



Ant-mediated biological control: a global meta-synthesis of antagonistic interactions against pests

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Abstract

Ants' deep and pervasive ecological impacts on terrestrial ecosystems also translate into several meaningful services and disservices for human activities, whose balance can often be complex to assess. Biological control of pest insects appears to be the most economically relevant in agricultural settings and Asian waver ants being also the first insect used as biocontrol agents to be known in history. However, several more ants participate in biological control across the world. We carried out a first comprehensive meta-synthesis of these antagonistic interactions, reviewing 182 articles published between 1953 and 2025 and documenting the action of ants against pests of 54 cultivated plants and zootechnical activities. A total of 134 ant species from 46 genera and 8 subfamilies were found to control 155 pest species from 126 genera, 57 families, and 19 orders including mostly insects but also mites, mammals, weeds, and fungal pathogens. This amounted to a total of 328 unique ant–pest combinations documented from 69 countries across all continents except Antarctica. Data are released through a public dataset organized in 403 rows, each detailing an ant–pest pair interaction from a specific article and country. In most cases, the biocontrol activity of ants occurs without the need of targeted management, but management can have a serious effect. We discuss the identity of the species involved, the settings and mechanisms of antagonistic interactions, as well as the development of management strategies to enhance ants' role in biocontrol and drawbacks of ant activity.

Keywords Formicidae · Biocontrol · Pest management · Plant protection · Systematic review

Introduction

Ants (Hymenoptera, Formicidae), the largest family of eusocial insects, have a pervasive ecological effect on most terrestrial ecosystems including through a myriad of interactions with animals (including other ants), bacteria, fungi, and plants (e.g. Le Moli et al. 1994; Rosumek et al. 2009; Lach et al. 2010; Steiner et al. 2011; Chomicki and Renner 2017; Parker and Kronauer 2021).

Ant activity is also significant in anthropogenic settings, from agroecosystems to urban areas, where many of their

interactions with other organisms and the environment translate into a complex mix of services and disservices for human activities (Lach et al. 2010; Parker and Kronauer 2021). In agricultural settings, these include soil enrichment and bioturbation (Frouz and Jilková 2008; Taylor et al. 2019; Viles et al. 2021), seed removal (Baraibar et al. 2009; 2011a; Lami et al. 2020; Uhey and Hofstetter 2022), suppression of plant pathogens (Offenberg & Damgaard 2019; Offenberg et al. 2022), facilitation of ant-mutualist honeydew-producing insect pests (Schifani et al. 2024), and (almost exclusively in the case of leafcutter ants) direct herbivory (Della Lucia et al. 2014). In urban settings, certain ants may become pests due to their habits of invading buildings, feed on stored products, stinging, or in some cases interfering with electrical equipment (Lach et al. 2010; Santos 2016; Perfecto and Philpott 2023). However, perhaps the most important or well-known service ants provide is biological control of a variety of (mostly insect) pests usually because of the predatory habits of most species (Way and Khoo 1992; Dejean et al. 2024).

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Indeed, ants represent the first organisms of which we have historical record for a use as biocontrol agents: it is the case of the Asian weaver ant *Oecophylla smaragdina* (Fabricius) whose leaf nests were sold in the market of Southeastern Asia about 1700 years ago to be put into citrus trees, thus ensuring the fruits from being damaged by pest insects (Huang & Yang 1987). This fascinating report by the Chinese botanist Ji Han was published in the flora text Nanfang Caomu Zhuang (南方草木狀, Plants of the Southern Regions) in 304 AD and reports on a strategy that in different variants is still in place today (Huang and Yang 1987; Van Mele 2008; Offenberg 2015).

Some specific characteristics of ants may be advantageous from a biological control standpoint: most are polyphagous, generalist predators that are able to adapt to a variety of prey species; being often territorial and aggressive, they may chase away even intruders that are unsuitable as prey; through recruitment, they can quickly react to sudden increases in prey densities; they can withstand significant periods of food shortage and use different resources such as honeydew-producing insects as a stable alternative; they are not easily susceptible to satiety due to building food stocks and rearing immature stages (Risch & Carroll 1982; Way and Khoo 1992). At the same time, some of these features could produce antagonistic interactions with other predators and parasitoids used as biocontrol agents (Anjos et al. 2022). However, mutualistic interactions with some honeydew-producing pests are deemed as the most concerning drawback (Choate and Drummond 2011; Anjos et al. 2022), which may be countered with a variety of tactics when needed: applying barriers to prevent ant access, using toxic baits against ant colonies, manipulating ant behaviour with alternative food sources, or bypassing ant protection by selecting appropriate biocontrol agents (reviewed in Schifani et al. 2024).

Several qualitative reviews have addressed the topic of ants in pest management. The first was authored by Way and Khoo (1992), who highlighted key specific characteristics of ants in biocontrol and seven important ant groups [*Anoplolepis* spp., *Azteca* spp., *Dolichoderus thoracicus* (Smith), *Formica rufa* group, *Oecophylla* spp., *Solenopsis* spp., and *Wasmannia auropunctata* (Roger)], as well as insights on favourable ecological management. Choate and Drummond (2011) analysed management practices to preserve ant populations or increase ant presence, analysed five examples of cropping types in which ants provide special services (cocoa, sweet potato, banana, mango, and cashew), and discussed the problems arising from ant–hemipteran mutualisms. Benckiser (2010) compared harvester and leafcutter ants to *Lasius* and honeydew-collecting European species, emphasizing the importance of services and disservices these insects can provide to agriculture. Offenberg (2015) focuses his review on the relatively well-explored role of *Oecophylla* weaver ants,

while also highlighting those traits that are shared with most other species. Sankovitz et al. (2024) published an overview of beneficial and harmful interactions of ants, their context dependency, and their importance for management assessments. Finally, we reviewed the problem of mutualistic interactions between ants and honeydew-producing pests and the different management tactics that have been developed (Schifani et al. 2024).

Fewer are the systematic reviews that have so far been carried out. Offenberg and Damgaard (2019) and Offenberg et al. (2022) worked on the ability of ants to suppress plant pathogens, a promising and still largely unexplored research field. They identified ant, plant, and pathogen species as well as the involved antibiotic substances from 19 and 14 publications, respectively. Anjos et al. (2022) worked on a meta-analysis that analysed 52 studies to address for the first time in a quantitative way the problem of the cost–benefit balance of ant activity in agricultural settings, providing a multifaceted overview that also addressed crop yield. They found mutualistic interactions between ant and honeydew-producing insects to be the main cause of problems but at the same time the positive effects of ant-mediated biocontrol to have a much stronger effect overall, establishing a positive balance at a general scale. More recently, Lutinski et al. (2024) carried out a meta-synthesis of ant–pest antagonistic interactions in agriculture but did not release a consultable dataset and limited their research only to open access articles and ended up reviewing a total of 47 of them.

We carried out a meta-synthesis of ant-mediated biological control focusing on the identity and context of the antagonistic interactions in which ants act as biocontrol agents by reviewing 182 articles. Our research was not limited geographically or by publication time and was extended to both open- and closed-access literature, leading to the review of more than three times the maximum number of publications achieved in past reviews. We aimed to provide a first comprehensive synthesis of the ant and pest species involved as well as of the cultivated plants and contexts in which pests were controlled, developing a consultable dataset to facilitate the fruition of these data and access to the original sources.

Materials and methods

We looked for publications describing antagonistic interactions between ants and pest organisms through laboratory or field observations and experiments. To our purpose, pests were defined as organism with a meaningful detrimental activity to human activities in the urban, agricultural, or agroforestry context. We selected only those studies in which ants were identified at least at the genus level and pests at the family level. An exception was made for articles

reporting on ants acting as biocontrol agents against weeds, whose taxonomic identity was usually not mentioned by the authors, which were nonetheless included since these ant–plant interactions are rarely reported in the first place. Only ant–pest antagonistic interactions that the authors of the studies described as impactful were selected, while non-significant or dubious interactions were discarded.

Relevant publications were searched on the Scopus (Elsevier) database using the query “(TITLE-ABS-KEY (ants) OR TITLE-ABS-KEY (formicidae) AND TITLE-ABS-KEY (biological AND control) OR TITLE-ABS-KEY (pest AND management)) AND DOCTYPE (ar OR re)”. The resulting list was then manually screened to select only papers compliant with our aims (e.g. excluding articles with ants as the receiver of biocontrol efforts by non-ant biocontrol agents, or those not detailing the identity of the interacting ant or pest species at a sufficient level). This research was last update on 19 April 2025. Additional relevant publications were found among the references of publications belonging to this set, contributing to the formation of the final dataset. The software R (v4.4.0) and RStudio (v2024.12.1) were used to analyse and visualize the data (Posit team 2025; R Core Team 2025).

Results

Our initial Scopus research produced a list of 1,975 publications. After removing those that were not relevant to our aims, and adding 31 more publications not obtained from the Scopus search, we built a final dataset comprising 182 publications (Way 1953; Buschmann et al. 1977; Miller 1977; Stapley 1981; Krispyin & Todd 1982; Elvin et al. 1983; Roche & Abreu 1983; Sterling et al. 1984; Huang and Yang 1987; Lockwood & Story 1986; Gravena & Pazetto 1987; Lemke & Kissam 1988; Way et al. 1989; 1992; 1999; 2002; Allen & Hagley 1990; Perfecto 1990; 1991; Lee et al. 1990; Jaffe et al. 1990; Way & Khoo 1991; Castiñeiras & Ponce 1991; Uronu 1992; Fernandes et al. 1994; Van Den Berg et al. 1995; Dejean et al. 1997; Peng et al. 1997a, b; 1999; 2005; 2011; 2012; 2013; 2014; Goitia & Cerda 1998; Perfecto & Castiñeiras 1998; Sporleder & Rapp 1998; Goebel et al. 1999; Peng 1999; 2000; 2002; Pomerinke 1999a, b; Coll et al. 2000; Kenne et al. 2000; López & Potter 2000; McCoy et al. 2000; Eubanks 2001; Jones et al. 2001; Sekamatte et al. 2001; 2003; Sileshi et al. 2001; Morris et al. 2002; 2015; Rocha Gonring et al. 2002; 2003; Stuart et al. 2002; Van Mele et al. 2002; 2007; 2009a; 2009b; Vandermeer et al. 2002; Hood et al. 2003; Mansfield et al. 2003; Mathews et al. 2003; 2004; 2011; Sujii et al. 2003; Nay & Perring 2005a, b; Peng & Christian 2005a,b; 2006; Seagraves & McPherson 2006; Abera-Kalibata et al. 2006; 2007; 2008; Nachappa et al. 2006; Perfecto & Vandermeer

2006; Velázquez et al. 2006; Wyckhuys & O'Neil 2006; Agarwal et al. 2007; Armbrecht & Gallego 2007; Ayenor et al. 2007; Litsinger et al. 2007; Orsini et al. 2007; De La Mora et al. 2008; Baraibar et al. 2009; Dwomoh et al. 2009; Lomeli-Flores et al. 2009a; Way & Heong 2009; Amaral 2010; Larsen & Philpott 2010; Silva-Torres et al. 2010; Xiao & Fadamiro 2010; Duyck et al. 2011; Pardee & Philpott 2011; Cao et al. 2012; De Oliveira et al. 2012; Hosetti & Rudresh 2012; Mollet et al. 2012; 2014; Ramos et al. 2012; Vu et al. 2012; Westerman et al. 2012; Carrero et al. 2013; Gonthier et al. 2013; Jiménez-Soto et al. 2013; Mañák et al. 2013; 2017; Offenberger et al. 2013; 2018; Olotu et al. 2013; Pierre & Idris 2013; Rashid et al. 2013; Adgaba et al. 2014; Armendariz et al. 2014; Bownes et al. 2014; Greenstone et al. 2014; Monzo et al. 2014; Otsuki & Yano 2014a, b; Welch & Lundgren 2014; Abdulla et al. 2015; 2016; 2017a; 2017b; Campolo et al. 2015; Dassou et al. 2015; Diamé et al. 2015; Egonny et al. 2015; Msogoya et al. 2015; Dahan et al. 2016; Evans & Gleeson 2016; Mahapatro & Mathew 2016; Minkey & Spafford 2016; Morris & Perfecto 2016; Bisseleua et al. 2017; Castracani et al. 2017; Forbes & Northfield 2017; Gossler et al. 2017; Odogol et al. 2017; Suenaga 2017; Wan Khairul Anuar et al. 2017; Bagny Beilhe et al. 2018; Nielsen et al. 2018; Olson et al. 2018; Pag-Ong et al. 2018; Sow et al. 2018; Ennis & Philpott 2019; Tresson et al. 2019; Baldwin et al. 2020; Koffi et al. 2020; 2023; Mabin et al. 2020; Sanchez et al. 2020a, b; Schifani et al. 2020; 2023a,b; Abbas et al. 2021; Ahissou et al. 2021; Bulgarini et al. 2021; Ferdous & Jahan 2021; Kamiyama et al. 2021; Kar et al. 2021; Martínez-Núñez et al. 2021; Newson et al. 2021; Sanchez et al. 2021; Trigos-Peral et al. 2021; Constantino-Chuaire et al. 2022; Eisawi et al. 2022; Giannetti et al. 2022; 2024; Kamala Jayanthi et al. 2022; Kheirodin et al. 2022; Schulze-Sylvester et al. 2022; Smargiassi et al. 2023; 2025; Jensen et al. 2023; 2024; Gualberto et al. 2024; Wen et al. 2025).

The selected studies were published between 1953 and 2025. One hundred and seventy-three consisted of journal articles, four were technical reports, two PhD theses, one a book chapter, one a conference proceedings volume, and one a Master's thesis. Journal articles were published in 69 different journals. The ten most frequent were Biological Control (18 articles), Environmental Entomology (13), International Journal of Pest Management (11), Bulletin of Entomological Research (8), Journal of Economic Entomology (9), Entomologia Experimentalis et Applicata (7), Agricultural and Forest Entomology (6), Agriculture, Ecosystem and Environment (6), Journal of Applied Entomology (6), and Pest Management Science (5). Of the 69 journals, 63 were Scopus-indexed (91%). Most publications were in English (176), except for 6 journal articles published in Spanish. This dataset, provided in the Supplementary material of this paper, consists of 402 rows, each reporting an antagonistic

interaction between an ant species as the biocontrol agent and a pest in a specific country and sourced from a specific publication. If the same source would contain more than one of such interactions, if the same interaction would be reported from multiple countries by the same source, or if multiple sources would report on the same ant–pest pair, this would lead to multiple rows reporting the same ant–pest pair or source. In total, we recovered antagonistic interactions involving 134 ant species belonging to 46 genera and 8 subfamilies involved in the control of 155 pest species belonging to 126 genera, 57 families, and 18 orders (8 of insects, one of arachnids, one of mammals, four of plants, and four of fungi). These correspond to 329 unique combinations of ant and pest species.

The geographic distribution of the studies on ant-mediated biological control

The studies we recovered for our dataset were conducted in 69 countries of all continents. Most of them were from the U.S.A. (33), followed by Australia (14), Mexico (12), and Brazil (10) (Fig. 1). Tropical and subtropical regions expectedly contributed more widely: we recovered studies from 10 Latin American countries from Argentina to Cuba and Mexico, from most countries in South-Eastern Asia, Oceania, and neighbouring regions (13 countries from Pakistan to Papua New Guinea and from Australia to Japan), and 14 from Afrotropical countries of both Eastern and Western Africa. Even within the USA, the state contributing the most was the Florida (eight publications), largely characterized by a tropical/subtropical climate. Nonetheless, temperate

regions still provided an important contribution, with ten Mediterranean or European countries also involved alongside many other USA states.

Ants involved as biocontrol agents

Subfamily Myrmicinae

With 175 antagonistic interactions reported, myrmicines were the prevailing subfamily among ants involved in biocontrol, which is unsurprising considering that they are the largest and most successful of the extant subfamilies, including a lot of (mostly generalist) predators as well as seed-eating species. Of these interactions, 132 involved either the genus *Solenopsis* (70), *Pheidole* (39), or *Crematogaster* (23), while 12 other genera were responsible for the remaining 43.

Solenopsis was the second most frequent ant genus in our study. Almost all *Solenopsis* species were “fire ants”, i.e. belonging to a famous New World lineage of large-sized, often aggressive species. Only *S. molesta* (Say) is a small-sized, endogean, and cleptoparasitic “thief” ants that steals the brood of neighbouring ant colonies, which is the typical lifestyle of most *Solenopsis* ants across the world. The most frequent species was the red imported fire ant *S. invicta* Buren (38 interactions), followed by the tropical fire ant *S. geminata* (Fabricius) (17), both being South American species that have become invasive across much of the world. *Solenopsis invicta* is considered a threat to environmental conservation and human activities and is ranked as the fifth costliest invasive species worldwide (Diagne et al. 2021). Nonetheless, it has also been intensively documented, especially in North America, as an effective generalist predator controlling a wide spectrum of pest insects

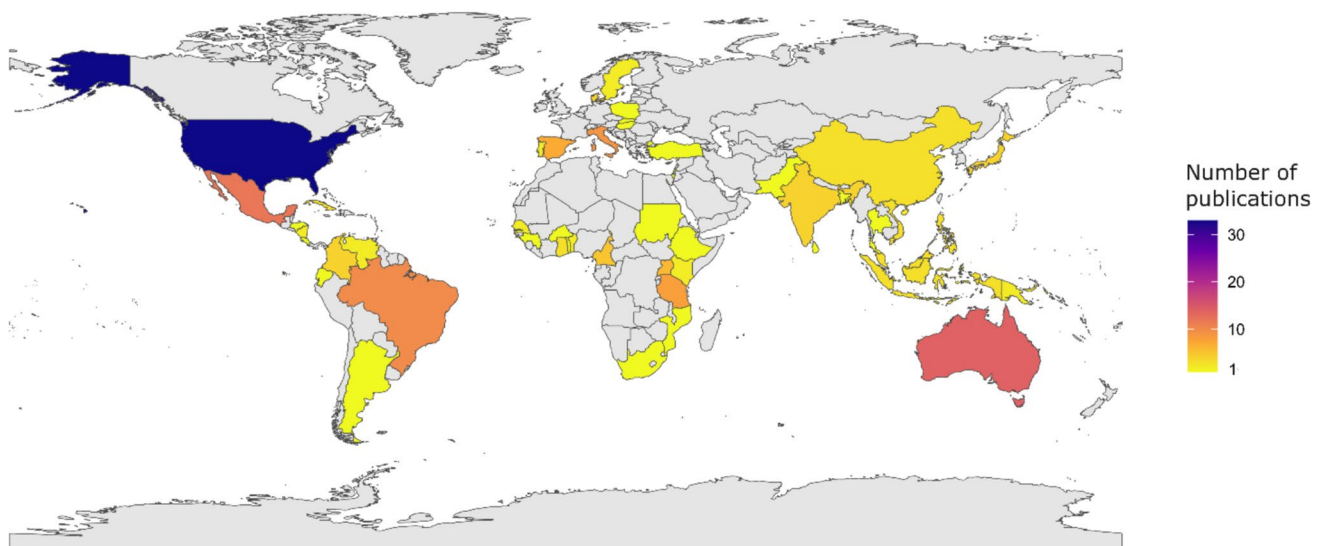


Fig. 1 Geographic distribution of publications on ants having an antagonistic effect against pests considered in this study. The colour scale indicates the number of publications per country, while countries with no publications are marked in grey

in different agricultural contexts, and to a lesser extent the same occurred with *S. geminata*.

Pheidole is the most diverse ant genus of the world (Bolton 2025), and with a total of 12 species found it also ranks as the most diverse genus in our dataset. In a stark contrast to *Solenopsis*, all interactions involving *Pheidole* species were documented within the boundaries of their supposed native range, including the invasive *P. megacephala* (Janicki et al. 2016; Guénard et al. 2017). The widespread genus *Crematogaster* comprises many dominant, arboreal nesting ant species, eight of which appeared in our dataset.

The remaining myrmicine genera were *Aphaenogaster*, *Cardiocondyla*, *Cephalotes*, *Messor*, *Monomorium*, *Myrmica*, *Myrmecaria*, *Nesomyrmex*, *Pogonomyrmex*, *Temnothorax*, *Tetramorium*, and *Wasmannia*.

Subfamily Formicinae

While comprising less than half of the described myrmicine diversity, formicine ants were the protagonists of almost as many antagonistic interactions in our dataset (163 in total). Over half of them (91) involved the genus *Oecophylla*, followed by *Formica* (17) and *Lasius* (17).

The weaver ants of the genus *Oecophylla* rank as the most represented in our dataset. There are just two weaver ant species of the genus *Oecophylla* currently recognized, namely *O. longinoda* (Latreille) in the Afrotropics and *O. smaragdina* in the Indomalayan and Oceanian regions, but these are well-known for their ecological impact. As already mentioned, *O. smaragdina* was the first insect to have been recorded as a biocontrol agent in human history (Huang and Yang 1987). With the highest number of recorded interactions in our dataset (64), *O. smaragdina* has not only been the subject of several studies across about its entire range, but, as mentioned before, there is ample testimony of cultural traditions regarding its use as a biocontrol agent in Southeastern Asia (Huang and Yang 1987; Van Mele 2008; Offenberg 2015). The similar use of *O. longinoda* as a biocontrol agent in the Afrotropics may not be rooted in a similarly old tradition but has been developed since at least 75 years (Way 1953) (27 interactions in our dataset).

Contrary to *Oecophylla*, *Lasius* and *Formica* ants (including the mound-building red wood ants and other species) contributed to biological control in temperate regions of the northern hemisphere. The other formicines ant genera were *Anoplolepis*, *Brachymyrmex*, *Camponotus*, *Cataglyphis*, *Lepisiota*, *Melophorus*, *Meranoplus*, *Nylanderia*, *Paratrechina*, *Polyrhachis*, and *Prenolepis*. While *Camponotus* is the second largest ant genus, with the global number of species approaching that of *Pheidole*, far fewer interactions (12) were reported.

Subfamily Dolichoderinae

Axinidris, *Azteca*, *Iridomyrex*, *Linepithema*, and *Tapinoma* were the dolichoderine genera found in our search,

for a total of 37 antagonistic interactions involving them. *Tapinoma* (14) and *Azteca* (9) were the genera most frequently participating, with records of the first coming from the Mediterranean, Senegal, Mexico, and the Philippines, and the Neotropical genus *Azteca* mostly recorded from Mexican coffee agroforestry.

Others

The remaining genera recorded were involved in 28 antagonistic interactions, and belonged to the subfamilies Amblyoponinae (*Myopopone*), Dorylinae (*Dorylus*, *Labidus*), Ectatomminae (*Ectatomma*), Ponerinae (*Neoponera*, *Odontomachus*, *Pachycondyla*), and Pseudomyrmecinae (*Pseudomyrmex*). This leaves 7 ant subfamilies with no interactions recorded (Agroecomyrmecinae, Aneuretinae, Apomyrminae, Leptanillinae, Martialinae, Myrmecinae, and Proceratiinae), as well as 300 other genera (out of 346, see Bolton 2025; Oberski et al. 2025).

Cultivated plants and context diversity

We recovered published evidence of ants' role against pests of 47 cultivated plant species (mostly of agricultural use and a few used in forestry), as well as zootechnical activities (apiculture, cattle pastures, poultry), and golf lawns. Coffee, cashew, banana, citrus, and soybean were the five most frequent crop types (Fig. 2).

Coffee

Forty-seven antagonistic interactions against coffee pests were found. A total of 14 ant genera, led by *Azteca*, *Pseudomyrmex*, *Solenopsis*, and *Wasmannia*, acted against a total of five coffee pests, in most cases being the coffee berry borer *Hypothenemus hampei* (Ferrari) (Coleoptera, Curculionidae) and the coffee leaf-miner *Leucopelta coffeella* (Guérin-Méneville) (Lepidoptera, Lyonetiidae). Studies were conducted in six countries of Africa, Asia, and South America, most of them in Mexico.

Cashew

Thirty-six antagonistic interactions against cashew pests were found. All interactions involved *Oecophylla* ants as control agents (either *O. smaragdina* in Asia and Oceania, or *O. longinoda* in Africa). Ants controlled pests from 10 genera, including at least six species of *Helopeltis* (Hemiptera, Miridae), two of *Amblypelta* (Hemiptera, Coreidae), and two of *Pseudotheraptus* (Hemiptera, Coreidae). Studies were conducted in eight countries, with Australia, Papua New Guinea, Vietnam, and Tanzania at the forefront.

Banana

Twenty-nine antagonistic interactions against banana pests were found across studies from eight countries from the Caribbean, Central and South America, Southeastern Asia, and the Afrotropical regions, with the higher number of studies being from Cuba and Martinique. Interactions with banana pests involved 14 ant genera, with *Pheidole*,

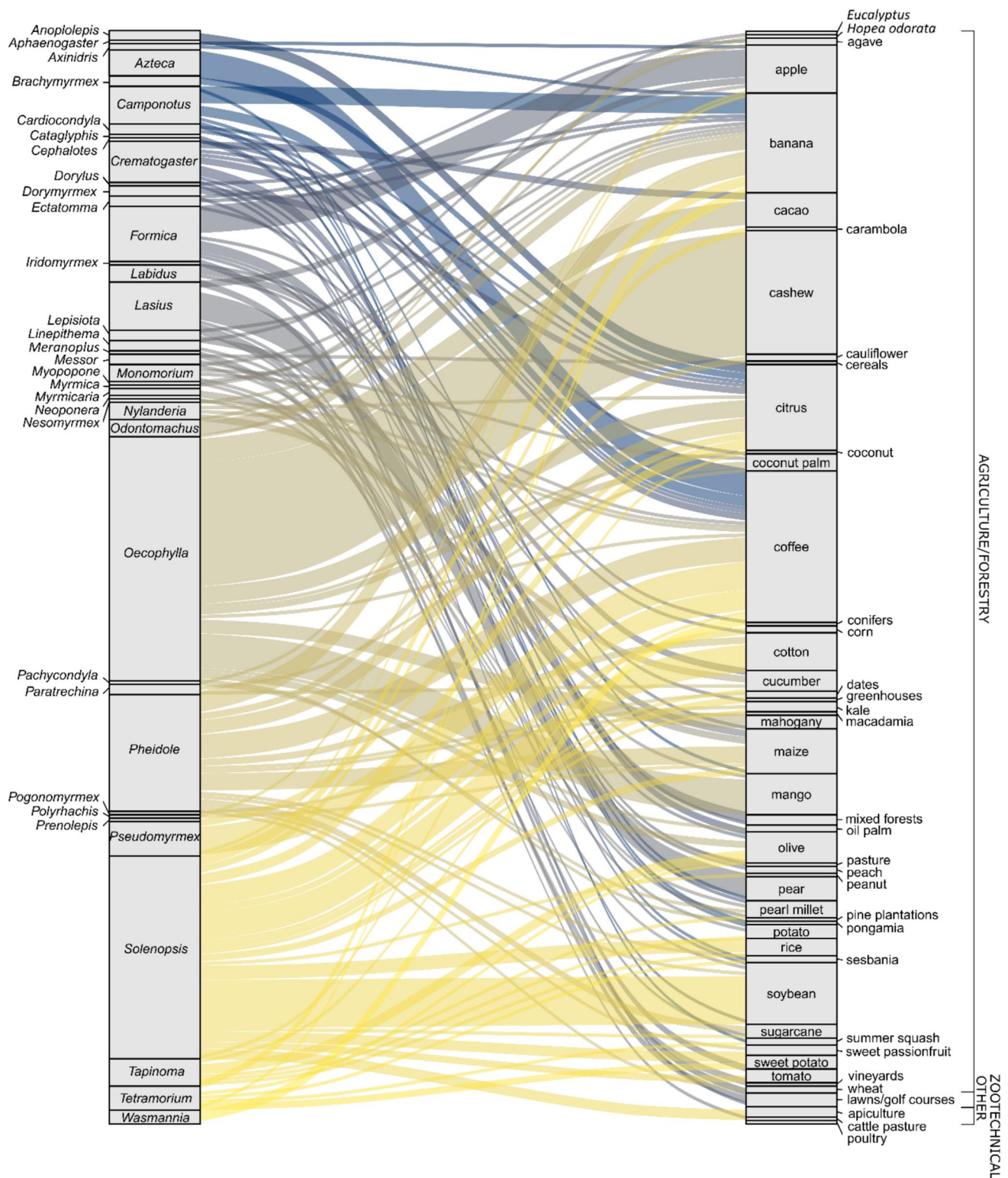


Fig. 2 Sankey diagram illustrating the contexts of antagonistic ant-pest interactions documented in the field studies we analysed

Camponotus, and *Odontomachus* being more frequent, in all cases controlling the banana root borer *Cosmopolites sordidus* (Germar) (Coleoptera, Curculionidae).

Citrus

Thirty-seven antagonistic interactions against citrus pests were found. Eleven ant genera participated in the control of

citrus pests, with *Oecophylla*, being far the most frequent. Citrus pests controlled by ants belonged to 19 different genera, with the citrus root weevil *Diaprepes abbreviatus* (L.) being by far the most frequent. Studies on ants' role as bio-control agents in citrus originated six countries in Africa, Asia, Europe, and North America, with most of them produced in Florida (USA), China, and South Africa. Interactions concerned grapefruit, mandarin, orange, and pomelo orchards.

Soybean

Twenty-two antagonistic interactions against soybean pests were found. Five ant genera were involved in controlling soybean pests, with *Solenopsis invicta* being by far the most frequent, while the pest genera were seven, with the moth *Anticarsia gemmatilis* Hübner (Erebidae) being the most frequent. Most studies concerning ant-mediated bio-control in soybean were carried out in the USA, with a few conducted in Indonesia.

Pest species controlled by ants

We reported ant–pest antagonistic interactions against pests classified into 154 species, 125 genera, and 19 orders of animals (383 interactions), plants (11), and fungi (8) (Fig. 3).

Butterflies and moths (Insecta, Lepidoptera)

With 124 records, lepidopterans are almost paired with coleopterans as the most frequent order of pests that ants are controlling. Antagonistic interactions against a total of 16 lepidopterans families were found, including 14 of moths (Crambidae, Erebidae, Gelechiidae, Geometridae, Gracilariidae, Lyonetiidae, Noctuidae, Notodontidae, Plutellidae, Praydidae, Pyralidae, Psychidae, Tortricidae, and Xylorictidae), and two of butterflies (Papilionidae and Pieridae), for a total of 40 genera. Noctuidae (31 interactions), Tortricidae (16), Lyonetiidae (14), Pyralidae (13), Crambidae (10), and Erebidae (10) were the most frequent families, while the most frequent genera were *Leucoptera* (Lyonetiidae), *Cydia* (Tortricidae), *Anticarsia* (Erebidae), *Spodoptera* (Noctuidae), *Diaphania* (Crambidae), and *Helicoperva* (Noctuidae).

Ants may play a role against eggs, larvae, and/or pupae of lepidopterans, depending on the examined case. Some types of eggs may be inaccessible to some ant species: for example, Schifani et al. (2023a, b, c, d) documented through laboratory experiments *Crematogaster scutellaris* (Olivier) and *Tapinoma magnum* Mayr predated on the first-instar caterpillars of the codling moth *Cydia pomonella* (L.) (Tortricidae) but ignoring its eggs. This ability can also extend to the larvae of leaf-miner species, with reports of ants capable of creating small holes of the leaves to access them (e.g. in the case of *Solenopsis invicta* ants against the citrus leaf-miner *Phyllocnistis citrella* Stainton, see Xiao et al. 2007). On the other hand, they are less likely to prey upon

the flight-capable adults. A potential dissuasion on the egg-laying behaviour of the adults as demonstrated with some beetle and fly species looks like a further plausible mechanisms, but no supporting literature was found in our analysis. Interactions against lepidopterans are widespread across 31 crop types.

Beetles (Insecta, Coleoptera)

A total of 126 recorded antagonistic interactions against coleopterans were found, making this the most frequent group of pests controlled by ants. These involved 7 families, with a total of 103 interactions being with Curculionidae, 15 with Chrysomelidae, and the rest split between Cerambycidae, Elateridae, and Scarabaeidae, for a total of 30 genera. The most frequent genera were *Hypothenemus* (30), *Cosmopolites* (29), and *Diaprepes* (20), all members of to Curculionidae. Ants may play a role against all beetle stages, including eggs, larvae, pupae, and adults, depending on the specific beetle species/stage and ant species involved. For example, Jaffe et al. (1990) documented the ant *Azteca delpini* Emery predated on all stages of *Diaprepes* spp. curculionids, *Pheidole fallax* Mayr and *Solenopsis geminata* predated on all stages except the eggs, *Mono-morium* spp. and an unidentified *Solenopsis* predated only the eggs whether or not with their protective shield intact, and finally *Camponotus* spp., an unidentified *Crematogaster*, *Ectatomma ruidum* Roger, *Paratrechina longicornis* (Latreille), *Tapinoma littorale* Wheeler, and *Wasmannia auropunctata* (Roger) being predators of unprotected eggs and larvae but having difficulties with first-instar larvae. Pest beetle species exhibit a wide range of lifestyles; at least some ant genera proved effective against the more secretive ambrosia and bark beetles that hide in the wood for part of their lifestyles, sometimes invading their galleries. For example, the red wood ant *Formica polyctena* controls *Ips* spp. bark beetles in European forests of multiple countries (Trigos-Peral et al. 2021), while laboratory experiments by Giannetti et al. (2022) found *Crematogaster scutellaris*, *Tapinoma magnum*, *Temnothorax affinis* (Mayr), and *T. algericus* Forel all having detrimental effects on the ambrosia beetle *Xylosandrus compactus* through both direct predation and a repellent effect of ant semiochemicals, but only *T. algericus* actively invaded its galleries. Interactions against beetles are reported from 22 crop types and plant species.

True bugs (Insecta, Hemiptera)

In total, 89 antagonistic interactions against hemipterans were reported. A total of 15 hemipteran families were reported to be involved. Miridae (24), Pentatomidae (24), and Coreidae (17) were the most frequent families. The remaining were Aleyrodidae, Aphididae, Aphrophoridae, Cicadellidae, Coreidae, Delphacidae, Dinidoridae, Ischnorhinidae, Membracidae, Plataspididae, Psyllidae, and Triozidae. The most frequently reported genera were *Helopeltis*, *Nezara* (11), and *Amblypelta*, (8), in most cases

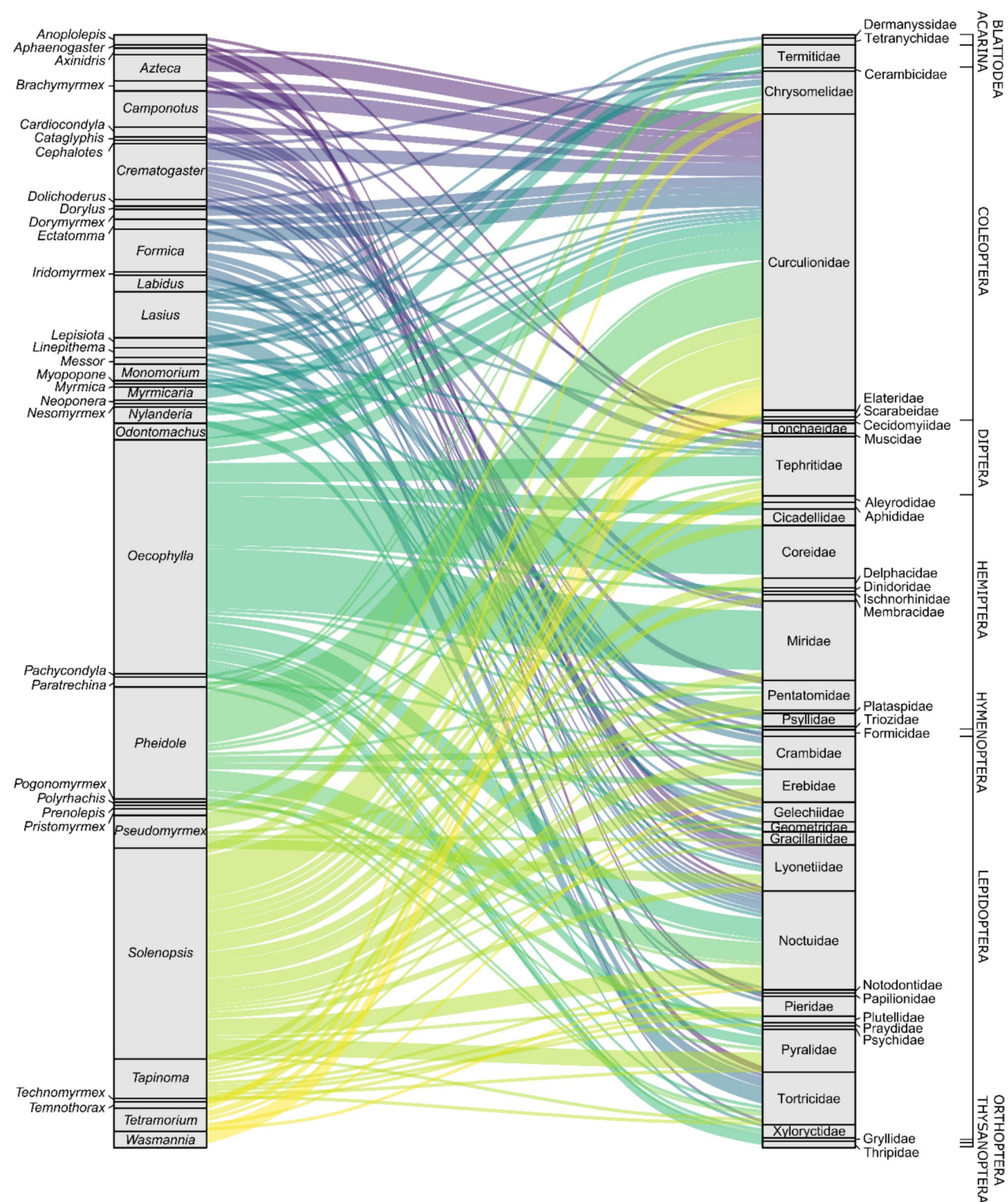


Fig. 3 Sankey diagram illustrating the interactions between ants and arthropod pests documented in the publications analysed in this study

controlled by *Oecophylla* ants in tropical fruit plantations. Ants may attack all stages, including eggs, nymphs, and adults, depending on the species involved. For example, *Solenopsis geminata* and an unidentified species of *Dolichoderus* were documented as predators of the eggs of the pentatomid stink bug *Nezara viridula* (L.) (Van Den Berg et al. 1995), while *Crematogaster scutellaris* and *Tapinoma magnum* increased nymph mortality but did not harm the eggs (Schifani et al. 2023a). Aggregated young nymphs of *N. viridula* also were less attractive for *Solenopsis invicta* and *Monomorium carbonarium* (Smith) but were normally attacked by *Pheidole dentata* Mayr and *Tetramorium guineense* (Bernard) (Lockwood & Story 1986). Among the pests controlled by the ant *Oecophylla smaragdina* were also two aphid species of the genus *Toxoptera* in Vietnamese citrus orchards, both not ant-mutualist (Van Mele et al. 2002). At least some of the ants that predate stink bugs ignore their egg parasitoids that are considered important biocontrol agents (Schifani et al. 2023a, b). Indirect interactions mediated by semiochemicals were documented between *Crematogaster scutellaris* and *Philaenus spumarius* (Aphrophoridae) (Smargiassi et al. 2025). Interactions against true bugs are reported from 23 crop types and plant species.

Flies (Insecta, Diptera)

A total of 28 documented antagonistic interactions against flies were found, involving four families (Cecidomyiidae, Lonchaeidae, Muscidae, and Tephritidae) for a total of six genera. Interactions against fruit flies (Tephritidae) were prevalent (23) and involved the genera *Bactrocera* (13), *Ceratitis* (8), and *Rhagoletis* (3). The remaining genera were *Dasiops* (Lonchaeidae), *Dasineura* (Cecidomyiidae), and *Haematobia* (Muscidae). The predatory role of ants is most common against larvae and pupae. In fruit flies, the most common target are larvae that have just left the fruits to pupate in the soil and pupae themselves. For example, Campolo et al. (2015) estimated about 27% of *Ceratitis capitata* larvae being eliminated by *Tapinoma magnum* in Italian citrus orchards, while *Oecophylla* spp. are involved in the control of six *Ceratitis* and *Bactrocera* species in mostly mango orchards. Indirect interactions in which ant chemical discourages fruit fly oviposition are also reported (Van Mele et al. 2009a; Kamala Jayanthi et al. 2022; Smargiassi et al. 2023). Interactions against flies were reported across six crop types, as well as in cattle pastures where the red imported fire ant *Solenopsis invicta* may control the horn fly *Haematobia irritans* (L.) (Lemke and Kissam 1988). Interactions against beetles are reported from eight crop types and plant species.

Other insects (Blattodea, Hymenoptera, Orthoptera, Thysanoptera)

The seven antagonistic interactions against Blattodea are due to ants' predatory ability against termites (Termitidae). Ants encompass many termite-specialist predators, and

many generalist species may opportunistically consider termites as an attractive prey.

The two against other hymenopterans were antagonistic interactions against other ants which acted as pests in specific contexts. In Ethiopia, *Crematogaster* ants were found to be effective at repelling the predatory raids of *Dorylus* army ants from beehives (Adgaba et al. 2014), while in South America *Linepithema* ants would prevent *Amoimyrmex* leafcutter ants from damaging the vines (Schulze-Sylvester et al. 2022).

One antagonistic interaction involved an orthopteran, a cricket from the genus *Myara* that is preyed upon in Australian mahogany plantations by *Oecophylla smaragdina* (Peng et al. 2013).

Oecophylla spp. were also involved in the control of *Selenothrips* (Thysanura, Thripidae) in Australia and Tanzania (cashew and mango, respectively) (Peng and Christian 2005b; Abdulla et al. 2015).

Mites (Arachnida, Acarina)

Mites from two genera and families were found to be attacked by ants, for a total of three records: *Dermanyssus* (Dermanyssidae) and *Tetranychus* (Tetranychidae). In both cases ants preyed upon adults and immature stages (Otsuki & Yano 2014a, b; Kar et al. 2021). Available field data only concern the ability of *Lasius* ants against the poultry red mite *Dermanyssus gallinae* (De Geer) in Türkiye (Kar et al. 2021).

Mammals

The African weaver ant *Oecophylla longinoda* was reported to repel frugivorous bats (Chiroptera, Pteropodidae) from cashew and mango in Guinea—in the same context, the aggressiveness of the ants was also deemed to discourage even human thieves from robbing fruits (Van Mele et al. 2009b).

Fungi

Eight antagonistic interactions against fungi were reported, involving five species from four genera and four orders (Eurotiales, Glomerellales, Helotiales, and Pleosporales): *Colletotrichium gloeosporioides*, *Monilia fructigena*, *Penicillium italicum*, *Venturia inaequalis*, and *V. pyrina* (Offenberg et al. 2018; Schifani et al. 2020). *Formica*, *Lasius*, and *Oecophylla* ants were involved in these interactions.

Weeds

A total of 11 antagonistic interactions were found. In most cases, as mentioned before, the taxonomic identity of the botanical species involved was not clear. *Melophorus*, *Messor*, and *Pheidole* ants were reported as weed controllers in Australian and Spanish agroecosystems of cereals and other plants, with effects at least against *Brassicaceae*, *Papaveraceae*, and *Poaceae* (Baraibar et al. 2009; Westerman et al. 2012; Evan and Gleeson 2016; Minkey and Spafford 2016).

Management tactics to promote ant effectiveness in biocontrol

A few tactics have been experimented to enhance the role of ants as biocontrol agents in certain contexts. Some of these, like the use of food provision, overlaps with very similar techniques used to reduce the damaging effects of interactions between ants and ant-mutualist honeydew-producing pests. Here we briefly review these tactics, yet it is important to note that the effects of ants on pests, are, in most documented cases, not the result of any targeted management strategy.

Transplanting nests

As already mentioned, the oldest documented use of ants in biological control reports farmers buying *Oecophylla smaragdina* nests in local markets and placing them into citrus trees (Huang and Yang 1987). Such peculiar nests that only a few ant species build are ideal for this practice. Weaver ants can be extremely common in many areas of the Old-World tropics, yet in some cases nests are still artificially transplanted (Van Mele 2008). Most ant species do not make nests that are as easy and manageable to move from one place to another as those of weaver ants, so that few other examples of such practices exist. Most recently, some experiments were highly successful in introducing red wood ants (*Formica polyctena* Förster) originating from the forests of Denmark into Danish apple plantations of the same region by transporting their mound nests (Nielsen et al. 2018; Offenberg et al. 2019; Jensen et al. 2023). These ants had a way superior impact on lepidopterans and fungi affecting the apple trees as compared to the resident *Lasius* ants, and although they would also more strongly promote honeydew-producing hemipterans, these effects could be balanced through sugary provision (Jensen et al. 2023). With both weaver ants and red wood ants, it is important to place transplanted nests in ways that lower the chance of inter-colonial fights which can severely hinder the effectiveness of this practice (Van Mele 2008).

Several ant species have become invasive in areas where they are non-native, outcompeting and excluding native ant species and having detrimental effects on arthropod and plant communities. Rarely, ants were voluntarily introduced as biocontrol agents before becoming a conservation concern: it is the case of red wood ants (*Formica paralugubris* Seifert) moved from the Alps to central Italy and Canada to fight the processionary moth *Thaumtopoea pytiocampa* (Denis & Schiffermülle) and other forest pests (Pavan 1959; Frizzi et al. 2018; Balzani et al. 2021). Predicting these interactions in advance can be very difficult and containing ants is challenging. Therefore, transplanting ants outside their native range should always be avoided and only moving species within the native range from natural to anthropogenic environment appears acceptable.

Artificial nests

Instead of introducing ant colonies, it is sometimes possible to attract or increase the presence of the desired species by providing suitable nesting sites that are otherwise lacking in a certain context. Wood-nesting, mostly arboreal ants may sometimes offer important services in tree plantations and orchards, but the lack of natural deadwood on those plants may limit their ability to build nests and reach optimal density levels (Philpott and Foster 2005). In natural systems, myrmecophytic plants host ant colonies that protect them by developing specialized structures named *domatia* (Rico-Gray and Oliveira 2008), while structures such as certain wooden galls in temperate forests may indirectly play a similar role (Giannetti et al. 2019). A few studies have successfully experimented with providing artificial nests for arboreal ants in agricultural settings. It has first been experimented in Mexican coffee agroecosystems to increase ant diversity and enhance the presence of twig-nesting ants (Philpott and Foster 2005; Jiménez-Soto and Philpott 2015). More recently, Giannetti et al. (2024) tested the use of artificial nests modelled upon oak galls induced by *Andricus* wasps, which several ant species naturally colonize in oak forests, by building similar structures and placing them on young olive plants that do not yet offer deadwood portion for ants to colonize and obtained positive results for the control of some insect pests.

Artificial food sources

A third tactic consists in manipulating ant behaviour by using artificial food sources to direct them on plants and enhance their predatory attitude. Myrmecophile plant species across many lineages have adapted to offer food to attract ant attention and manipulate ant behaviour to their convenience, using them as ‘defenders’ against herbivory from arthropods and mammals (Grasso et al. 2015). These partnerships, most of the time mediated by extrafloral nectaries (Rico-Gray and Oliveira 2008), may involve the provision of sophisticated foods that alter ant behaviour in complex ways, promoting fidelity to the plants and enhanced aggressivity against other organisms (Nepi et al. 2015). In ant management, a somewhat similar use of food provision has also been tested with successful results, even if artificial foods have not yet tried to mimic the sophistication of natural ones. Protein- and sugar-based baits were used by Sekamatte et al. (2001) in maize fields of Uganda to increase ant activity and thus protect the crops from *Macrotermes* termites. In Italian pear orchards, dispensing a water-sucrose solution through “artificial nectaries” has also proved effective at increasing ant abundance on trees and directing them to the protection of their fruits: very interestingly, this allowed for an effective ant-mediated biocontrol which unmanipulated ants would not provide to an appreciable level (Schifani et al. 2020).

In parallel, providing alternative sugary food sources also has important applications when it comes to disrupting mutualistic relationships between ants and honeydew-producing pests and may thus serve this goal in parallel with enhanced predatory or antifungal activity (Nagy et al. 2013, 2015; Wäckers et al. 2017; Parrilli et al. 2021; Pérez-Rodríguez et al. 2021; Borbély and Nagy 2022; Correa et al. 2023; Jensen et al. 2023; Schifani et al. 2024; Burgio et al. 2025).

Habitat and landscape composition

Finally, habitat management may play an important role in enhancing the role of ants as biocontrol agents by shaping ant communities and promoting the activity of certain species by lowering inter- and intra-specific competition. Ant communities, which may comprise a dozen species to more than one hundred of them in tropical forests, are regulated by complex interactions and may greatly vary in response to environmental changes (Lach et al. 2010). In artificial habitats such as agroecosystems, human planning and management may shape the richness, composition, and structure of ant communities. These characteristics then have cascading effects on the services (and disservices) ants provide.

Comparing shaded and sunny coffee plantations of Colombia, Armbrecht and Gallego (2007) revealed much higher predation rates of the coffee berry borer by ants in shaded plantations, and further studies in shaded coffee plantations of Colombia and Mexico revealed practices promoting ant diversity and reducing drawbacks caused by ant-hemipteran mutualisms (Livingston et al. 2014; Perfecto et al. 2014; Ibarra-Isassi et al. 2021). Seguni et al. (2011), working in Tanzanian citrus orchards, demonstrated how clearing the ground vegetation would be highly detrimental to the important biological control services provided by the African weaver ant *Oecophylla longinoda* by propelling the big-headed ant *Pheidole megacephala* to eliminate and replace *O. longinoda* from most tree canopies. Restoring ground vegetation would invert the process, but still it took two years for *O. longinoda* to re-colonize tree canopies (Seguni et al. 2011). In a similar system involving *O. smaragdina* and *P. megacephala*, planting soursop trees (*Annona muricata* L.) would favour the presence of *O. smaragdina* which uses its associated honeydew-producing hemipterans as an important food source. In Brazilian organic farms, Frizzo et al. (2020) reported higher biocontrol effectiveness of richer ant species assemblages that were associated with higher crop diversity, low intensity soil management, proximity to fallow areas, the use of living ground cover or mulching as well as complementary biological pest control products with little to no impact on ants. In Spanish olive orchards, the maintenance of herb cover at intermediate landscape complexity had a significant effect on ant abundance and potential for pest control (Martínez-Núñez et al. 2021). Tillage and irrigation in Spanish cereals eliminated

Messor harvester ants and the weed seed removal service they provide (replaced only at a much lower level by *Mus* rodents), while no or minimum tillage systems with the establishment of field edge vegetation would benefit from an enhanced beneficial activity of these ants (Baraibar et al. 2009; 2011b).

However, no general rules have been drafted for management measures to take, and this will be likely only possible for very specific contexts.

Discussion

Our review provides for the first time a comprehensive synthesis of published information detailing the identity of the ant and pest species involved in ant-mediated biological control and of the contexts in which these interactions take place. While our research dataset is naturally limited by the research method and source database we used, it is the most comprehensive to have been assembled on this topic and its public release will allow others to further keep building on it. Of course, it is first meant to be a resource for those interested in ants' role in pest management and biological control. However, in a broader sense it provides a systematic synthesis of an important volume of information especially on ant–animals interactions that is relevant for the biology and ecology of hundreds of species.

Out of over 15,000 described ant taxa, only a handful have been documented to have a role as biocontrol agents: 133 species represent < 1% of those currently described, while 46 genera are about 13% of the 346 currently valid genera (Bolton 2025; Oberski et al. 2025). This is for the most part most likely due to a lack of knowledge and studies, since thousands of specie share very similar morphological, behavioural, and ecological characteristics to those whose role has been documented (Risch and Carrol 1982; Way and Khoo 1992; Offenberg 2015). Depending on their management, agroecosystems may also pose strong limits to the survival of many ant species. Organic farming and agroecological approaches tend to allow for richer and more functionally diverse ant communities that provide more significant biocontrol services, and much may still be done to understand these synergies (e.g. Frizzo et al. 2020; Anjos et al. 2022; Zina et al. 2022).

While *Oecophylla* weaver ants have received unparalleled attention historically (Offenberg 2015), and retain their position as the most documented group, they still account for less than 20% of the documented interactions we reviewed. On the other hand, the second most recorded ant species is the red imported fire ant *Solenopsis invicta*. It is usually only known for its detrimental role as one of the worse invasive species, highly damaging to the environment and human activities (Tschinkel 2013; Luque et al. 2014; Diagne et al.

2021), its continuous expansion across the world being very worrying (Menchetti et al. 2023; 2024). Particularly in the USA, where the invasion is the oldest and covers an extreme range, this ant also plays the role of major biocontrol agent of several pests across a variety of crop systems, a service whose seemingly important economic value has never been comprehensively assessed.

While we focused on ant–pest antagonistic interactions, mutualistic relationships with honeydew-producing species may have a significant impact in certain contexts, even if their overall global impact is considered less significant for agriculture as compared to ant predation of pests (Anjos et al. 2022). Predatory ants may simultaneously control certain pests and assist others: sometimes, this balance can already be favourable for plant health with honeydew-producing insects ensuring the continuous ant presence and defence against more damaging herbivores (Styrsky and Eubanks 2007; 2010). Ants may also be able to reduce some forms of plant damage even if caused by ant-mutualistic pests (Anjos et al. 2022), which may be explained by mechanisms such as ant ability to prevent the spread of pathogens caused by uncollected honeydew (Styrsky and Eubanks 2007). However, a variety of management options may facilitate harmonizing these functions, among which the provision of alternative food sources or specialized biocontrol agents is the most compatible with preserving (or even enhancing) the services ants provide in plant protection (Schifani et al. 2024). The generalist predatory nature of most ants involved in pest control (as well as most ant species in general, Dejean et al. 2024) can also raise the concern of intra-guild antagonistic interactions against other biological control agents, including predators and parasitoids. However, these interactions are more likely to pose a threat to other generalist natural enemies than to specialists, with the latter more often having developed adaptations to cope with ants (Anjos et al. 2022). Antagonistic interactions between ants and other predators and parasitoids should not be automatically assumed to take place, but rather investigated case by case (e.g. Schifani et al. 2023a, b, c). Some interference with the activity of pollinators has also been documented in certain natural settings but never documented to have a significant detrimental effect on agricultural systems so far (Nogueira et al. 2021).

In any context, the specific identity of the involved ant–pest pairs appeared as a very meaningful aspect that should not be overlooked. Different ants may not only provide different services and disservices, but some species may have opposite effects. We have already mentioned how, under certain management conditions, *Pheidole megacephala* would displace *Oecophylla longinoda* from canopy trees without replacing the biocontrol services the latter offered (Stapley 1981; Seguni et al. 2011). At the same time, *P. megacephala* was reported as an effective biocontrol agent

in other contexts (Castiñeiras and Ponce 1991; Goebel et al. 1999; Jones et al. 2001; Bownes et al. 2014; Koffi et al. 2020; 2023; Ahissou et al. 2021). Many more examples also exist. For instance, Dejean et al. (1997) documented *Crematogaster gabonensis* Emery controlling the leaf-miner chrysomelid beetle *Coelaenodera minuta* Uhmann in oil palms of Cameroon, but in the same context *Tetramorium gabonense* (André) favoured the beetles instead. Suppressing the tropical fire ant *Solenopsis geminata* from coffee farms of Costa Rica allowed other ant species to thrive and control the coffee berry borer (Tribble & Carroll 2014). Even among ants of the same genus or species group differences may be remarkable: *Formica* ants were recorded as predators of the black cutworm *Agrotis ipsilon* (Hufnagel) (Lepidoptera, Noctuidae) in the USA, but *F. pallidefulva* Latreille was much more effective and exhibited different behaviours than the similar species *F. subsericea* Say (López and Potter 2000).

Stable interactions between attending ants and aphid and scale insect colonies are usually much more obvious to the observer than the predatory and antagonistic behaviours of ants against other pests; predatory interactions may last just a few seconds, or the case of the suppression of fungal pathogens, they remain essentially invisible to human eyes (Offenberg et al. 2022; Jensen et al. 2024). Not only living ants (as reviewed in our analysis) but also extracts from ant-associated microbes are attracting increasing attention for their ability to suppress fungal pathogens, with still very few ant species that have been thoroughly examined (Offenberg & Damgaard 2019; Offenberg et al. 2022; Jensen et al. 2024). Another aspect that can be hidden from human eye concerns chemical dissuasion against phytophagous insects, which may avoid areas characterized by the semiochemicals of their ant predators, avoiding laying their eggs or spending time where they are abundant (Van Mele et al. 2009a; Giannetti et al. 2022; Kamala Jayanthi et al. 2022; Smargiassi et al. 2023; 2025). An independent use of the repellent activity of these substances may also be explored in the future.

Research over management tactics to improve ant effectiveness seemingly still has a lot left to explore, yet in most cases ants already quietly provide these services without any targeted human intervention as per most of the literature we investigated. However, their needs must be considered when potentially interfering management actions are evaluated. Less ant-friendly settings (e.g. very intensively managed agroecosystems) should be expected to be unlikely to offer the same services as those in which more diverse ant communities thrive (Anjos et al. 2022), while the effect of different management approaches on ant communities is still unexplored for a considerable part. Conservation of ant diversity in contexts such as agricultural settings should there be considered important both safeguarding biodiversity and preserving economically valuable services.

Our work provides an important step forward towards categorizing ant–pest interactions for basic and applied research, summarizing existing knowledge and identifying knowledge gaps and limitations such as the uneven amount of investigation carried out across different regions of the world, the small percentage of ant diversity so far investigated, or the very limited knowledge of some interactions (e.g. suppression of fungal pathogens, or indirect dissuasion of insect through chemical cues). On the other hand, our review work is limited to mostly indexed literature, which unsurprisingly turned out to be mainly written in English and published in academic journals. This translates into a bias towards relatively recent scientific literature, and implies an unquantified amount of unscanned grey literature, including non-indexed journals and reports, especially those written in other languages—potentially superimposing a geographic and cultural bias—or with an older date of publication. It is also important to remind that the studies we have gathered were carried out with diverse methodologies across a variety of contexts and includes interactions whose significance is context-dependent and heterogeneous. However, the dataset we have assembled and made available through this publication is the largest and most comprehensive of its kind to the current date. Its structure welcomes further updates and expansions, while also promoting deeper investigations at individual subtopics that were here only briefly covered.

Author contributions

ES conceived the study, conducted the systematic literature review and meta-synthesis, prepared the illustrations, and wrote the first draft of the manuscript. DG and DAG participated in the conceptualization, writing, and secured funding. DAG supervised the work. All authors contributed to the final draft.

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Data availability The dataset generated in this study is available as an online supplementary file.

Declarations

Conflict of interests The authors declare no conflict of interests.

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