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Semiochemicals associated with the monitoring of ant traces (Hymenoptera: Formicidae): a systematic review

Semioquímicos asociados al seguimiento de rastros de hormigas (Hymenoptera: Formicidae): una revisión sistemática

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ABSTRACT

Ants are very diverse hymenopterans with a wide geographical distribution. They are social insects and their communication is based on chemical signals. Within the group of semiochemicals that regulate the search for foods are the trail pheromones on the roads. The purpose of this review is to document the main tracking pheromones on the trails that guide ants to feeding sources. A systematic review was carried out based on the guidelines of the PRISMA statement of research found in PubMed, Web of Science and Google Scholar of the pheromones trails. Reported 26 chemical compounds were reported in 14 species of ants, the main sources of obtaining were extracts of the whole body, abdomen and glands. The detection of the semiochemicals were electrophysiological responses of Hymenoptera and chromatographic methods, recording short and long-chain organic compounds (C05-C18). The study of trial chemical compounds has been carried out on a small number of species, this type of research has great potential for the control of invasive ants, since their distribution has had negative repercussions on ecosystems and economic damage to man.

Keywords: Chromatography-mass spectrometry, electroantennography, glands, bioassay, trail.

RESUMEN

Las hormigas son himenópteros muy diversos y de amplia distribución geográfica. Son insectos sociales y su comunicación se basa en señales químicas. Dentro del grupo de semioquímicos que regulan la búsqueda de alimentos están las feromonas de rastro en los caminos. El propósito de esta revisión es documentar las principales feromonas de seguimiento en los senderos que guían a las hormigas hacia las fuentes de alimentación. Se realizó una revisión sistemática basada en las directrices de la declaratoria PRISMA de las investigaciones encontradas en PubMed, Web of Science y Google Scholar de las feromonas de rastro. Se reportaron 26 compuestos químicos de 14 especies de hormigas, las principales fuentes de obtención fueron extractos de cuerpo completo, abdomen y glándulas. La detección de los semioquímicos fueron respuestas electrofisiológicas de los himenópteros y métodos cromatográficos,

registrando compuestos orgánicos de cadena corta y larga (C05-C18). El estudio de compuestos químicos de rastro se ha realizado a un número reducido de especies, este tipo de investigaciones tiene gran potencial para el control de hormigas invasoras, ya que su distribución ha tenido repercusiones negativas en los ecosistemas y daños económicos para el hombre.
Palabras clave: Cromatografía de gases-espectrometría de masas, electroantenografía, glándulas, bioensayo, sendero.

INTRODUCTION

Insects are the most diverse terrestrial invertebrates on the planet, counting about 30 million species (Stork, 2018). In the order Hymenoptera the most representative are bees, wasps and ants. Ants belong to the family Formicidae, the largest of the order Hymenoptera. They are insects of great diversity, as about 11,000 to 16,000 species (26 subfamilies and 428 genera) have been identified. It is estimated that for every 10 kg of insects, 3 to 4 kg are ants (Azhagu *et al*., 2017; Huber, 2017; Diamé *et al*., 2018; Vander Meer & Alonso, 2019; Csősz *et al*., 2021). These invertebrates are of great relevance for the ecosystem services they provide in most terrestrial environments where they establish their colonies, as they modify or create habitats for other species, and are therefore considered ecosystem engineers (Leite *et al*., 2018; Wills & Landis, 2018; De Almeida *et al*., 2020). Ants are able to decompose and recycle nutrients, changing soil structure and energy flow, collect and transport seeds favoring plant distribution (Bologna *et al*., 2017; Eubanks *et al*., 2019; Li *et al*., 2019; Swanson *et al*., 2019; Jílková *et al*., 2020; Ortiz *et al*., 2021; Zhong *et al*., 2021; Ouattara *et al*., 2021).

Formiids are used as bioindicators to estimate the diversity of other taxa, reflect the conservation or pollution status of ecosystems and ecological restoration (Forbes & Northfield, 2017; Tibcherani *et al*., 2018; Casimiro *et al*., 2019; Thurman *et al*., 2019; Carvalho *et al*., 2020; Oberprieler & Andersen, 2020; Okrutniak & Grześ, 2021). In addition, they are an important pest control (Stüber *et al*., 2021; Trigos-Peral *et al*., 2021) and some species are even used for human consumption at different stages of development (immature and adult stages) (Pino Moreno & Blasquez, 2021).

Ants are a dominant and widely dispersed group globally. With the exception of Antarctica and regions with perpetual snow, ants are present in a wide variety of habitats; they are able to colonize new areas to survive environmental changes and find new resources to ensure the reproduction and survival of their colonies (Escárraga & Guerrero, 2014; Guénard *et al*., 2017; Hakala *et al*., 2019; Lessard, 2019). The survival development success, reproduction and foraging of ants is due to the fact that they are social organisms, where the division of labor is collaborative, based on castes and with the plasticity of changing roles by body size and age (Cristín *et al*., 2020; De Gasperin *et al*., 2020; Ortiz-Alvarado *et al*., 2021; O'Shea-Wheller *et al*., 2021).

Ant communication is based on chemical traces, which can differentiate colony odor and congener identification (cuticular hydrocarbons); these compounds are involved in specific responses and are secreted by exocrine glands (Kleeberg *et al*., 2017; Pask *et al*., 2017; Gordon, 2021). Ants are nearly blind, but have a very acute olfactory system in the antennae, which are equipped with specialized chemoreceptors to pick up airborne odor molecules, so the perception and interpretation of odors, in ant brains, is of vital importance for their survival (D'Ettorre *et al*., 2017; Kleeberg *et al*., 2017). Pheromones coordinate nest defense (alarm system), queen and brood care, colony immigration, reproduction, foraging and recruitment (Wyatt, 2017; Du *et al*., 2019; Vander Meer & Alonso, 2019; Ge *et al*., 2020). Trail pheromones is one of the main guidance mechanisms to food sources, when a forager finds food, it deposits a trail of pheromones while returning to the nest, inciting recruitment of its mates to the same resource. Recruited foragers deposit additional trail pheromones, reinforcing the original one, the more abundant and higher quality the food, the higher the pheromone concentration over the trail (Hu *et al*., 2018; Du *et al*., 2019; Renyard, 2019; Kolay *et al*., 2020).

There are two types of pheromones that allow communication between ants: primers and releasers. The former are associated with the development of long-term complex physiological behaviors, while releasers have a simple and immediate behavioral response (Vander Meer & Alonso, 2019). The marking of chemical traces (odor) on trails generates a response, almost immediately, in the recruitment of other foraging ants. Excreted pheromones are produced by a gland (or two in some species), and depending on the family or subfamily in which they are classified, these can be tibial, pygidial, procoxal, Dufour, Pavan, etc (Hölldobler, 2019; Billen *et al*., 2020). Secreted pheromones are a particular mixture of cuticular (HC) or glandular hydrocarbons, they are metabolites that regulate specific behavior. One of the most widely used tools for metabolite identification is metabolomics with targeted and non-targeted approaches. The former involves the analysis of known chemical compounds (use of standards) and the latter aims to find all possible compounds (Ribbenstedt *et al*., 2018). Through different metabolomics techniques, pheromones that regulate various behaviors of social insects have been identified, including chemicals associated with trail following of different families and subfamilies of ants (Hefetz, 2019), which are used for the creation of synthetic versions as methods to control invasive species that negatively affect the trophic relationships of ecosystems, agricultural crops and architectural structures with different uses for humans (Angulo *et al*., 2022; Chen *et al*., 2020; Tay *et al*., 2020). Currently, several review articles report the chemical compounds used by ants as a guidance system towards food sources (Morgan, 2009; Cerdá *et al*., 2014; Fox & Adams, 2022), however, these contributions do not specify the methodology used in the search for sources and the quality criteria to select them and include them in their research, so it is necessary to conduct a review of the semiochemicals reported in ants, since it is indispensable information for the development of studies with ants from Mexico. To ensure that a review is reproducible, accurate and transparent, there is the PRISMA statement, which has been applied in a wide variety of disciplines to perform thematic reviews (Page *et al*., 2021), but there is no precedent of being used to report information on semiochemicals reported with ants. The PRISMA statement is a set of guidelines for conducting a systematic review, which is a rigorous synthesis of knowledge to identify, sift, select and critically analyze the most relevant research on a specific topic and include them in the review (Rethlefsen *et al*., 2021; Sarkis-Onofre *et al*., 2021). In this sense, the objective of the present review is to document the main trail-following pheromones, as a guidance system to food sources, reported in the last seven years, and to identify the different techniques for their chemical synthesis and methods to evaluate their effectiveness.

MATERIAL AND METHODS

In this research, a systematic review of scientific literature has been carried out, using the guidelines of the PRISMA statement (Page *et al*., 2021), which allows synthesizing, through a bibliometric analysis, the state of knowledge of pheromones associated with tracking and foraging of different ant species, specifically those secreted by glands or other part of the body. The systematic review was structured in five steps: a) systematic review questions, b) initial search, c) systematic search, d) selection of publications (inclusion and exclusion criteria), e) quality analysis and critical evaluation, which are explained below:

(a) **Systematic review questions.** The purpose of the systematic review was to address the following research questions:

In which ant species have trace pheromones been reported in the last seven years?

What are the methods of pheromone extraction and which body parts have been analyzed?

What techniques were used for the detection of chemical compounds as a physical response of ants?

What are the methods of preparation of trace chemical and/or pheromonal compounds?

What are the compounds that have been identified in ant foraging trails?

What experimental designs (bioassays) were conducted to obtain the results?

b) Initial search. This consisted of initial searches in Web of Since, Scopus, PubMed and Google Scholar in December 2021, the terms used were the combination of 'Ants' and 'pheromones trails'. The results obtained identified a large number of publications, many duplicated, or others that were not useful because they included ethological studies on breeders (queens), or even belonged to other insect families (e.g., termites, beetles and arachnids). To delimit the searches, Boolean operators OR and AND were used as appropriate.

c) Systematic search. This was conducted in January 2022 including searches from 2017 to the present. The terms and language used, by search engine type, were: i) Web of Since; (TI= (Ants) OR TI=(Hymenoptera: Formicidae)) AND TI=(pheromones trails) AND TI=(trails following). ii) Scopus; TITLE (ants OR "Hymenoptera: Formicidae" AND pheromones AND "trails following"). iii) PubMed and Google Scholar; Ants OR (Hymenoptera: Formicidae) AND (pheromones trails) AND (Trail-Following). The search terms were in English, since the most current scientific production on ant trail pheromones is in this language. This criterion increased the visibility of articles indexed in international databases, and identified the results with the highest number of formic acid subfamilies.

d) Selection of publications

Inclusion criteria

Research that reported chemical tracer compounds in ant trails obtained from glandular extracts and other parts of the body (e.g. head, thorax, abdomen, etc.). In addition, we identified those contributions that conducted bioassays with the application of extracts and/or synthetic pheromones. Such experiments had to use food attractants or evidence trail following, in addition to reporting the bias and/or design effects of each experiment by subjecting them to a probabilistic test.

The search only included trail pheromones; research that reported alarm pheromones (presence of predators or rival colonies) or pheromones that regulate colony reproduction were not considered.

Exclusion criteria

Publications where bioassays were based on essential oil extracts were not included. Priority was given to screening investigations that synthesized pheromones from ant body parts or commercial mixtures. Another exclusion criterion was experiments designed to test biological relationships (e.g., mimicry) with insect families other than ant prey. Finally, trail tracking will not be based on mathematical models.

e) Quality analysis and critical evaluation

The individual quality of the selected articles was evaluated, considering case selection (number of ant colonies), pheromone extraction methods, designs and repetitions in the bioassays. After meeting these criteria, each article was read in full. All of them were characterized by using experimental designs that allowed them to perform statistical tests and/or different adjustments of probabilistic models; in general, the analytical methods (obtaining trace semiochemicals and/or pheromones) can be adapted or repeated in other investigations with Formicids.

Functional group analysis

After applying the PRISMA statement, and identifying the ants' trace semiochemicals, we proceeded to classify the information as described below; a) chemical functional groups, b) chain length (number of carbons) and c) chemical compounds. With this information and the total frequencies of the classification, a descriptive analysis was performed using Minitab® 18.1.

RESULTS

212 sources containing the keywords of interest were identified in two databases and an Internet search engine. With this information, 206 publications were selected, which were scientific articles from the last 7 years. After excluding duplicates and analyzing titles and abstracts, 178 records were excluded. The remaining 25 articles were screened using the inclusion/exclusion criteria, of which seven were chosen for the systematic review because they met the quality and critical appraisal criteria (Table 1).

The investigations by Chalissery *et al.* (2021), Chalissery *et al.* (2019) and Renyard *et al.* (2019) were conducted in Canada, by Simon Fraser University, Burnaby, BC (Department of Biological Sciences). In the study by Hamilton *et al.* (2018) they obtained the samples (anthills) in Soberania National Park, Panama, under the direction of The Ohio State University, Columbus, OH, USA (Dept. of Evolution, Ecology and Organismal Biology). The research of Nakamura *et al.* (2019) was conducted at Kyoto Institute of Technology, Japan (Laboratory of Applied Entomology). Stringer *et al.* (2017) developed their study in New Zealand, New Zealand Institute (Institute of Plants and Food). Finally, Xu *et al.* (2021) obtained biological material in Guangdong (ants) and Hebei (cotton aphids) provinces in China, the research development was a collaboration between Hebei University and South China Agricultural University (among other institutions).

Table 1. Quality analysis of articles included in the results

Reference	**Sample size** 1=Not clear 2=Present	**Glandular extracts or other body parts 1=Not clear**	**Bioassays** 0=Not present 1=Not clear 2=It is clear	**Treatments** 1=Different treatments and a control 2=Different treatments with replicates and a control	**Response variable** 0=Qualitative (ordinal) 1=Numeric (discrete and/or continuous)	**Statistical analysis** 0=Not present 1=Not clear 2=Present	**Results** 0=Incomplete 2=Complete	**Total**
Chalissery *et al*. (2021)	1	2	2	2	1	2	2	12
Chalissery *et al*. (2019)	2	2	2	2	1	2	2	13
Hamilton *et al*. (2018)	2	2	0	1	1	0	2	8
Nakamura *et al*. (2019)	2	2	2	2	1	2	2	13
Renyard *et al*. (2019)	2	2	2	2	1	2	2	13
Stringer *et al*. (2017)	2	2	2	2	1	2	2	13
Xu *et al*. (2021)	2	2	2	2	1	2	2	13

The result of the review identified a total of 26 trace semiochemicals from 14 ant species, belonging to the subfamilies Myrmicinae (ten species), Formicinae (three species), and Dolichoderinae (one species) (Table 2). The most studied ants to conduct the experiments were *Camponotus modoc* and *Linepithema humile* (Stringer *et al*., 2017; Chalissery *et al*., 2019).

Table 2. Trace semiochemicals and analysis methodologies in systematic search

Reference	Species (s)	Source(s) for pheromone procurement	Solvent used in the extracts	Configuration of roads and/or structures used in the bioassays	Pheromone detection analysis	Identified trace pheromones	Results
Chalisser *et al*. (2021)	*Tetramorium immigrans*	Venom gland and whole body (abdomen, thorax and head)	Dichloromethane (DCM)	i) Circular structure ii) Labyrinth in the shape of a "V". iii) Field path with two paper strips (0° and 180°). DCM was used as control in all experiments.	(i) Gas chromatography-electroantenography (GC-EAD) to identify the most responsive compounds in the antennae. (ii) Gas chromatography-mass spectrometry (GC-MS) for analysis of candidate pheromone(s).	Methyl 2-methoxy-6-methylbenzoate (MMMB) as a candidate pheromone.	Ants followed extract trails (HSRE).

Chalisser *et al*. (2019)	Sympatric distribution: i) *Camponotus modoc* ii) *Lasius niger* iii) *Myrmica rubra* Allopatric distributioni v) *Tetramorium caespitum* v) *Novomessor albisetosus* vi) *Linepithema humile*	Synthetic blend of six trace pheromones (6-TPB)	Pentane	Circular structures of different diameters In all experiments pentane was used as control	GC-EAD	i) (2S,4R,5S)-2,4-dimethyl-5-hexanolide (“hexanolide”, 6-TPB) and 2,4, dimethyl-5-hexanolide (EAD) ii) 3,4-dihydro-8-hydroxy-3,7-trimethylisocoumarin (“isocoumarin”, 6-TPB) and 3,4-dihydro-8-hydroxy-3,5,7-trimethylisocoumarin (EAD). iii) 3-ethyl-2,5-dimethylpyrazine (6-TPB and EAD). iv) 2,5-dimethylpyrazine (6-TPB and EAD) v) 4-methyl-3-heptanone (6-TPB and EAD) vi) (Z)-9-hexadecenal (6-TPB and EAD)	Ants followed the traces of the synthetic mixture (HSRMS).
Hamilton, *et al*. (2018)	*Cyphomyrmex rimosus* *C. salvini* *C. costatus* *C. muelleri* *C. longiscapus*	Head, mesosoma (thorax) and gaster (abdomen)	Metanol	Chemical compounds compared to a phylogenetic sample	GC-MS	i) 2,5-dimethyl-3-isoamylpyrazine ii) Six putative trace pheromones: (3Z, 6E)-α-farnesene, (3Z, 6E)-α-7-ethylhomofarnesene, α-6-ethyl-bishomofarnesene, Bishomofarnesene-2, Bishomofarnesene-1, Trishomofarnesene	The most abundant compounds were (3Z, 6E)-α-7-ethylhomofarnesene and α-6-bishomofarnesene in three species of the *C. wheeleri* group. The mesosome region did not yield volatile compounds.
Nakamura *et al*. (2019)	*Tetramorium tsushimae* Emery	Extract of whole body, head-mesosoma, gaster, venom gland, Dufour's gland, upper intestine and abdominal residues.	Mixture of n-hexane and diethyl ether	Straight lines of various lengths (10 and 5 cm). In all experiments, n-hexane and diethyl ether were used as controls. diethyl ether were used as controls	GC, GC preparative coupled with a thermal conductivity detector and GC-MS	Methyl 6-methylsalicylate	HSRE Ants more frequently chose the extract marked with poison gland than any of the others (Dufour's gland, upper gut and abdominal residues).

Renyard *et al*. (2019)	*Camponotus modoc*	Hindgut and venom gland	DCM	i) Metal scaffolding to a circular structure ii) "V" labyrinth iii) "Y" labyrinth DCM was used as control in all experiments.	i) GC-EAD to identify the most responsive compounds in the antennae and GC-MS for analysis of candidate pheromone(s). (ii) GC-MS to quantify the amount of candidate upper gut pheromone components	i) 2, 2,2,4-dimethylhexanoic acid ii) 2,4-dimethyl-5-hexanolide iii) Pentadecane iv) Dodecanoic acid v) 3,4-dihydro-8-hydroxy-3,5,7-trimethylisocoumarin	HSRE Poison gland components did not cause any trace tracking
Stringer *et al*. (2017)	*Linepithema humile*	Gaster	Hexane with 50 ng of dodecyl acetate	i) Cotton thread (20 cm × 0.33 mm) (ii) Straight line drawn on a sheet of paper iii) Parallel paths (1cm) In all experiments 70% ethanol was used as a control	GC-MS	(Z)-9-hexadecenal	HSRE Trail following was most effective with physical cues (yarn). Trail following was slightly improved at high concentrations upwind
Xu *et al*. (2021)	*Solenopsis invicta*	Full body excerpt	Hexane	i) Filter paper strips (1 cm) placed inside a Petri dish (9 cm). ii) Growth of aphid populations on the leaf area of cotton seedlings by applying ant extracts. In the experiments, hexane was used as a control.	i) Electroantennogram (EAG) in the antennae of *Aphis gossypii* Glover. (ii) GC-MS for the analysis of crude extract of worker ants in six fractions.	Z,E-a-farnesene E,E-a-farnesene	i) Aphids showed responses to extracts of all fractions. ii) *S. invita* trace semiochemicals suppress the dispersal of *A. gossypii.* iii) Application of the trace extracts led to faster aphid population growth on cotton seedlings.

*To avoid synonymy of the trace chemical compounds, discrepancies and confusion with the acronyms used by the authors, these were reported in English

The method for obtaining trace semiochemicals were by extracts, using organic solvents of three chemical groups; alkane (C_5H_{12} and C_6H_{14}), ester ($C_4H_{10}O$), alcohol (CH_3OH) and a chlorinated aliphatic (CH_2Cl_2). Regarding the body parts for obtaining the semiochemicals, Nakamura *et al*. (2019), Chalissery *et al*. (2021), and Xu *et al.* (2021) employed full-body ants. Chalissery *et al.* (2021) additionally used venom gland, while Nakamura *et al.* (2019) obtained extracts from head-mesosoma, abdomen, venom gland, and upper intestine. Likewise, Stringer *et al*. (2017) and Hamilton *et al*. (2018) dissected gasters (Table 2).

The electrophysiological detection and response method used in ants was GC-EAD in two publications (Chalissery *et al*., 2021; Chalissery *et al*., 2019) and electroantennogram (EAG) in *Aphis gissypii* in a mutualistic relationship with *Solenopsis invicta* (Xu *et al*., 2021) (Table 2). The preparation, production and purification of trace semiochemicals (26 in total), in general, was by GC-MS. In the retrieved articles, gas chromatographic intensities were analyzed and identifying molecules obtained from extracts of different ant body parts, with the exception of Chalissery *et al*. (2019) who used EAD for species of sympatric and allopatric distribution (Table 2).

It was identified that all authors used different terms to name trace semiochemicals, including candidate pheromones in the contributions of Stringer *et al*. (2017), Renyard *et al*. (2019and Chalissery *et al*. (2021); unlike Hamilton *et al*. (2018) who used putative pheromones derived from extracts of the genus *Cyphomyrmex* (Table 2).

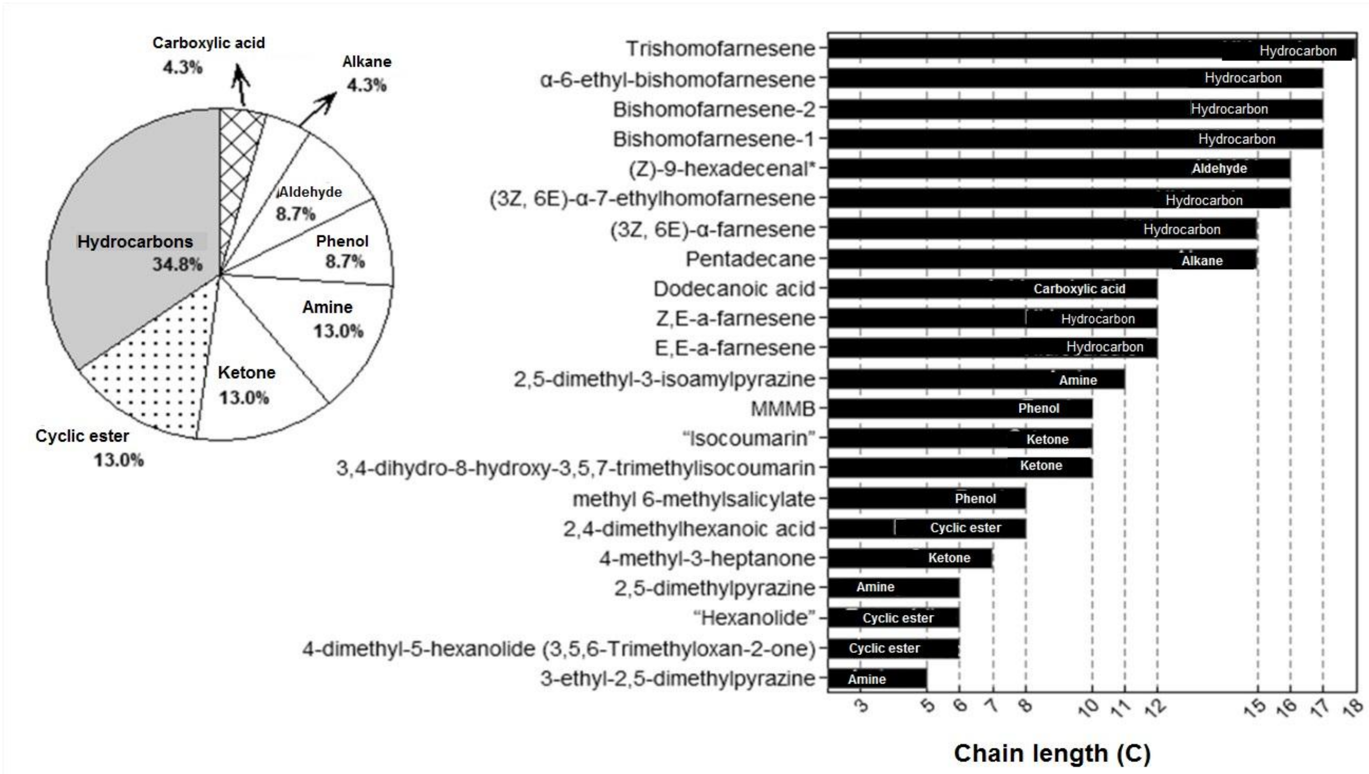
The direction of the bioassays was with physical structures of various shapes and dimensions, to which chemical compounds of single or different concentrations (extracts and even synthetic pheromones) were applied to simulate trail following on paths with or without reward. For example, Chalissery *et al*. (2019) employed circular structures, Chalissery *et al*. (2021) "V" shaped mazes, Renyard *et al*. (2019)) circular structure and "V" and "Y" mazes. The other designs were in scaffolds or straight line walkways like that of Nakamura et al. (2019), and even some hybrid designs; such as the case of Stringer et al. (2017) with straight line cotton thread and Xu *et al*. (2021) who used straight paths placed on Petri boxes (Table 2). The review identified that ants responded to trace chemical compounds from their own pheromones, but also to that of other species (Chalissery et al., 2019). In the identification methodologies for trace volatiles, Chalissery et al. (2019), Nakamura *et al*. (2019), and Stringer *et al*. (2017) used commercial standards, accounting for 19 % of the total chemical compounds characterized (Table 3). Research by Renyard *et al*. (2019), Chalissery *et al*. (2021) and Xu *et al*. (2021) synthesized their own standards. While other authors obtained them externally from other researchers, oh well, they used commercial standards, but do not give specifications of trademarks or patents (Table 3).

Table 3. Standards used for the synthesis of trace chemical compounds

Reference	Semiochemicals identified	Standard
Chalissery *et al*. (2021)	MMMB	Internal standard synthesized by the authors
Chalissery *et al*. (2019)	i) "Hexanolide" ii) "Isocoumarin" iii) 3-ethyl-2,5-dimethylpyrazine iv) 2,5-dimethylpyrazine v) 4-methyl-3-heptanone vi) (Z)-9-hexadecenal	i,ii) Synthesis of *Camponotus modoc* hindgut extracts. (Renyard *et al*., 2019) iii) Acros Organics, New Jersey, USA iv) Aldrich Chem Co. Milwau, USA v) Sigma-Aldrich, St. Louis, MO, USA vi) Sigma-Aldrich
Hamilton *et al*. (2018)	i) 2,5-dimethyl-3-isoamylpyrazine Punitive trace pheromones:ii) (3Z, 6E)-α-farnesene iii) (3Z, 6E)-α-7-ethylhomofarnesene iv) α-6-ethyl-bishomofarnesene v) Bishomofarnesene-2 vi) Bishomofarnesene-1 vii) Trishomofarnesene	Direct comparison with commercial products
Nakamura *et al*. (2019)	Methyl 6-methylsalicylate	External standard provided Shigeru Matsuyama. University of Tsukuba, Tsukuba, Japan
Renyard *et al*. (2019)	i) 2,4-dimethylhexanoic acid ii) 2,4-dimethyl-5-hexanolide (3,5,6-Trimethyloxan-2-one) iii) Pentadecane iv) Dodecanoic acid v) 3,4-dihydro-8-hydroxy-3,5,7-trimethylisocoumarin	Internal standards synthesized by the authors
Stringer *et al*. (2017)	(Z)-9-hexadecenal	Bedoukian Research, Danbury, CT, USA.
Xu *et al*. (2021)	Z,E-a-farnesene E,E-a-farnesene	Internal standards synthesized by the authors

*They do not specify, however, that initial comparisons were made with the NIST Mass Spectral Data base, V.2 and published literature spectra.

The amine functional group 3-ethyl-2,5-dimethylpyrazine pheromone was the shortest chain (C05) used in experiments with *Myrmca rubra* (Chalissery *et al*., 2019). In contrast, the longest chain hydrocarbon was Trishomofarnesene in the bioassays with *Cyphomyrmex rimosus* and *Cyphomyrmex salvini* (C18) (Hamilton *et al*., 2018). The most commonly used organic compounds were hydrocarbons with chains of C12, C15, C16, C16, C17 and C18 accounting for 34.8 %, followed by cyclic esters and ketones (C06, C08 and C07, C10) with 13 % (Figure 1).



Source: Own elaboration with data obtained from articles analyzed with the PRISMA statement

Figure 1. Identification of the functional groups of trace chemical compounds

For *Camponotus modoc*, "hexanolide" was reported (Chalissery *et al*., 2019; Renyard *et al*., 2019), a compound that has possibly never been reported for the species before. However, this semiochemical has been identified in other ant species of the same genus (*Camponotus socius*, *C. pennsylvanicus* and *C. vagus*) in the chiral configuration (2S,4R,5S)-2,4-Dimethyl-5-hexanolide in trace pheromone biosynthesis experiments using electrophysiological and behavioral evidence (Bestmann *et al*., 1999).

DISCUSSION

At present, it is possible, that there are no systematic reviews that have used the PRISMA statement to report ant trail semiochemicals as the one developed in this study, so it is important this synthesis of knowledge about different characteristics of semiochemicals reported in various publications. The 14 Formicid species studied have diverse geographical distribution categories (native, exotic, introduced, etc.) (Janicki *et al*., 2016), highlighting: *Linepithema humile* and *Solenopsis invicta* as introduced and/or exotic ants; which have invaded almost all continents, caused damage to ecosystems and economic losses to man (Angulo *et al*., 2022; Chen *et al*., 2020; Seko *et al*., 2021).

An alternative in the control of pest ants is the use of pheromones, mentioned in five investigations. Three through the use of lethal baits (Chalissery *et al*., 2019; Renyard *et al*., 2019; Chalissery *et al*., 2021), and two with the disruption of trail communication by increasing pheromone concentration (Stringer *et al*., 2017; Nakamura *et al*., 2019). Invasive species control with baits and pheromones is a recent practice, for example, Welzel & Choe (2016) use hydrogel adding (Z)-9-hexadecenal and insecticides for Argentine ant control, a strategy that appears to be more effective with pheromone-assisted baits vs. to other residual contact baits such as sprays, granules and other liquids (Suiter *et al*., 2021). This tactic has also been used with the invasive fire ant *Myrmica rubra*, causing significant mortality by carrying and sharing insecticide-added food within the colony (Hoefele *et al*., 2021).

Not all research mentioned ant control through semiochemicals as a direct method. For example, Xu *et al*. (2021) analyzed an ecological relationship, through a bioassay, to verify if the pheromone trail of *Solenopsis invicta* can impact the population dynamics of *Aphis gossypii*. They highlight a positive mutualistic relationship between these two insects of wide geographic distribution, and how the red fire ant exerts control in the reproduction and dispersal of the apterous hemiptera. This type of ecological relationship has been investigated between the mealybug *Planoccocus citri* and the ant *Lasius grandis*, when introducing an alternate feeding of sugar, decreased the care of the prey insect and consequently increased the infestation of the mealybug in a citrus orchard (Navel Powell cultivar orange trees) (Pérez-Rodríguez *et al*., 2021).

Ants are widely used for the biological control of other insect pests in agricultural and forestry crops. Such is the case of *Wasmannia auropunctata* in a coffee agroforestry system, which reduced the survival of *Hypothenemus hampei* inside the fruits, and with little significant effect *Solenopsis invicta* depredated adult borers of *H. hampei* outside the fruits (Newson *et al*., 2021). The ethology and chemical communication of formicides allowed the development of a biological control of the fruit fly *Bacterocera zonata* that attacks mangoes of the Chaunsa variety, this through the exposure of fruits to chemical signals from an ant colony, managing to deter oviposition of *B. zonata* (Rimsha *et al*., 2019). In another contribution, with seven ant species (five genera; *Camponotus*, *Pheidole*, *Oecophylla*, *Brachyponera*, and *Megaponer*), they investigated the predation of *Spodoptera frugiperda* (J. E. Smith) budworm larvae on maize crops in fields without insecticide treatment, proving to be a potentially useful *S. frugiperda* control method (Dassou *et al*., 2021). At present, relatively few pheromones are reported from ant trail trails (Czaczkes, 2018). In this research, (Z)-9-hexadecenal was identified in two contributions (Chalissery *et al*., 2019; Stringer *et al*., 2017), this compound and its pheromonal analogues are of particular interest in the integrated management of insects of different orders, particularly in mating disruption (Rizvi *et al*., 2021).

In the review developed in this work, a great similarity was observed in the choice of methodologies for the detection, identification and production of trace semiochemicals, however, there was a great variability of results. This tendency may be due to the biology and ecology of the ant species studied, sources of pheromone extraction (body parts) and different methods in the bioassays. The use of GC-MS used in the synthesis of chemical compounds, despite having been the most recurrent methodology, had differences in the solvents used for the preparation of extracts, characteristics of the columns (polar affinity) and the use of targeted and non-targeted metabolomics. The identification of useful functional groups in the analyzed articles, and their derivatization (synthesis) to significant molecular ions (Attygalle *et al*., 1998), apparently depended on the diagnosis of the chromatographic peak (m/z), but also on the sources of emission of the semiochemicals, which were through extracts from different parts of the body of arthropods.

Four high-risk invasive ant species have been identified in Mexico (*Linepithema humile*, *Nylanderia fulva*, *Solenopsis invicta* and *Pheidole megacephala*) (Rosas-Mejía & Milan, 2017). The results of this review can be used for the creation of synthetic pheromonal compounds and mark artificial pathways that guide ants to lethal baits or function as a disruptor of this behavior. These volatiles can be extracted from various parts of the ant's body (glands, gaster, head, thorax, etc.), characterized with chromatographic or electroantennographic techniques (even combining both technologies), and tested for their effectiveness through bioassays. The aforementioned strengthens the knowledge of ant trace semiochemicals, and supports decision making for the control and/or eradication of species considered pests.

CONCLUSIONS

In all the articles analyzed, it was demonstrated that pheromone synthesis through extracts is effective in the Myrmicinae, Formicinae and Dolichoderinae families, the most outstanding functional group was long chain hydrocarbons (C12: C18), in all the bioassays the ants responded to the chemical compounds marked on the trails. The identification and synthesis of trail semiochemicals remain through electrophysiological responses of the hymenopterans and gas chromatography combining mass spectrometry. To conduct trail following experiments, the use of traditional mazes was emphasized, however, increasingly novel designs and the use of technology, such as cameras and ant counting software, are being chosen to prevent the decision of whether or not to take a path by formicids from biasing the results.

The overview of the trace semiochemical use has great potential for control of invasive ant species, as they are not only capable of following their own trails, but also those of other Formiid species. Ants are a very diverse group, and many of the chemicals that regulate their behaviors and how they can be used in other taxonomic groups have yet to be discovered.

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Errata Erratum

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