For the reasons considered above, the potential benefits and costs of ants–aphids interactions on host plants in different habitats need to be examined in more detail from different perspectives. When evaluated in terms of biological control, the presence of ants reduces the effectiveness of natural enemies that put pressure on aphid populations as they provide strong protection against these natural enemies such as predators and parasitoids (Herbert & Horn, 2008; Novgorodova & Gavriluk, 2012). Also, ant presence has positive effects on important biological features of aphids such as population growth (Rice & Eubanks, 2013). Conversely, the removal of ants from the environment reduces the intensity of the aphid population and the damages they cause (Nagy *et al.*, 2013; Devegili *et al.*, 2020). From an ecological perspective, the honeydew and cuticular hydrocarbons secreted by aphid species play an important role in the aphid partner selectivity of ants, as it helps ants recognize and not kill aphids (Endo & Itino, 2013; Hayashi *et al.*, 2015). Moreover, the presence of a trophobiotic organ consisting of a shortened cauda and a perianal ring of setae in some subterranean myrmecophilous aphids has been interpreted as an adaptation to living underground, in their interactions with ants, and to living in galls (Heie, 1987). Kanturski *et al.* (2017) examined the external morphology of the trophobiotic organ of six aphid species belonging to subfamilies Anoeciinae, Eriosomatinae and Lachninae and concluded that the development and character of the trophobiotic organ in aphids is far from being accurately proven and explained.

The studies on tritrophic interactions among ants and aphids in different habitats worldwide are still very limited. A review study conducted so far showed that there are 972 aphids–ants interactions and 915 ants–aphids interactions between 284 species of aphids and 193 species of ants (Siddiqui *et al.*, 2019). Detailed faunal trophobiosis studies should be conducted by different disciplines of science to better understand and interpret these ants–aphids interactions based on benefits and costs. Separate faunal studies of ants and aphids in Turkey have been carried out by many researchers for more than a century (Rigler, 1852; Trotter, 1903; Donisthorpe, 1950; Çanakçıoğlu, 1975; Özdemir *et al.*, 2005; Kiran & Aktaş, 2006; Kiran & Karaman, 2012; Kök *et al.*, 2016; Kök & Kasap, 2019). These studies so far revealed that the ant and aphid fauna of Turkey is represented by 362 ant and 591 aphid species, respectively (Kiran & Karaman, 2020; Kök & Özdemir, 2021). Although the faunal diversity of ants and aphids is quite rich, the studies on the interactions

of these organisms are still limited both in Turkey and in the world. Accordingly, the purpose of this study conducted in the northwestern part of Turkey was to increase the data that will form a basis for a better understanding of the tritrophic interactions between ants and aphids on host plants in different habitats. Also, we wondered how interactions of the ants–aphids and aphids–host plants will respond to the different habitats such as cultivated, uncultivated and urban areas. Therefore, we hypothesized that these interactions in cultivated areas, where the diversity of cultivated plants, trees and herbaceous plants which is one of the most important factors in increasing the diversity of both aphids and ants, are richer and should be higher and complex than in other areas.

Materials and methods

Sampling site

The sampling site of this study was in the northwestern part of Turkey; it consists of the South Marmara region, which constitutes an important crossroads between Europe and Asia. This region has a continental climate in the southeastern parts, a milder climate in parts close to the coastal area, and a Mediterranean climate in regions of the gulf and islands. The sampling area contains the Biga Peninsula, Edremit Gulf, Gallipoli Peninsula and Ida Mountains, which are known to have a high degree of endemic floristic and faunistic biodiversity (Özhatay & Özhatay, 2005). The sampling areas include cultivated areas consisting mostly of fruit, vegetable and cereal areas, uncultivated areas including forests and natural areas free from human activity, and urban areas including the centers of city settlement of Çanakkale and Balıkesir Provinces and their county in the South Marmara region of the northwestern part of Turkey (Fig. 1).

Collection, preparation and identification of ants and aphids

To register interactions between ants and aphids on host plants, yearly insect sampling was carried out on herbaceous plants, shrubs and trees in different habitats such as cultivated (1), uncultivated (2) and urban areas (3) in the South Marmara region of the northwestern part of Turkey between April and October from 2017 to 2020. To determine whether aphids detected on host plants in the sampling area were myrmecophilous, the presence or absence of ants on or near aphid colonies was observed for a few minutes since it is known that the behaviour of myrmecophilous and nonmyrmecophilous aphids differ significantly (Dixon, 1958; Novgorodova, 2002). Classification of aphids as myrmecophilous was based on behaviours such as ants actively collecting honeydew from aphid colonies and aphids not showing any defensive behaviour against ants (Novgorodova & Ryabinin, 2018). Once the interactions between aphid colonies and ants were determined, sufficient numbers of both apterous—alate specimens of aphids and ant individuals were separately put in an Eppendorf tube containing 70% ethyl alcohol using a soft brush and then brought to the laboratory for identification. Collected ant specimens were mounted on small cardboards and pinned with stainless insect needles.

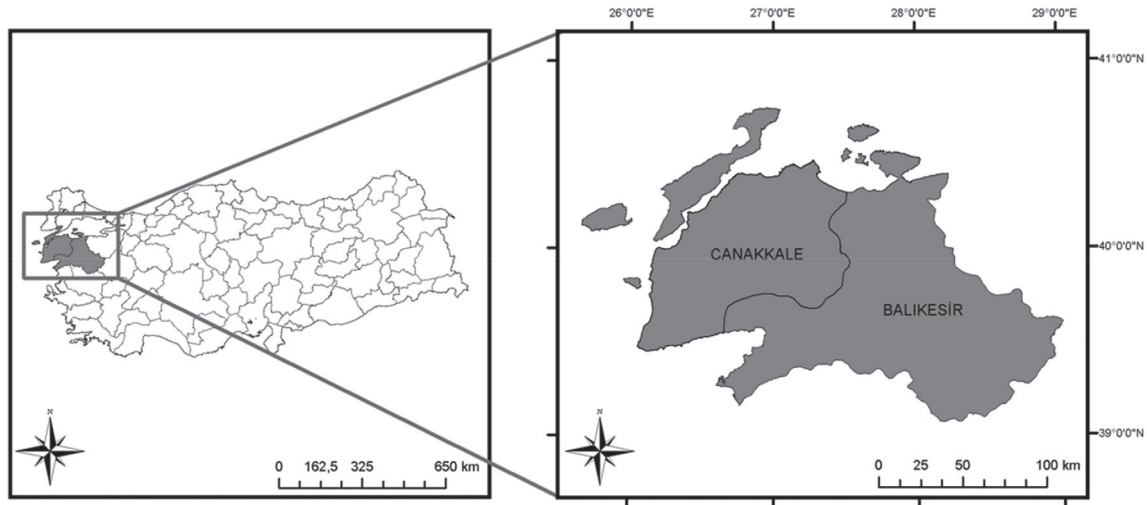


Figure 1 Map showing the overall sampling site in the South Marmara region including Çanakkale and Balıkesir provinces of Northwest Turkey.

Ant species were identified using Olympus SZ51 microscope according to Agosti & Collingwood (1987), Seifert (1992), Czechowski *et al.* (2002), Aktaç & Radchenko (2002), Karaman & Aktac (2013). The preparation of the aphid specimens followed the method of Hille Ris Lambers (1950). The aphid specimens were identified using a LEICA DM 2500 light microscopy mounted HD camera and LAS 4.1 version software according to Blackman & Eastop (2006, 2021). For the identification of aphid specimens, measurements of morphological characters, ratios of different body parts and chaetotaxy were also examined. The current taxonomic status and species names of all aphids followed Favret (2021), and ants followed Bolton's Catalogue (Bolton, 2017). The vouchers of all aphids and ants are, respectively, deposited in the Aphid Collection of S. KOK (Department of Plant Protection, Agricultural Faculty, Çanakkale Onsekiz Mart University, Turkey) and CNA (Collection of N. AKTAC—Department of Biology, Faculty of Science, Trakya University, Turkey).

Data analysis

The graphs of bipartite network interactions in the cultivated, uncultivated and urban areas were constructed based on data of ants and aphids relative abundances for ants–aphids and aphids–host plants interactions for all years. The nestedness (N) (NODF) and modularity (M) (Beckett) were calculated for the networks of ants–aphids and aphids–host plants in the cultivated, uncultivated and urban habitats using the 'nested' and 'metaComputeModules' functions, respectively, and then to reveal observed differences in nestedness and modularity in the networks for different habitats, we compared the observed values to null expectations computed from nulls created using the method of 'r2dtable' in the bipartite package in the R software version 3.6.1. Also, we used analysis of covariances to test the differences in the values of nestedness and modularity for the ants–aphids and aphids–host plants networks in the cultivated, uncultivated and urban areas (R Development Core Team, 2021).

Results

Results of the survey carried out to better understand the interactions of ants–aphids in the different habitats of the northwestern part of Turkey identified 26 ant species belonging to 13 genera in 3 subfamilies from the family Formicidae (Hymenoptera) associated with 52 aphid species belonging to 22 genera from the family Aphididae (Hemiptera: Aphidoidea) on 66 host plant species. Surveys in the different habitats revealed 132 tritrophic ants–aphids–host plants interactions including new association records for the world and Turkey.

The trophobiosis list of ants associated with aphids on host plants in the different habitats of the northwestern part of Turkey is given below.

Family Formicidae

Subfamily Dolichoderinae

Genus *Dolichoderus* Lund, 1831

Dolichoderus quadripunctatus (Linnaeus, 1771)

**Cinara* (*Cupressobium*) *oxycedri* Binazzi, 1996 on *Juniperus oxycedrus* L. (Cupressaceae), 07.IV.2019, Çanakkale (2).

*Note: The association between *D. quadripunctatus* and *C. (C.) oxycedri* is recorded for the first time. There are reports of associations between *D. quadripunctatus* and some aphid species belonging to genus *Aphis*, *Betulaphis*, *Brachycaudus*, *Calaphis*, *Callipterinella*, *Cavariella*, *Chaitophorus*, *Chromaphis*, *Cinara* (*C. pini*, *C. pinea* and *C. pilosa*), *Drepanosiphum*, *Eucallipterus*, *Euceraphis*, *Lachnus*, *Myzocallis*, *Myzus*, *Panaphis*, *Periphyllus*, *Pterocomma*, *Schizaphis*, *Stomaphis*, *Thelaxes*, *Tuberculatus* and *Tuberolachnus* from Poland and Ukraine (Stukalyuk, 2018; Czechowski *et al.*, 2019; Stukalyuk *et al.*, 2019).

Genus *Tapinoma* Foerster, 1850

Tapinoma erraticum (Latreille, 1798)

**Aphis* (*Aphis*) *spiraecola* Patch, 1914 on *Prunus avium* (L.) L. (Rosaceae), 16.V.2017, Çanakkale (1); **Aphis* (*Aphis*) *rumicis* Linnaeus, 1758 on *Rumex pulcher* L. (Polygonaceae), 12.V.2018, Balıkesir (2); **A. (A.) spiraecola* and *Aphis* (*Aphis*) *nerii* Boyer de Fonscolombe, 1841 on *Nerium oleander* L. (Apocynaceae),

20.V.2018, Çanakkale (3); *Aphis* (*Aphis*) *craccivora* Koch, 1854 on *Vicia* sp. (Leguminosae), 07.V.2020, Çanakkale (1); *A. (A.) craccivora* on *Trifolium* sp. (Leguminosae), 11.VI.2020, Balıkesir (1).

*Note: This is a new ant–aphid association. Previously, associations between *T. erraticum* and some aphid species belonging to genus *Aphis*, *Brachycaudus*, *Chaitophorus* and *Cinara* were reported from Iran and Turkey (Mortazavi et al., 2015; Latibari et al., 2016; Kök et al., 2018).

Subfamily Formicinae

Genus *Camponotus* Mayr, 1861

Camponotus aethiops (Latreille, 1798)

**Aphis* (*Aphis*) *solanella* Theobald, 1914 on *Urtica urens* L. (Urticaceae), 31.III.2017, Çanakkale (1); **Myzocallis* (*Pasekia*) *komareki* on *Quercus ithaburensis* subsp. *macrolepis* (Kotschy) Hedge & Yalt. (Fagaceae), 22.IV.2017, Çanakkale (2); **Rhopalosiphum maidis* (Fitch, 1856) on *Triticum aestivum* L. (Poaceae) 22.IV.2017, Balıkesir (1); *Aphis* (*Aphis*) *fabae* Scopoli, 1763 on *Rumex crispus*, 06.V.2017, Çanakkale (1); **A. (A.) rumicis* on *R. crispus* L. (Polygonaceae), 14.V.2017, *A. (A.) solanella* and *Brachycaudus* (*Prunaphis*) *cardui* (Linnaeus, 1758) on *Cirsium* sp. (Compositae), 24.V.2017, Çanakkale (1); Balıkesir (1); *Lachnus roboris* (Linnaeus, 1758) on *Q. ithaburensis* subsp. *macrolepis* 20.V.2018, Balıkesir (2); * *A. (A.) craccivora* on *Tribulus terrestris* L. (Zygophyllaceae), 18.VII.2018, Balıkesir (1); **Aphis* (*Aphis*) *gossypii* Glover, 1877 on *Punica granatum* L. (Lythraceae), 14.V.2020, Çanakkale (1); **Dysaphis* (*Pomaphis*) *plantaginea* (Passerini, 1860) on *Malus domestica* Borkh. (Rosaceae), 21.V.2020, Çanakkale (1); **Myzus* (*Myzus*) *cerasi* (Fabricius, 1775) on *P. avium* (Rosaceae), 21.V.2020, Çanakkale (1).

*Note: This is a new ant–aphid association. Also, the association between *Camponotus aethiops* and *Aphis* (*Aphis*) *craccivora* is recorded for the first time in Turkey. Also, the associations between *C. aethiops* and some aphid species belonging to genus *Aphis*, *Brachycaudus*, *Lachnus*, *Sipha* and *Thelaxes* were reported from Spain and Turkey (Özdemir et al., 2008; Hernández-Castellano & Hidalgo, 2014; Akyürek et al., 2016).

Camponotus gestroi Emery, 1878

**Aphis* (*Aphis*) *fabae* on *Rumex crispus* (Polygonaceae), 06.V.2017, Çanakkale (2); **Lachnus roboris* on *Quercus cerris* L. (Fagaceae), 13.VI.2018, Balıkesir (2).

*Note: This is a new ant–aphid association. Also, the associations between *C. gestroi* and some aphid species belonging to the genus *Thelaxes* and *Lachnus* were reported from Iraq (Starý, 1969).

Camponotus lateralis (Olivier, 1792)

**Chaitophorus leucomelas* Koch, 1854 on *Populus* sp. (Salicaceae), 13.V.2017, Balıkesir (2); **M. (M.) cerasi* on *Prunus avium* (Rosaceae), 12.VI.2017, Çanakkale (1); **A. (A.) fabae* on *Chenopodium album* L. (Amaranthaceae), 21.VII.2017, Balıkesir (1).

*Note: This is a new ant–aphid association. Also, the associations between *C. lateralis* and some aphid species belonging to genus *Aphis* and *Hyadaphis* were reported from Malta Island and Turkey (Mifsud et al., 2011; Akyürek et al., 2016).

Camponotus piceus (leach, 1825)

**Brachycaudus* (*Thuleaphis*) *amygdalinus* (Schouteden, 1905) on *Prunus persica* (L.) Batsch (Rosaceae), 22.IV.2017, Çanakkale (1); **Sitobion* (*Sitobion*) *fragariae* (Walker, 1848) on *Hordeum murinum* subsp. *leporinum* (Link) Arcang. (Poaceae), 06.V.2017, Çanakkale (2); **Macrosiphum* (*Macrosiphum*) *rosae* (Linnaeus, 1758) on *Rosa* sp. (Rosaceae), 13.V.2017, Balıkesir (2); * *Myzocallis* (*Pasekia*) *komareki* on *Quercus ithaburensis* subsp. *macrolepis* (Fagaceae), 22.IV.2018, Balıkesir (2).

*Note: This is a new ant–aphid association. Also, the associations between *C. piceus* and some aphid species belonging to genus *Aphis*, *Brachycaudus*, *Hyadaphis* and *Staegeriella* were reported from Italy and Turkey (Starý, 1966; Özdemir et al., 2008).

Camponotus samius Forel, 1889

**Aphis* (*Aphis*) *arbuti* Ferrari, 1872 and *Wahlgreniella nervata arbuti* (Davidson, 1910) on *Arbutus unedo* L. (Ericaceae), 13.VI.2017, Çanakkale (2).

*Note: This is a new ant–aphid association. Also, the associations between *C. samius* and *Cinara pini* were reported from Turkey (Kök et al., 2018).

Camponotus sanctus Forel, 1904

Myzus (*Myzus*) *cerasi* on *Prunus avium* (Rosaceae), 08.VI.2019, Balıkesir (1).

Note: There is a record of the association between *C. sanctus* and *M. (M.) cerasi* from Turkey (Kök et al., 2018).

Genus *Formica* Linnaeus, 1758

Formica cunicularia Latreille, 1798

Macrosiphum (*Macrosiphum*) *rosae* on *Rosa* sp. (Rosaceae), 04.IV.2017, Çanakkale (3); **Patchiella reaumuri* (Kaltenbach, 1843) on *Tilia tomentosa* Moench (Malvaceae), 01.V.2017, Çanakkale (3); **Cinara* (*Cinara*) *tujafilina* (Del Guercio, 1909) on *Platycladus orientalis* (L.) Franco (Cupressaceae), 21.V.2017, Çanakkale (3); *Aphis* (*Aphis*) *pomi* De Geer, 1773 on *Malus floribunda* Siebold ex Van Houtte (Rosaceae), 21.V.2017, Çanakkale (3); *Aphis* (*Aphis*) *solanella* and **Brachycaudus* (*Prunaphis*) *cardui* on *Cirsium* sp. (Compositae), 24.V.2017, Çanakkale (1); **M. (M.) cerasi* on *P. avium* (Rosaceae), 12.VI.2017, Çanakkale (1); **Hyalopterus amygdali* (Blanchard, 1840) on *Prunus persica* (Rosaceae), 21.V.2018, Balıkesir (3); *Aphis* (*Aphis*) *spiraecola* on *Spiraea* × *vanhouttei* (Briot) Zabel (Rosaceae), 11.V.2018, Balıkesir (3); **Cinara* (*Cinara*) *fresai* Blanchard, 1939 on *Cupressus arizonica* Greene (Cupressaceae), 15.IV.2019, Balıkesir (3); **Aphis* (*Aphis*) *rumicis* on *Rumex* sp. (Polygonaceae), 30.IV.2020, Balıkesir (1); *Dysaphis* (*Pomaphis*) *plantaginea* on *Malus domestica* (Rosaceae), 30.IV.2020, Çanakkale (1); * *Brachycaudus* (*Brachycaudus*) *helichrysi* (Kaltenbach, 1843) on *Prunus domestica* L. (Rosaceae), 06.V.2020, Çanakkale (1); **Hyalopterus pruni* (Geoffroy, 1762) on *Phragmites australis* (Cav.) Trin. ex Steud. (Poaceae), 28.V.2020, Balıkesir (1); **B. (P.) cardui* on *Carduus pycnocephalus* L. (Compositae), 28.V.2020, Balıkesir (1); *Aphis* (*Aphis*) *fabae* on *Chenopodium album* (Amaranthaceae), 28.V.2020, Çanakkale (1).

*Note: This is a new ant–aphid association. Also, the associations between *Formica cunicularia* and *Aphis* (*Aphis*) *pomi* and *D. (P.) plantaginea* are recorded for the first time in Turkey. Also, the associations between *F. cunicularia* and some

aphid species belonging to genus *Acyrtosiphon*, *Aphis*, *Brachycaudus*, *Chaitophorus*, *Cinara*, *Macrosiphoniella*, *Macrosiphum* and *Sipha* were reported from Iran, Russia and Turkey (Novgorodova, 2005; Özdemir *et al.*, 2008; Mortazavi *et al.*, 2015; Akyürek *et al.*, 2016; Latibari *et al.*, 2017; Kök *et al.*, 2018).

Genus *Lasius* Fabricius, 1804

Lasius alienus (Foerster, 1850)

**Aphis* (*Aphis*) *umbrella* (Börner, 1950) on *Malva* sp. (Malvaceae), 04.IV.2017, Balıkesir (1); **Dysaphis* (*Dysaphis*) *radicola radicola* (Mordvilko, 1897) on *Rumex* sp. (Polygonaceae), 16.IV.2017, Çanakkale (1); **Aphis* (*Aphis*) *spiraecola* on *Viburnum tinus* L. (Adoxaceae), 27.IV.2017, Balıkesir (3); **Brachycaudus* (*Thuleaphis*) *amygdalinus* on *Prunus persica* (Rosaceae), 22.IV.2017, Çanakkale (1); **Trama* (*Neotrampa*) *caudata* Del Guercio, 1909 on *Tragopogon porrifolius* subsp. *longirostris* (Sch. Bip.) Greuter (Compositae), 01.V.2017, Çanakkale (1); *Aphis* (*Aphis*) *craccivora* on *Vicia faba* L. (Leguminosae), 01.V.2017, Çanakkale (1); *Aphis* (*Aphis*) *solanella* on *Rumex* sp. (Polygonaceae), 01.V.2017, Balıkesir (1); **Aphis* (*Aphis*) *catalpae* Mamontova, 1953 on *Catalpa bignonioides* Walter (Bignoniaceae), 11.V.2017, Çanakkale (3); **Cinara* (*Cinara*) *brauni* Börner, 1940 on *Pinus nigra* subsp. *pallasiana* (Lamb.) Holmboe (Pinaceae), 13.V.2017, Balıkesir (2); **Aphis* (*Aphis*) *rumicis* on *R. crispus* (Polygonaceae), 14.V.2017, Balıkesir (1); **Aphis* (*Aphis*) *spiraecola* on *Viburnum opulus* (Adoxaceae), 08.VI.2017, Balıkesir (3); **A. (A.) umbrella* on *Malva sylvestris* L. (Malvaceae), 07.IV.2018, Balıkesir (2); *Myzus* (*Myzus*) *cerasi* on *Prunus avium* (Rosaceae), 15.V.2018, Çanakkale (1) **Aphis* (*Aphis*) *fabae mordvilko* Börner & Janich, 1922 on *Philadelphus coronarius* L. (Hydrangeaceae), 11.V.2019, Çanakkale (3);

*Note: This is a new ant–aphid association. Also, the associations between *Lasius alienus* and some aphid species belonging to genus *Aphis*, *Brachycaudus*, *Capitophorus*, *Chaitophorus*, *Cinara*, *Dysaphis*, *Myzus*, *Neobetulaphis*, *Periphyllus*, *Pterocomma*, *Rhopalosiphum*, *Sipha*, *Schizoneuraphis* and *Toxoptera* were reported from Italy, Iran, Spain, Turkey and U.S.A. (Starý, 1966; Özdemir *et al.*, 2008; Favret *et al.*, 2010; Akyıldırım *et al.*, 2014; Barton & Ives, 2014; Mortazavi *et al.*, 2015; Akyürek *et al.*, 2016; Latibari *et al.*, 2016).

Lasius brunneus (Latreille, 1798)

**Cinara* (*Cinara*) *pini* on *Pinus* sp. (Pinaceae), 13.VIII.2019, Çanakkale (2).

*Note: The association between *L. brunneus* and *C. (C.) pini* is recorded for the first time. Also, the associations between *L. brunneus* and some aphid species belonging to genus *Aphis*, *Brachycaudus*, *Cinara*, *Dysaphis*, *Hyalopterus*, *Periphyllus*, *Prociphilus*, *Pterocomma* and *Stomaphis* were reported from Europe, Iran, Italy, Poland, Slovakia, Spain and Turkey (Espalder *et al.*, 2006; Loi *et al.*, 2012; Depa & Kanturski, 2014; Akyürek *et al.*, 2016; Depa *et al.*, 2017; Mirzamohamadi *et al.*, 2019; Purkart *et al.*, 2019).

Lasius niger (Linnaeus, 1758)

**Aphis* (*Aphis*) *fabae* on *Chenopodium album* (Amaranthaceae), 21.V.2020, Balıkesir (1); **Dysaphis* (*Pomaphis*) *plantaginea* on *Malus domestica* (Rosaceae), 21.V.2020, Çanakkale (1).

*Note: This is a new ant–aphid association new in Turkey. Also, the associations between *L. niger* and some aphid species belonging to genus *Aphis*, *Brachycaudus*, *Calipterina*, *Chaitophorus*, *Chromaphis*, *Cinara*, *Dysaphis*, *Lachnus*, *Metopeurum*, *Myzocallis*, *Symydobius* and *Trama* were reported from England, India, Japan, Russia and Spain (Tizado *et al.*, 1993; Müller & Godfray, 1999; Kaneko, 2003; Novgorodova, 2005; Kataria & Kumar, 2013).

Genus *Lepisiota* Santschi, 1926

Lepisiota frauenfeldi (Mayr, 1855)

**Aphis* (*Aphis*) *vallei* Hille Ris Lambers & Stroyan, 1959 on *Euphorbia rigida* M.Bieb. (Euphorbiaceae), 06.V.2017, Çanakkale (2); **Dysaphis* (*Pomaphis*) *plantaginea* on *M. domestica* (Rosaceae), 11.V.2017, Çanakkale (3); **Lachnus roboris* on *Quercus infectoria* G. Olivier (Fagaceae), 13.V.2017, Balıkesir (2); **Aphis* (*Aphis*) *spiraecola* on *P. avium* (Rosaceae), 16.V.2018, Çanakkale (3); *Aphis* (*Aphis*) *fabae* on *Nerium oleander* (Apocynaceae), 31.V.2018, Balıkesir (3); **Hyperomyzus* (*Hyperomyzus*) *lactucae* (Linnaeus, 1758) and **Uroleucon* (*Uroleucon*) *sonchi* (Linnaeus, 1767) on *Sonchus* sp. (Compositae), 11.VI.2020, Çanakkale (1).

*Note: This is a new ant–aphid association. The association between *L. frauenfeldi* and *A. (A.) fabae* is recorded for the first time in Turkey. Also, the associations between *L. frauenfeldi* and some aphid species belonging to genus *Aphis*, *Greenidea*, *Hyadaphis*, *Macrosiphoniella*, *Ovatus*, *Pterochloroides*, *Tinocallis* and *Tuberolachnus* were reported from India, Iran, Malta Island and Pakistan (Mifsud *et al.*, 2011; Mortazavi *et al.*, 2015; Rakhshani & Ahmad, 2015; Gull-E-Fareen *et al.*, 2020).

Genus *Plagiolepis* Mayr, 1861

Plagiolepis pallescens Forel, 1889

**A. (A.) spiraecola* on *Viburnum opulus* L. (Adoxaceae), 08.VI.2017, Çanakkale (3); *Aphis* (*Aphis*) *craccivora* on *Trifolium purpureum* Loisel. (Leguminosae), 28.V.2020, Balıkesir (1).

*Note: This is a new ant–aphid association. Also, the associations between *P. pallescens* and some aphid species belonging to genus *Acyrtosiphon*, *Aphis*, *Brachycaudus*, *Callaphis*, *Hyalopterus* and *Tinocallis* were reported from Iran and Turkey (Özdemir *et al.*, 2008; Shiran *et al.*, 2013; Mortazavi *et al.*, 2015).

Plagiolepis pygmaea (Latreille, 1798)

A. (A.) craccivora on *Amaranthus retroflexus* L. (Amaranthaceae), 16.VII.2017, Balıkesir (1); **Acyrtosiphon* (*Acyrtosiphon*) *pisum* (Harris, 1776) and *A. (A.) craccivora* on *Medicago sativa* L. (Leguminosae), 24.V.2017, Çanakkale (1); **Rhopalosiphum maidis* and *Schizaphis* (*Schizaphis*) *graminum* (Rondani, 1852) on *Setaria* sp. (Poaceae), 21.VII.2017, Çanakkale (1); **S. (S.) graminum* on *Sorghum* sp. (Poaceae), 21.VII.2017, Balıkesir (1); **Myzus* (*Myzus*) *lythri* (Schränk, 1801) on *Prunus armeniaca* L. (Rosaceae), 25.IV.2020, Çanakkale (1); **Brachycaudus* (*Brachycaudus*) *helichrysi* on *Anthemis* sp. (Compositae), 07.V.2020, Çanakkale (1); **Myzus* (*Myzus*) *cerasi* on *Prunus avium* (Rosaceae), 21.V.2020, Balıkesir (1); **Brachycaudus* (*Appelia*) *tragopogonis* (Kaltenbach, 1843) on *Tragopogon* sp., 28.V.2020, Çanakkale (1).

*Note: This is a new ant–aphid association. The association between *P. pygmaea* and *A. (A.) craccivora* is recorded for the first time in Turkey. Also, the associations between *P. pygmaea* and some aphid species belonging to genus *Aphis*, *Brachycaudus*, *Chromaphis*, *Dysaphis*, *Melanaphis*, *Panaphis*, *Prociphilus* and *Sipha* were reported from Iran, Malta Island, Spain and Turkey (Mifsud *et al.*, 2011; Hernández-Castellano & Hidalgo, 2014; Mortazavi *et al.*, 2015; Akyürek *et al.*, 2016; Kök *et al.*, 2018).

***Plagiolepis vindobonensis* Lomnicki, 1925**

**Aphis (Aphis) solanella* and *Brachycaudus (Prunaphis) cardui* on *Cirsium* sp. (Compositae), 24.V.2017, Balıkesir (1); **Aphis (Aphis) ruborum* (Börner & Schilder, 1931) on *Rubus* sp. (Rosaceae), 13.VI.2017, Çanakkale (1); **B. (P.) cardui* on *Carduus pycnocephalus* (Compositae), 12.V.2018, Çanakkale (2); **Aphis (Aphis) spiraeicola* on *P. avium* (Rosaceae), 02.IX.2019, Balıkesir (1); **Aphis (Aphis) lamiorum* (Börner, 1950) on *Lamium purpureum* L. (Lamiaceae), 16.IV.2020, Çanakkale (1); **Aphis (Aphis) frangulae* Kaltenbach, 1845 on *Lamium amplexicaule* L. (Lamiaceae), 25.IV.2020, Balıkesir (1); **Dysaphis (Pomaphis) plantaginea* and *Aphis (Aphis) gossypii* on *Malus domestica* (Rosaceae), 30.IV.2020, Çanakkale (1); **Aphis (Aphis) craccivora* on *Vicia* sp. (Leguminosae), 07.V.2020, Çanakkale (1); **A. (A.) craccivora*, *Therioaphis (Pterocallidium) trifolii* (Monell, 1882) and *Acyrtosiphon (Acyrtosiphon) pisum* on *Trifolium spumosum* L. (Leguminosae), 07.V.2020, Çanakkale (1); **Myzus (Nectarosiphon) persicae* (Sulzer, 1776) and *A. (A.) gossypii* on *Prunus armeniaca* (Rosaceae), 14.V.2020, Çanakkale (1); **A. (A.) craccivora*, *Ovatus (Ovatus) insitus* (Walker, 1849) and *A. (A.) gossypii* on *Malus* sp. (Rosaceae), 14.V.2020, Çanakkale (1); **B. (A.) tragopogonis* on *Tragopogon* sp. (Compositae), 28.V.2020, Balıkesir (1).

*Note: This is a new ant-aphid association. There is a record of the association between *Plagiolepis vindobonensis* and *Staegeriella necopinata* from Turkey (Özdemir *et al.*, 2008).

Genus *Prenolepis* Mayr, 1861

***Prenolepis nitens* (Mayr, 1853)**

**Aphis (Aphis) ruborum* on *Rubus caesius* L. (Rosaceae), 29.III.2017, Balıkesir (1); **Aphis (Aphis) gossypii* on *Veronica* sp. (Plantaginaceae), 01.V.2017, Çanakkale (1); **Aphis (Aphis) fabae* on *Silybum marianum* (L.) Gaertn. (Compositae), 24.V.2017, Çanakkale (1); **Cinara (Cinara) pini* (Linnaeus, 1758) on *Pinus* sp. (Pinaceae), 26.IX.2017, Balıkesir (2); **Cinara (Cinara) oxycedri* on *Juniperus oxycedrus* (Cupressaceae), 07.IV.2018, Çanakkale (2); **Aphis (Aphis) rumicis* on *Rumex* sp. (Polygonaceae), 16.IV.2020, Balıkesir (1); **Phorodon (Phorodon) humuli* (Schrank, 1801) on *Prunus* sp. (Rosaceae), 30.IV.2020, Çanakkale (1).

*Note: This is a new ant–aphid association. Also, an association between *P. nitens* and *Prociphilus fraxini* was reported from Slovakia (Purkart *et al.*, 2019).

Genus *Proformica* Ruzsky, 1902

***Proformica korbi* (Emery, 1909)**

**Dysaphis (Pomaphis) plantaginea* on *Malus domestica* (Rosaceae), 21.XI.2019, Çanakkale (1).

*Note: The association between *P. korbi* and *D. (P.) plantaginea* is recorded for the first time. Also, there is no record of the association between *P. korbi* and aphids in the world.

Subfamily Myrmicinae

Genus *Crematogaster* Lund, 1831

***Crematogaster ionia* Forel, 1911**

**Chaitophorus leucomelas* on *Populus* sp. (Salicaceae), 06.V.2017, Çanakkale (2); **A. (A.) ruborum* on *R. caesius* (Rosaceae) 06.V.2017, Çanakkale (1, 3); **Aphis (Aphis) viticis* Ferrari, 1872 on *Vitex agnus-castus* L. (Lamiaceae) 06.V.2017, Çanakkale (1); **Aphis (Aphis) hederæ* Kaltenbach, 1843 on *Hedera helix* L. (Araliaceae), 27.IV.2017, Balıkesir (3); **Brachyunguis (Brachyunguis) tamaricis* (Lichtenstein, 1886) on *Tamarix* sp. (Tamaricaceae), 05.VI.2018, Çanakkale (3).

*Note: This is a new ant–aphid association. Also, there is a record of the association between *Crematogaster ionia* and *Aphis nerii* from Turkey (Kök *et al.*, 2018).

***Crematogaster scutellaris* (Oliver, 1792)**

**Chaitophorus leucomelas* on *Populus* sp. (Salicaceae), 13.V.2017, Çanakkale (2); **Periphyllus obscurus* Mamon-tova, 1955 on *Acer campestre* L. (Sapindaceae), 13.VI.2018, Çanakkale (2); *Aphis (Aphis) fabae* on *Chenopodium album* (Amaranthaceae), 11.VI.2020, Balıkesir (1).

*Note: This is a new ant–aphid association. Also, the associations between *C. scutellaris* and some aphid species belonging to genus *Aphis*, *Pemphigus* and *Pterocomma* were reported from Italy and Turkey (Akyürek *et al.*, 2016; Masoni *et al.*, 2017).

***Crematogaster sordidula* (Nylander, 1849)**

**Aphis (Aphis) craccivora* on *T. stellatum* L. (Leguminosae), 22.IV.2018, Çanakkale (2); **Brachycaudus (Brachycaudus) helichrysi* on *Carduus pycnocephalus* (Compositae), 20.VII.2019, Balıkesir (2).

*Note: This is a new ant–aphid association. Also, the associations between *C. sordidula* and some aphid species belonging to genus *Aphis*, *Cinara*, *Brachycaudus* and *Thelaxes* were reported from Iran, Iraq and Turkey (Starý, 1969; Özdemir *et al.*, 2008; Mortazavi *et al.*, 2015).

Genus *Monomorium* Mayr, 1855

***Monomorium monomorium* Bolton, 1987**

**B. (B.) helichrysi* on *C. pycnocephalus* (Compositae), 16.X.2019, Çanakkale (2).

*Note: The association between *M. monomorium* and *B. (B.) helichrysi* is recorded for the first time. Also, there is a record of the association between *M. monomorium* and *Aphis (Aphis) gossypii* from Palau (Idechiil *et al.*, 2007).

Genus *Pheidole* Westwood, 1839

***Pheidole pallidula* (Nylander, 1849)**

**Myzus (Myzus) cerasi* on *Prunus avium* (Rosaceae), 16.V.2017, Çanakkale (1); **Aphis (Aphis) craccivora* on *Amaranthus albus* L. (Amaranthaceae), 21.VII.2017, Balıkesir (1); **A. (A.) craccivora*, *A. (A.) gossypii* and **Ovatus (Ovatus) insitus* on *Malus* sp. (Rosaceae), 14.V.2020, Çanakkale (1); **Myzus (Nectarosiphon) persicae* and **A. (A.) gossypii* on *Prunus armeniaca* L. (Rosaceae), 15.V.2020, Çanakkale (1).

*Note: This is a new ant–aphid association. Also, the associations between *P. pallidula* and some aphid species belonging to genus *Aphis*, *Brachycaudus*, *Cinara*, *Hyalopterus*, *Myzus*, *Sipha*

and *Thelaxes* were reported from Iraq, Iran, Italy, Malta Island, Spain and Turkey (Starý, 1966, 1969; Mifsud *et al.*, 2011; Shiran *et al.*, 2013; Hernández-Castellano & Hidalgo, 2014; Latibari *et al.*, 2016; Kök *et al.*, 2018).

Genus *Tetramorium*

Tetramorium caespitum (Linnéus, 1758)

Brachycaudus (*Prunaphis*) *cardui* on *Cynara* sp. (Compositae), 04.IV.2017, Çanakkale (1); *Aphis* (*Aphis*) *fabae* on *Rumex* sp. (Polygonaceae), 16.V.2017, Çanakkale (1).

Note: The associations between *T. caespitum* and some aphid species belonging to genus *Aphis*, *Protaphis*, *Brachycaudus*, *Macrosiphoniella* and *Myzus* were reported from Iran, Japan, Spain and Turkey (Tizado *et al.*, 1993; Katayama & Suzuki, 2003; Shiran *et al.*, 2013; Akyıldırım *et al.*, 2014; Akyürek *et al.*, 2016).

Tetramorium ferox Ruzsky, 1903

*A. (*A.*) *fabae* on *Vicia* sp. (Leguminosae), 12.VI.2019, Balıkesir (2).

*Note: The association between *T. ferox* and *A. (A.) fabae* is recorded for the first time. Also, there is no record of the association between *T. ferox* and aphids in the world.

Tetramorium hippocratis (Agosti & Collingwood, 1987)

**Aphis* (*Aphis*) *craccivora* on *Vicia* sp. (Leguminosae), 07.V.2020, Çanakkale (1).

*Note: The association between *Tetramorium hippocratis* and *A. (A.) craccivora* is recorded for the first time. Also, there is no record of the association between *T. ferox* and aphids in the world.

From the identified ants, the species that most interacted with aphids were *Formica cunicularia* with 15 aphids, *Plagiolepis vindobonensis* with 13 aphids, *Lasius alienus* with 12 aphids, and *Camponotus aethiops* with 11 aphids. On the other hand, the ant species that least interacted with aphids were *Dolichoderus quadripunctatus*, *Camponotus gestroi*, *Camponotus sanctus*, *Lasius brunneus*, *Proformica korbi*, *Monomorium monomorium*, *Tetramorium ferox* and *Tetramorium hippocratis*; all interacting with one aphid species. In the case of the aphids to ants interaction, the most common aphids associated with ants were *Aphis* (*Aphis*) *fabae* associated with 11 ant species, *A. (A.) craccivora* with 9 ant species, and *Myzus* (*Myzus*) *cerasi* with 7 ant species. Also, the aphids, *A. (A.) arbuti*, *A. (A.) catalpae*, *A. (A.) fabae mordvilkoii*, *A. (A.) frangulae*, *A. (A.) hederiae*, *A. (A.) lamiorum*, *A. (A.) nerii*, *A. (A.) pomi*, *A. (A.) umbrella*, *A. (A.) valleii*, *A. (A.) viticis*, *Brachyunguis* (*Brachyunguis*) *tamaricis*, *Cinara* (*Cinara*) *brauni*, *C. (C.) freisai*, *C. (C.) tujafilina*, *Dysaphis* (*Dysaphis*) *radicola radicola*, *Hyalopterus pruni*, *Hyperomyzus* (*Hyperomyzus*) *lactucae*, *M. (M.) lythri*, *Pachyiella reaumurii*, *Periphyllus obscurus*, *Phorodon* (*Phorodon*) *humuli*, *Schizaphis* (*Schizaphis*) *graminum*, *Sitobion* (*Sitobion*) *fragariae*, *Therioaphis* (*Pterocallidium*) *trifolii*, *Trama* (*Neotrama*) *caudata*, *Uroleucon* (*Uroleucon*) *sonchi* and *Wahgreniella nervata arbuti* were only visited by one ant species.

The nestedness and modularity values of different habitats in ants–aphids and aphids–host plants networks were determined and results showed that the nestedness values of different habitats for ants–aphids networks were cultivated ($N = 17.26$), uncultivated ($N = 1.56$) and urban ($N = 8.88$) areas, and for aphids–host plants networks as cultivated ($N = 2.83$),

uncultivated ($N = 0.33$) and urban ($N = 1.66$) areas. The modularity values of different habitats for ants–aphids networks were estimated as cultivated ($M = 0.54$), uncultivated ($M = 0.80$) and urban ($M = 0.66$) areas and were estimated as cultivated ($M = 0.80$), uncultivated ($M = 0.90$) and urban ($M = 0.88$) areas for aphids–host plants networks.

The values of nestedness and modularity of different habitats within ants–aphids and aphids–host plants networks were tested against its null models to estimate whether different habitats in networks are significant nested or modular. As a result of testing the nestedness and modularity values of each habitat in different networks against null models, the habitats in ants–aphids networks were significantly nested (cultivated: $F = 91.54$, $P < 0.001$; uncultivated: $F = 183.27$, $P < 0.001$; urban: $F = 32.00$, $P < 0.001$) and the habitats in aphids–host plants networks were significantly nested (cultivated: $F = 918.41$, $P < 0.001$; uncultivated: $F = 268.09$, $P < 0.001$; urban: $F = 10.55$, $P < 0.001$). Similarly, the habitats in ants–aphids networks were significantly modular (cultivated: $F = 431.54$, $P < 0.001$; uncultivated: $F = 111.21$, $P < 0.001$; urban: $F = 279.71$, $P < 0.001$) and the habitats in aphids–host plants networks were significantly modular (cultivated: $F = 576.32$, $P < 0.001$; uncultivated: $F = 187.34$, $P < 0.001$; urban: $F = 725.72$, $P < 0.001$). Also, we used null models to reveal the effect of changes in the number of interactions and the distribution of interactions on differences in nestedness and modularity of networks in the cultivated, uncultivated and urban areas. Based on the interactions network values, the interactions of ants–aphids in the cultivated areas were more nested than the uncultivated and urban areas ($F_{1,3} = 24.54$, $P < 0.001$), and the interactions of aphids–host plants in the cultivated areas were more nested than the other areas ($F_{1,3} = 156.55$, $P < 0.001$). On the other hand, the interactions of ants–aphids in the uncultivated and urban areas were more modular than the cultivated areas ($F_{1,3} = 27.41$, $P < 0.001$), and the interactions of aphids–host plants in the uncultivated areas were more modular than the cultivated and urban areas ($F_{1,3} = 87.14$, $P < 0.001$).

Discussion

The mutualistic interactions between ants and aphids are largely based on the contents of different habitats such as host plant biodiversity, host plant quality, the presence of natural enemies and climate factors (Stadler *et al.*, 2002; Stutza & Entling, 2011; Canedo-Júnior *et al.*, 2017). In this context, investigation of ants–aphids interactions on host plants in different habitats provides an understanding of how ants and aphids have a great impact on food webs and how their interactions affect trophic levels. Also, these ants–aphids interactions provide the basis for our better understanding of phenomena such as pest management, biological control of pests, insect ecology and evolution. For this reason, we investigated the interactions between ants and aphids on host plants in different habitats such as cultivated, uncultivated and urban areas. When the tritrophic interactions of ants–aphids–host plants were evaluated in terms of different habitats, our field surveys revealed that 85 ants–aphids–host plants interactions occurred in cultivated areas, 27 ants–aphids–host plants interactions occurred

in uncultivated areas and 20 ants–aphids–host plants interactions occurred in urban areas. Around 19 ant species belonging to 11 genera from the family Formicidae associated with 30 aphid species belonging to 14 genera from the family Aphididae found on 39 host plant species were identified on cultivated and herbaceous plants in cultivated areas (Figs 2 and 3). In uncultivated areas with trees, shrubs and herbaceous plants, 17 ant species belonging to 10 genera from the family Formicidae associated with 18 aphid species belonging to 10 genera from the family Aphididae on 18 host plant species were identified (Figs 2 and 3). In urban areas with ornamental and herbaceous plants, 6 ant species belonging to 6 genera from the family Formicidae associated with 15 aphid species belonging to 7 genera from the family Aphididae on 17 host plant species were identified (Figs 2 and 3).

Our results draw attention to the fact that the number of tritrophic interactions of ants–aphids–host plants in cultivated areas is higher and more complex than in uncultivated and urban areas. This situation can be explained by the diversity of host plants including cultivated plants, trees and herbaceous plants in cultivated areas, the high number of aphid species, the presence and diversity of ant species. While the diversity and distribution of ants can be affected by environmental factors, such as soil structure, host plant vegetation and insolation, the diversity of aphid species is closely related to the presence of host plants as well as suitable densities of ant nests (Hopkins & Thacker, 1999). The correct understanding of the interactions between ants and aphids on host plants in different habitats sheds light on the studies of pest management and biological control strategies in agriculture and urban areas including landscape areas. In this context, the basic tritrophic interactions data obtained in this study can be the basis for studies to be conducted on these subjects in the future. In our surveys, numerous new interactions have been revealed between ants and aphids on host plants in different habitats. For example, the interactions of the ant, *Dolichoderus quadripunctatus*—*Cinara* (*Cinara*) *oxycedri*, an important aphid pest of forest trees, on the host plant, *Juniperus oxycedrus* (Cupressaceae); the ant, *Camponotus lateralis*—*Myzus* (*Myzus*) *cerasi*, an important aphid pest of cherry trees, on the host plant, *Prunus avium* (Rosaceae); the ant, *Pheidole pallidula*—*Myzus* (*Nectarosiphon*) *persicae*, an important aphid pest of peach trees, on the host plant, *Prunus armeniaca* (Rosaceae) and the ant, *Formica cunicularia*—*Brachycaudus* (*Brachycaudus*) *helichrysi*, an important aphid pest of plum trees, on the host plant, *Prunus domestica* (Rosaceae) are recorded for the first time. A better understanding of these new interactions between some ant species and aphids that can cause significant damages in agricultural areas is very important in terms of the efficiency of natural enemies in biological control strategies and some biological parameters of aphid pests. A study exploring the effect of ants on some aphids, *Dysaphis* (*Pomaphis*) *plantaginea*, *Eriosoma lanigerum* (Hausmann, 1802), *Aphis* (*Aphis*) *pomi* and *Aphis* (*Aphis*) *spiraecola*, on apple orchards revealed that the presence of ants was important, especially for *D. (P.) plantaginea* to perform well, and also ants had a significant negative effect on the abundance of natural enemies that are good suppressors of aphid pests (Minarro *et al.*, 2010). In parallel with this, our results showed that the aphid species, *D. (P.) plantaginea* was associated with six ant species on apple trees (*Malus domestica*) in

cultivated areas in northwest Turkey. Also, our qualitative observations in these fields reveal that the population density of *D. (P.) plantaginea* on apple trees was high in the presence of ants and natural enemies activity was low compared to other apple trees without aphids. According to Sadeghi-Namaghi & Amiri-Jami (2018), ant attendance positively affected the population growth rate of the aphid species, *Aphis* (*Aphis*) *gossypii*, while other aphid species, *Brachycaudus* (*Prunaphis*) *cardui* was negatively affected by the presence of ants. The parasitism rate of *A. (A.) gossypii* decreased significantly with the presence of the ant, *Lasius turcicus*, but the ant, *Crematogaster sordidula*, significantly increased the parasitism of *B. (P.) cardui*. As a result, the authors emphasized that the effects of the presence of ants differ between ants and aphids interactions. This inference is important in terms of understanding and leading the investigation on the possible effects of the many different interactions in our results. Also, the interactions of ants–aphids are an important issue in urban areas with ornamental plants as well as in cultivated and uncultivated areas. Korányi *et al.* (2020) emphasize that the abundance of ants decreased with urbanization but did not affect the abundance of aphids. This negative impact of urbanization on ants also clarifies our results on ants–aphids interactions in different habitats including urban areas. Correspondingly, our data show that while the diversity of ants and aphids in cultivated and uncultivated areas and the number of tritrophic interactions of them are high, the diversity of ants remained very low in urban areas despite the relatively high diversity of aphids.

As far as we know, studies on the responses of the interactions of ants–aphids and aphids–host plants in cultivated, uncultivated and urban areas are very limited. In this study, we also revealed that the interactions of ants–aphids and aphids–host plants were more nested in the cultivated areas compared to other areas. On the other hand, the interactions of ants–aphids and aphids–host plants areas were more modular in the uncultivated areas than in other areas. These results reveal that the specialization in cultivated areas is lower than in other areas because there are many different host plants for aphids and this provides them the opportunity to migrate between hosts. Also, the lower number of polyphagous aphid species having a large diversity of host plants in uncultivated and urban areas and the fact that these aphids generally spend their lives on the same host during the year may have caused the networks in these habitats to be less complex. Based on these results, we can emphasize that the negative or positive effects of aphids on host plants are less widespread in uncultivated and urban areas than in cultivated areas. Correspondingly, the interactions of ants–aphids–host plants in cultivated areas are becoming more diverse and complex.

As a result, it seems clear that the interactions between ants and aphids are affected by habitat differences, and these interactions positively or negatively affect the biological features of aphids, the effectiveness of natural enemies and biological control strategies. With this study, numerous data on the many new interactions between ants and aphids on host plants in different habitats such as cultivated, uncultivated and urban areas are presented. It is thought that our data will provide a basis for a better understanding of the interactions between ants and aphids in different habitats and there will be a guide for the studies to be carried out in different disciplines such as pest management, biological control of pests, insect ecology and evolution.

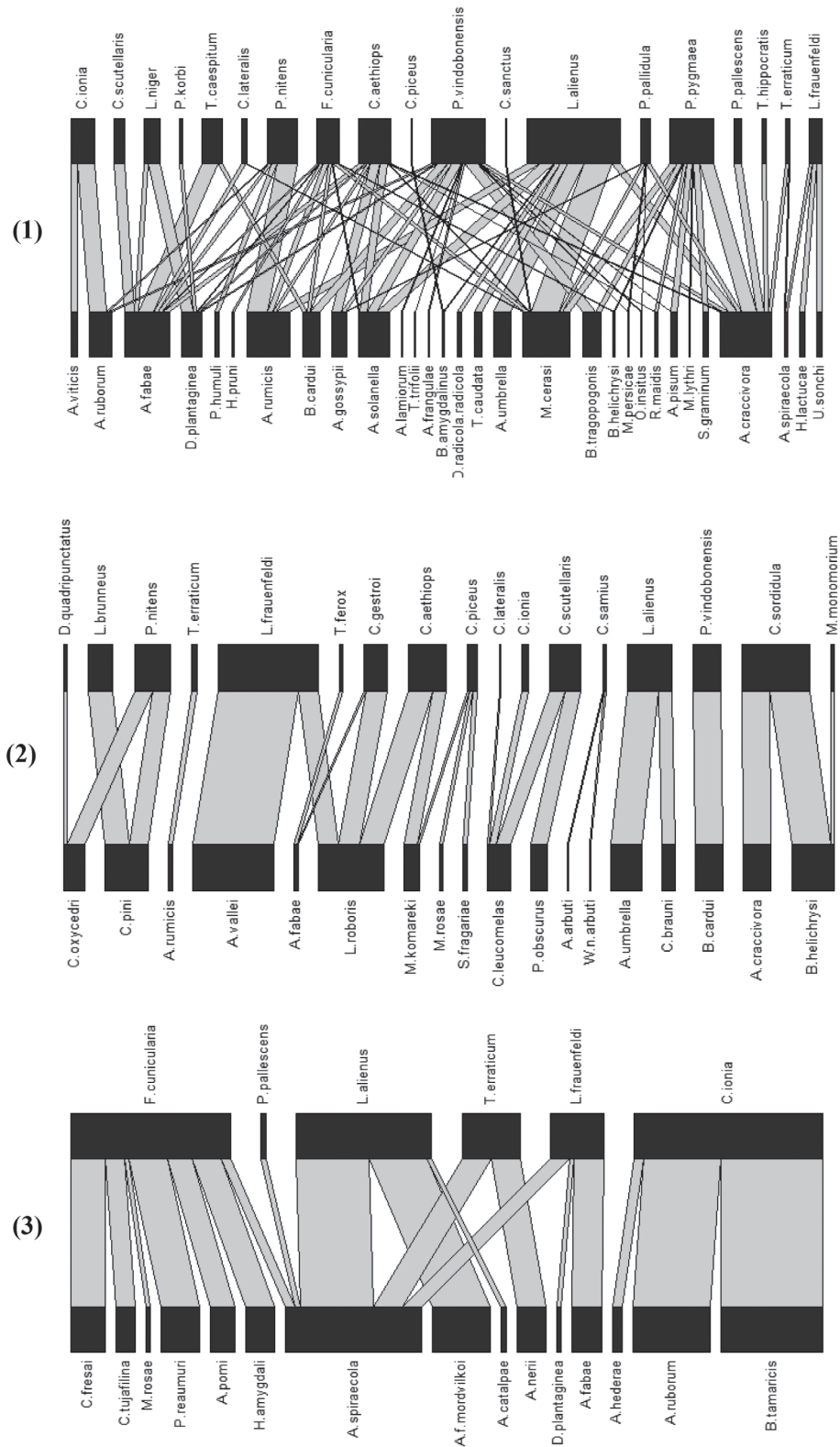


Figure 2 Bipartite networks interaction between ants (top) and aphids (bottom) species in cultivated (1), uncultivated (2) and urban (3) areas in Northwest Turkey. Black bars represent the abundance of the species and grey bars represent interactions.

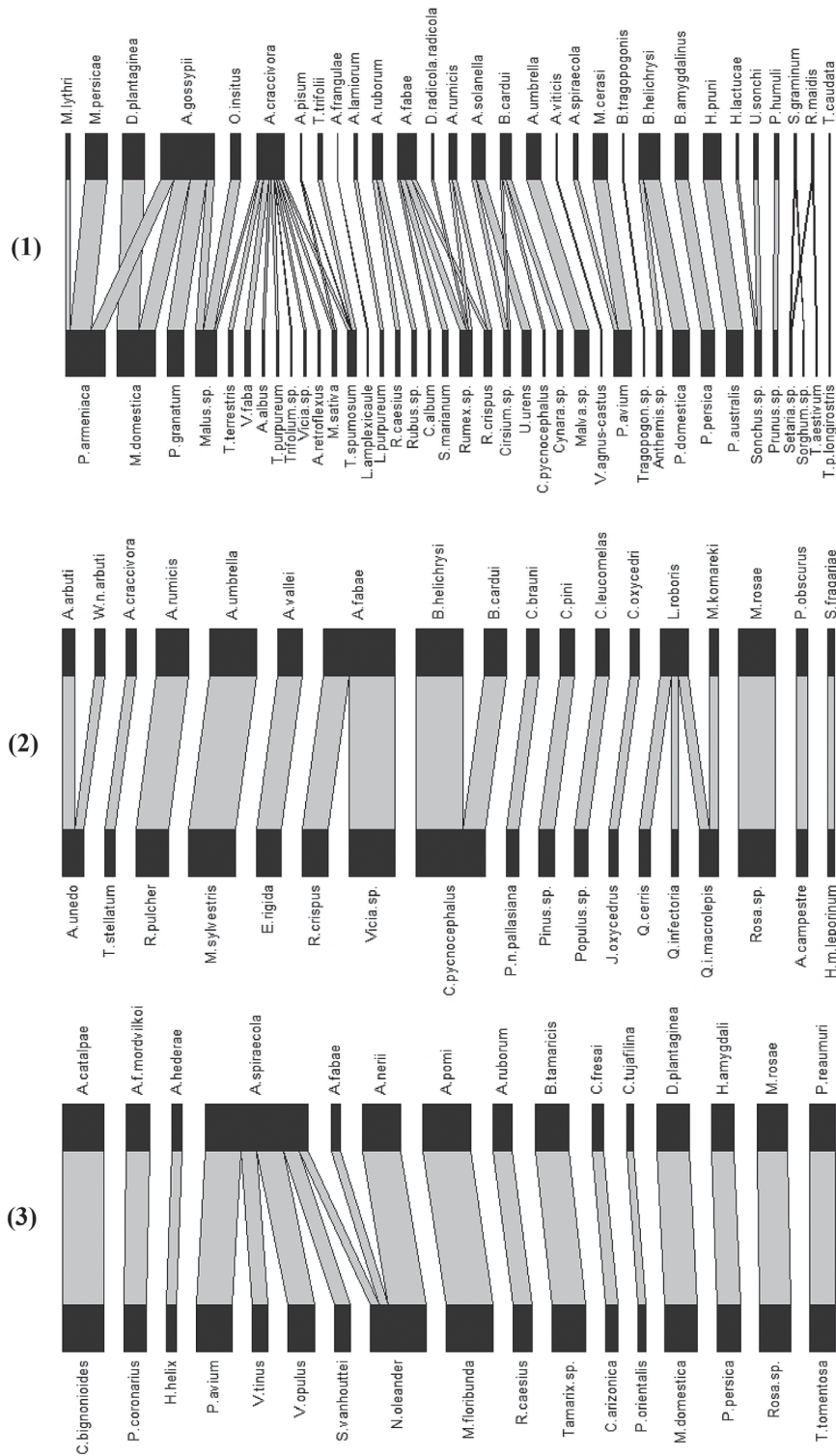


Figure 3 Bipartite networks interaction between aphids (top) and host plants (bottom) species in cultivated (1), uncultivated (2) and urban (3) areas in Northwest Turkey. Black bars represent the abundance of the species and grey bars represent interactions.

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Author contributions

ŞK conceived and designed the study. ŞK and İK performed the insect sampling, ŞK and NA performed the identity of aphids and ants. ŞK analysed the data and wrote the manuscript and reviewed the final version. Also, all authors contributed to reviewing and editing the manuscript.

Data availability statement

Data available on request from the authors

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