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Scale insects (Hemiptera: Coccomorpha) on coffee roots (*Coffea arabica* L.) in Colombia, with records of associated ants (Hymenoptera: Formicidae)

Los insectos escama (Hemiptera: Coccomorpha) de raíces de café (*Coffea arabica* L.) en Colombia, con registros de hormigas (Hymenoptera: Formicidae) en asociación

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Abstract

Scale insects (Hemiptera: Coccomorpha) that feed on roots are considered of economic importance in crops such as coffee. Although noteworthy developments on the knowledge about the alpha taxonomy of such insects exist, more information concerning their diversity is necessary. The aim of this study was to update the list of scale insect species found on coffee roots in Colombia as well as to recognize their trophobiotic ants. Field trips were carried out in nine Colombian departments, where 541 samples were obtained. In total, 4,762 scale insect specimens and 450 ants were analyzed; Coccomorph specimens were prepared in microscopy-slides and ants were pinned in points and entomological pins. Likewise, 250 scale insect samples preserved in seven Colombian entomological collections were also examined. Lastly, scale insect records associated with coffee in Colombia were also revised based on available published literature. The current study provides a list of scale insect species on coffee in Colombia, including their geographical distribution and associated ants. The checklist of scale insects associated to coffee roots is updated to 61 species, 52 of which correspond to samples collected in the field and nine from entomological collections; 20 species were recorded for the first time in association with coffee and 15 species are new records for Colombia. *Puto barberi*, *Geococcus coffeae*, the *Dysmicoccus* complex *texensis*, *Rhizoecus colombiensis* and *Pseudococcus elisae*, were the most frequently observed scale insect species on coffee in Colombia. Furthermore, 32 morphospecies of ants were found, of which 30 are known to be in facultative trophobiotic relationships with hemipterans, and two species of the *Acropyga* genus are known for their trophophoresy with scale insects.

Keywords: Coccoidea, hemiptera-ant association, pest insect, Neotropical region, Ortheziidae

Resumen

Los insectos escama asociados a raíces son de interés económico en cultivos como el café. Aunque existen desarrollos notables en el conocimiento sobre la taxonomía alfa de tales insectos, se requiere más información sobre su diversidad. El objetivo de este trabajo fue actualizar la lista de especies de insectos escama huéspedes en raíces de café en Colombia, así como reconocer sus hormigas trofobióticas. Se recolectaron 541 muestras en nueve departamentos de Colombia; se analizaron 4.762 especímenes de insectos escama y 450 hormigas. Los coccomorfos se prepararon en láminas para microscopía y las hormigas, en doble montaje en seco. Asimismo, se examinaron 250 muestras de escamas conservadas en siete colecciones entomológicos de Colombia. Por último, se revisó la literatura relacionada con registros previos de escamas en café para el país. La presente investigación provee una lista actualizada de especies de insectos escama para el cultivo en el país, incluida su distribución geográfica y hormigas asociadas. Se actualiza la lista de insectos escama asociadas a raíces de café a 61 especies, 52 de ellas obtenidas a partir de las muestras analizadas y nueve por registros de literatura; se hacen 20 nuevos registros de asociación con café y 15 nuevos registros para Colombia. Las especies con mayor presencia en el cultivo fueron *Puto barberi*, *Geococcus coffeae*, complejo *Dysmicoccus texensis*, *Rhizoecus colombiensis* y *Pseudococcus elisae*. Además, se obtuvieron 32 morfoespecies de hormigas, de las cuales 30 se conocen en relaciones trofobíoticas facultativas con hemípteros, y dos del género *Acropyga* en trofoforesia.

Palabras clave: asociación hemíptero-hormiga, Coccoidea, insectos dañinos, Neotrópico, Ortheziidae

Introduction

Coffee (Rubiaceae: *Coffea* spp.) is one of the most marketed plant-based products worldwide and generates about 24 billion dollars for the seven million tons produced per year (Food and Agriculture Organization of the United Nations [FAO], 2015). Coffee is the most important export crop for Colombia, with 30 % of the total planted area in the country (903,000 ha), followed by sugar cane (19 %), African palm (16 %), and cocoa (6.6 %), among others (National Administrative Department of Statistics [DANE], 2016). The economic importance of coffee and the interest to improve yields and lower production costs results in having to carry out research in multiple areas of the agronomy of this crop (Waller, Bigger, & Hillocks, 2007). In this context, insect taxonomy is one of the most active research areas in coffee farming, seeking to recognize the insect species associated with this crop (Le Pelley, 1973; Waller et al., 2007).

The term *scale insects* groups in a broad sense, insects belonging to the infraorder Coccomorpha, suborder Sternorrhyncha, order Hemiptera (Williams & Hodgson, 2014). They are the most diverse group of the suborder, with small sizes (< 5 mm), cryptic habits and with diverse reproductive processes; likewise, they show contrasting sexual dimorphism, reduced mobility —mainly in adult females— and the ability to secrete waxy substances that offer protection from environmental conditions and natural controllers. These insects also have trophobiotic relationships with other insects, mainly ants (Ben-Dov & Hodgson, 1997; Gavrilov & Kuznetsova, 2007; Gullan & Cranston, 2005; Gullan & Martin, 2003; Kondo & Gullan, 2010; Kondo, Ramos, & Vergara, 2008; Ramos & Serna, 2004). Nearly 8,000 scale insect species are known and have been grouped into 47 families (32 existing and 15 extinct), of which 187 species are recorded for coffee (García-Morales et al., 2016). The general richness of Coccomorpha for Colombia is estimated at 244 species, grouped into 14 families, including Diaspididae (78 species), Pseudococcidae (60), Coccidae (46) and Rhizoecidae (22), among others (Ben-Dov, 1994; Ramos-Portilla, Gil, & Benavides, 2018; García Morales et al., 2016; Kondo, 2001; Kondo, Rodríguez, Díaz, Dix, & Palacio, 2018). In Colombia, 45 of these species are associated with plants of the genus *Coffea* Linnaeus, 1753 (Balachowsky, 1959; Beardsley, 1970; Caballero et al., 2018; Gallego & Vélez, 1992; García Morales et al., 2016; Granara de Willink, 2009; Hambleton, 1946, 1976, 1977; Kondo, 2001, 2013; Kondo et al., 2008; Murillo, 1931; Posada, 1989; Ramos & Serna, 2004; Ramos-Portilla & Caballero, 2016; Williams & Granara de Willink, 1992).

These insects are characterized by having an exclusive phytosuccivorous habit, which can generate direct and indirect physiological problems to the plants, such as weakening by extraction of photoassimilates, transmission of phytopathogenic microorganisms, and in severe cases, the death of the plant (Gullan & Martin, 2003). The first record of scale insects in coffee was published by Nicolás Sáenz in 1893, who detected *Saissetia coffeae* (Walker, 1852) (Coccidae) and *Pseudococcus longispinus* (Targioni Tozzetti, 1867) (Pseudococcidae), but with no record of economic affectation (Bustillo, 2008). The first phytosanitary problem caused by scale insects in roots of Colombian coffee plantations was recorded in the thirties, when the population of *Puto antioquensis* (Murillo, 1931) (Putoidae) increased to the point of generating economic losses (Federación Nacional de Cafeteros, 1932). Later, in the sixties and seventies, species such as *Neochavesia caldasiae* (Balachowsky, 1957) and *Rhizoecus coffeae* Laing, 1925 (Rhizoecidae) were recorded, with damage focused on the departments of Antioquia and Caldas (Benavides-Gómez & Cárdenas-Murillo, 1977). Since 2008, this group regained economic importance with the increase of the mealybug populations, mainly *Puto barberi* (Cockerell, 1895) (Putoidae), *Dysmicoccus brevipes* (Cockerell, 1893) and *Pseudococcus jackbeardsleyi* Gimpel and Miller, 1996 (Pseudococcidae) in areas of the coffee-growing area or Eje Cafetero (Gil, Benavides, & Villegas, 2015; Villegas, Benavides, Zabala, & Ramos, 2009; Villegas-García & Benavides-Machado, 2011). In 2013, the first severe attack caused by the coccid *Toumeyella coffeae* Kondo, 2013, was recorded in roots of coffee plantations in the department of

Norte de Santander (Gil & Benavides, 2017; Gil et al., 2015; Kondo, 2013).

Prior to the current study, 32 scale insect species had been recorded for Colombia in association with coffee roots: *Toumeyella coffeae* Kondo, 2013 (Coccidae); *Mixorthezia minima* Koczné Benedicty and Kozar, 2004 (Ortheziidae); *Dysmicoccus brevipes*, *D. caribensis* Granara de Willink, 2009, *D. grassii* (Leonardi, 1913), *D. mackenziei* Beardsley, 1965, *D. neobrevipes* Bearsdley, 1959, *D. radicis* (Green, 1933), *D. texensis* (Tinsley, 1900), *D. varius* Granara de Willink, 2009, *Phenacoccus solani* Ferris, 1918, *Planococcus citri* (Risso, 1813), *Planococcus minor* (Maskell, 1897), *Pseudococcus elisae* Borchsenius, 1947, *Pseudococcus jackbeardsleyi* Gimpel and Miller, 1996, *Pseudococcus landoi* (Balachowsky, 1959) (Pseudococcidae); *Puto antioquensis* and *Puto barberi* (Putoidae); *Capitisetella migrans* (Green, 1933), *Geococcus coffeae* Green, 1933, *Neochavesia caldasiae*, *N. eversi* (Beardsley, 1970), *N. trinidadensis* (Beardsley, 1970), *Pseudorhizoecus proximus* Green, 1933, *Rhizoecus americanus* (Hambleton, 1946), *R. arabicus* (Hambleton, 1976), *R. coffeae*, *R. colombiensis* Ramos and Caballero, 2016, *R. compotor* Williams and Granara de Willink, 1992, *R. mayanus* (Hambleton, 1946), *R. setosus* (Hambleton, 1946) and *Ripersiella andensis* (Hambleton, 1946) (Rhizoecidae) (Balachowsky, 1959; Benavides-Gómez & Cárdenas-Murillo, 1977; Caballero et al., 2018; Granara de Willink, 2009; Hambleton, 1946, 1977; Kondo, 2001, 2013; Kondo et al., 2008; Murillo, 1931; Ramos-Portilla & Caballero, 2016; Villegas et al., 2009; Williams & Granara de Willink, 1992).

Regarding the trophobiosis association between hypogeous scale insects and ants (Hymenoptera: Formicidae), Colombia shows records of *C. migrans*, *N. trinidadensis* and *Ps. proximus*, attended by *Acropyga goeldii* Forel, 1893; *D. brevipes*, attended by *Prionopelta* sp. and *Solenopsis geminata* (Fabricius, 1804); *D. neobrevipes* and *D. texensis*, by *S. geminata*; *G. coffeae*, by *Solenopsis* sp. and *Tranopelta* sp.; *N. caldasiae*, by *Acropyga fuhrmanni* (Forel, 1914); *P. barberi*, by *Acropyga exsanguis* (Wheeler, 1909), *S. geminata*, *Tranopelta gilva* Mayr, 1886 and *Wasmannia auropunctata* (Roger, 1863); *R. caladii* and *R. coffeae*, by *A. exsanguis*, and *R. setosus*, by *Acropyga* sp. (Benavides-Gómez & Cárdenas-Murillo, 1977; Kondo et al., 2008; Villegas et al., 2009; Williams, 1998).

It is necessary to maintain an updated inventory of the scale insect species associated with coffee crop and expand their biological and ecological information, aspects in which the trophobiosis scale insects-ants are highlighted. For this reason, the aim of this study was to know the taxonomic composition of insects of the infraorder Coccomorpha in the rhizosphere of coffee cropping and their associated ants in Colombia, in order to contribute to the elaboration of integrated management plans.

Materials and methods

Samples of scale insects and associated ants were collected manually between January 2015 and July 2017, by officials of Servicio de Extensión Rural de la Federación Nacional de Cafeteros de Colombia (FNC) and of Instituto Colombiano Agropecuario (ICA), as well as well as by the authors AC, AARP, ZNG and PB, in the Colombian departments of Antioquia, Caldas, Casanare, Cauca, Huila, Nariño, Quindío, Risaralda and Santander. The plots from where the samples were taken were randomly selected based on the information included in Sistema de Información Cafetera (SICA) managed by Centro Nacional de Investigaciones de Café (Cenicafé), and also considering that farms should be under the supervision of ICA. Furthermore, plants should have less than, or up to two years of age of being planted. For ant collections, their interaction with the scale insects was verified, either because the former were stimulating the latter for the excretion of honey dew or transporting them.

In addition, scale insect specimens conserved in entomological collections of several research institutions were studied, including the following. Museo Entomológico "Universidad Nacional Agronomía Bogotá" (UNAB) and the Arthropod Collection of Instituto de Ciencias Naturales (ICN) (Universidad Nacional de Colombia, sede Bogotá); Museo

Entomológico "Francisco Luis Gallego" (MEFLG) (Universidad Nacional de Colombia, sede Medellín); Museo de Entomología de la Universidad Nacional - Sede Palmira (UNCP) (Universidad Nacional de Colombia, sede Palmira); Museo Entomológico Marcial Benavides (MEMB) (Cenicafé, Caldas); Colección Entomológica Luis María Murillo (CTNI) (AGROSAVIA, Cundinamarca), and entomological collection of Centro de Investigación Palmira (MECP) (AGROSAVIA, Valle del Cauca). The list was supplemented with information gathered from scientific literature.

The collected scale insect specimens and entomological collections were preserved in 70 % alcohol and prepared in plates for microscopy, based on the modified protocol of Sirisena, Watson, Hemachandra and Wijayagunasekara (2013). The macroscopic observations were made with a Nikon MSZ-1 stereomicroscopes, and the microscopic ones with an Olympus CX31 optical microscope and Nikon Eclipse E600 and a Zeiss Axio Lab A1 phase contrast microscope. Photographs were taken and analyzed with a Lumenera 1-5C camera and the Image Pro Insight 8.0 software, respectively. The postharvest curation process was carried out mainly in the UNAB Entomological Museum and the Abraham Willink Higher Institute of Entomology of Universidad Nacional de Tucumán (Argentina). The specimens collected are largely conserved in the Central Taxonomic Collection of the UNAB museum with backup copies in MEMB. The identification of the material was made based on the study of the external morphology of the adult female. The identification of some specimens of the genus *Rhizoecus* Kunckel d'Herculais, 1878, was based on the recognition of genital chambers. The following taxonomic keys and descriptions were employed: Balachowsky (1959), Cox (1978), Gill (1988), Gill, Nakahara and Williams (1977), Gimpel and Miller (1996), Granara de Willink (2009), Granara de Willink and Szumik (2007), Kondo (2013), Kondo and Williams (2004), Kosztarab (1996), Kosztarab and Kozár (1988), Kozár and Konczné-Benedicty (2007), McKenzie (1967, 1967), Miller and McKenzie (1971, 1973), Ramos-Portilla and Caballero (2016), Schneider and Lapolla (2011), von Ellenrieder and Watson (2016), Williams (2004a, 2004b), Williams and Granara by Willink (1992), Williams and Watson (1988), and Williams and Kosztarab (1972).

Ants were collected and kept in 70 % alcohol; later, they were mounted in entomological pins and their taxonomic identification was made by observing the morphology of minor and older worker ants. The Nikon MSZ-1 stereomicroscopes was used with 10 X, 20 X and 30 X eyepieces; the diagnoses and taxonomic keys of Fernández (2003), Jiménez, Fernández, Arias and Lozano-Zambrano (2007), LaPolla (2004), LaPolla, Brady and Shattuck (2010), LaPolla and Fisher (2014), and Longino (2009), Longino and Fernández (2007), Pacheco and Mackay (2013), Sarnat, Fischer, Guénard and Economo (2015), Wild (2007) and Wilson (2003) were used, as well as the comparison of specimens with cured specimens from the Central Taxonomic Collection of the Entomological Museum UNAB and digital resources such as AntWeb[1], AntWiki[2] and Bolton[3].

Results and discussion

Coccomorpha

A total number of 4,762 specimens were analyzed from 541 samples collected, and about 250 from the entomological collections of UNAB and MEMB. The other entomological collections consulted do not conserve specimens collected in coffee roots. From all the specimens studied, 52 species of Coccomorphs were identified in seven families: Coccidae (4 spp.), Diaspididae (2 spp.), Margarodidae (1 sp.), Ortheziidae (4 spp.), Pseudococcidae (22 spp.), Putoidae (1 sp.), and Rhizoecidae (18 spp.) (table 1).

[1] https://www.antweb.org/
[2] http://www.antwiki.org/wiki/Welcome_to_AntWiki
[3] http://antcat.org

Akermes colombiensis Kondo & Williams, 2004 (Coccidae), *Eurhizococcus colombianus* Jakubski, 1965 (Margarodidae), *Phenacoccus solani* Ferris, 1918 (Pseudococcidae) and *Rhizoecus variabilis* Hambleton, 1978 (Rhizoecidae) are recorded for the first time for coffee. *A. colombiensis* is recorded as a host in the epigeous plant stratum of the botanical families Lauraceae, Melastomataceae and Myrtaceae (Kondo & Williams, 2004); *E. colombianus* is a hypogeous species and is recorded on roots of plant species of the families Apiaceae, Lauraceae, Rosaceae and Vitaceae (Figueroa, 1946; Jakubski, 1965; Kondo & Gómez, 2008); *P. solani* is polyphagous (Ben-Dov, 1994, 2005; Chatzidimitriou et al., 2016; Kondo et al., 2008), without precise records of the plant structure that it colonizes; Rhizoecidae are recorded on *Agave* sp. (Asparagaceae), *Musa* sp. (Musaceae) and *Wedelia fructicosa* Jacq. 1760 (Asteraceae) (García Morales et al., 2016; Kondo et al., 2008). On the other hand, *Mixorthezia neotropicalis* (Silvestri, 1924) (Ortheziidae), *Chorizococcus caribaeus* Williams & Granara by Willink, 1992, *Dysmicoccus mackenziei* Beardsley, 1959, *D. perotensis* Granara by Willink, 2009, *D. quercicolus* Granara by Willink, 2009, *D sylvarum* Williams & Granara by Willink, 1992, *Ferrisia uzinuri* Kaydan & Gullan, 2012, *Phenacoccus parvus* Morrison, 1924, *P. sisalanus* Granara by Willink, 2009, *Spilococcus mamillariae* (Bouche, 1844), *S. pressus* Ferris, 1950 (Pseudococcidae), *Coccidella ecuadorina* Konczné Benedicty & Foldi, 2004, *Rhizoecus atlanticus* (Hambleton, 1946), *R. spinipes* (Hambleton, 1946) and *R. stangei* McKenzie, 1962 (Rhizoecidae) are recorded for the first time in association with coffee, and their distribution has now expanded to Colombia.

Rhizoecus cacticans (Hambleton, 1946) and *Rhizoecus caladii* Green, 1933 were previously recorded in Colombia, associated with other hosts. *Rhizoecus cacticans* is recorded in Colombia and associated to *Agave* sp. (Asparagaceae) and *Fragaria* sp. (Rosaceae) (Posada, 1989; Williams & Granara de Willink, 1992); its record on coffee comes from Guatemala (Williams & Granara de Willink, 1992). *Rhizoecus caladii* Green, 1933, is recorded in Colombia associated with roots of *Andropogon* sp., and *Brachiaria* sp. (Poaceae), and its record on coffee comes from Surinam (Hambleton, 1976; Williams & Granara de Willink, 1992).

Table 1. List of Coccomorpha species and their associated ants to coffee roots in Colombia

Taxon	Collection		Ent. Col.	Literature information	
	Associated ants	Distribution	Distribution	Author(s)	Distribution
Coccidae					
Akermes colombiensis Kondo & Williams, 2004[1]	*Brachymyrmex* sp., *Linepithema* sp., *Pheidole biconstricta* Mayr, 1870, *Solenopsis* sp., *Tapinoma* sp., *Wasmannia auropunctata* (Roger, 1863)	An, Cal, Cau, Q			
Coccus viridis (Green, 1889)		Cal, Cau, Ri, To			

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(Continuation of table 1)

Taxon	Collection		Ent. Col.	Literature information	
	Associated ants	Distribution	Distribution	Author(s)	Distribution
Coccidae					
Saissetia coffeae (Walker, 1852)		Cal, Q, Ri			
Toumeyella coffeae Kondo, 2013	*Pheidole* sp., *Tapinoma* sp., *Wasmannia auropunctata* (Roger, 1863)	Cau, Q	VC	3, 10	NS, VC
Diaspididae					
Hemiberlesia sp.	*Linepithema* sp., *Solenopsis* complejo *geminata*	Cal			
Odonaspis sp.		An			
Margarodidae					
Eurhizococcus colombianus Jakubski, 1965[1]			Cun		
Ortheziidae					
Insignorthezia insignis (Browne, 1887)	*Acropyga exsanguis* (Wheeler, 1909)	An, Cau, Q, Ri			
Mixorthezia minima Koczné Benedicty & Kozár, 2004	*Tranopelta gilva* Mayr, 1866, *Wasmannia auropunctata* (Roger, 1863)		NS	3	NS
Mixorthezia neotropicalis (Silvestri, 1924)[1, 2]		To			
Praelongorthezia praelonga (Douglas, 1891)	*Nylanderia steinheili* (Forel, 1893), *Linepithema* sp.	Cal, Q, To			
Pseudococcidae					
Chorizococcus caribaeus Williams & Granara de Willink, 1992[1, 2]	*Brachymyrmex* sp., *Pheidole* sp., *Tranopelta gilva* Mayr, 1866	Cal			

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(Continuation of table 1)

Taxon	Collection		Ent. Col.	Literature information	
	Associated ants	Distribution	Distribution	Author(s)	Distribution
Pseudococcidae					
Dysmicoccus brevipes (Cockerell, 1893)	*Acropyga exsanguis* (Wheeler, 1909), *Acropyga* pos. *guianensis, Acropyga smithii* Forel, 1893, *Brachymyrmex patagonicus* Mayr, 1868, *Brachymyrmex* sp., *Linepithema* sp., *Pheidole biconstricta* Mayr, 1870, *Pheidole* sp., *Prionopelta* sp., *Solenopsis* complejo *geminata*, *Solenopsis* sp., *Tranopelta gilva* Mayr, 1866, *Wasmannia auropunctata* (Roger, 1863)	An, Cal, Cau, Q, Ri, To	NS, Q, VC	3, 4, 11, 13, 15	NS, VC
Dysmicoccus caribensis Granara de Willink, 2009	*Acropyga* sp., *Brachymyrmex* sp., *Leptanilloides caracola* Donosos, Vieira y Wild, 2006, *Pheidole* sp.	Cal, Hu, Q, To	NS, VC	3, 5	NS, To, VC
Dysmicoccus complejo *joannesiae*		*Cau, To*			
Dysmicoccus complejo *texensis*	*Acropyga* pos. *guianensis*, *Acropyga* sp., *Brachymyrmex pictus* Mayr, 1887, *Brachymyrmex* sp., *Cryptopone holmgreni* (Wheeler, 1925), *Hypoponera* sp., *Linepithema* sp., *Myrmelachista* sp., *Nylanderia* sp., *Nylanderia steinheili* (Forel, 1893), *Odontomachus* sp., *Pheidole biconstricta* Mayr, 1870, *Pheidole subsphaerica* Wilson, 2003, *Pheidole* sp., *Prionopelta* sp., *Solenopsis geminata* (Fabricius, 1804), *Solenopsis* sp., *Tranopelta gilva* Mayr, 1866, *Wasmannia auropunctata* (Roger, 1863)	An, Cal, Cau, Q, Ri, To	NS, VC		

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(Continuation of table 1)

Taxon	Collection		Ent. Col.	Literature information	
	Associated ants	Distribution	Distribution	Author(s)	Distribution
Pseudococcidae					
Dysmicoccus grassii (Leonardi, 1913)		Cau, Q, To	NS	11	Cau
Dysmicoccus mackenziei Beardsley, 1965[1, 2]	*Solenopsis* complejo *geminata*	Cal			
Dysmicoccus neobrevipes Beardsley, 1959				3, 15	VC
Dysmicoccus perotensis Granara de Willink, 2009[1, 2]		Cal			
Dysmicoccus quercicolus (Ferris, 1918)[1,2]	*Pheidole* sp.	Cal, Cau			
Dysmicoccus radicis (Green, 1933)[1, 2]					
Dysmicoccus sylvarum Williams & Granara de Willink, 1992[1, 2]	*Solenopsis* complejo *geminata*	Cal, Cau, To			
Dysmicoccus texensis (Tinsley, 1900)				3, 11, 15	Cal, Cau, Q, To
Dysmicoccus varius Granara de Willink, 2009	*Solenopsis* complejo *geminata*	An, Cal, Cau, To	NS	3, 5	NS
Ferrisia uzinuri Kaydan & Gullan, 2012[1, 2]		To			
Phenacoccus parvus Morrison, 1924[1, 2]	*Pheidole* sp.	An			
Phenacoccus sisalanus Granara de Willink, 2007[1, 2]	*Acropyga exsanguis* (Wheeler, 1909), *Acropyga* sp., *Acropyga smithii* Forel, 1893, *Brachymyrmex* sp., *Linepithema* sp., *Pheidole* sp., *Solenopsis* complejo *geminata*	An, Cal, Q, Ri	VC		

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(Continuation of table 1)

Taxon	Collection		Ent. Col.	Literature information	
	Associated ants	Distribution	Distribution	Author(s)	Distribution
Pseudococcidae					
Phenacoccus solani Ferris, 1918	*Brachymyrmex* sp., *Linepithema* sp., *Pheidole* sp., *Solenopsis* sp., *Tranopelta gilva* Mayr, 1866, *Wasmannia auropunctata* (Roger, 1863)	An, Cal, Cau, Q, Ri, To	VC	3	VC
Planococcus citri (Risso, 1813)				11	Cau
Planococcus complejo *citri-minor*	*Solenopsis* complejo *geminata*	Cal	Cau, VC		
Planococcus minor (Maskell, 1897)				3	VC
Pseudococcus elisae Borchsenius, 1947	*Acropyga* pos. *guianensis*, *Acropyga smithii* Forel, 1893, *Acropyga* sp., *Brachymyrmex pictus* Mayr, 1887, *Brachymyrmex* sp., *Carebara* sp., *Linepithema* sp., *Pheidole* sp., *Solenopsis* sp., *Tapinoma* sp., *Tranopelta gilva* Mayr, 1866, *Wasmannia auropunctata* (Roger, 1863)	An, Cal, Cau, Q, Ri, To	VC, NS	3	VC, NS
Pseudococcus jackbeardsleyi Gimpel & Miller, 1996	*Acropyga* sp., *Pheidole* sp., *Tranopelta gilva* Mayr, 1866, *Wasmannia auropunctata* (Roger, 1863)	Cal, Cau, Ri, Q	Q	15	¿?
Pseudococcus landoi (Balachowsky, 1959)	*Acropyga smithii* Forel, 1893, *Brachymyrmex pictus* Mayr, 1887	An, Cal, Q, Ri, To	VC	3	VC
Spilococcus mamillariae (Bouche, 1844)[1, 2]		Q			
Spilococcus pressus Ferris, 1950[1, 2]		Cau, Ri			

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(Continuation of table 1)

Taxon	Collection		Ent. Col.	Literature information	
	Associated ants	Distribution	Distribution	Author(s)	Distribution
Putoidae					
Puto antioquensis (Murillo, 1931)				4, 9, 12	An
Puto barberi (Cockerell, 1895)	*Acropyga exsanguis* (Wheeler, 1909), *Acropyga* pos. *guianensis*, *Acropyga smithii* Forel, 1893, *Acropyga* sp., *Brachymyrmex aphidicola* Forel, 1909, *Brachymyrmex pictus* Mayr, 1887, *Brachymyrmex* sp., *Carebara* sp., *Crematogaster* sp., *Cryptopone holmgreni* (Wheeler, 1925), *Cyphomyrmex* sp., *Hypoponera* sp. *Linepithema* sp., *Nylanderia* sp., *Odontomachus* sp., *Pheidole biconstricta* Mayr, 1870, *Pheidole radoszkowskii* Mayr, 1884, *Pheidole* sp., *Prionopelta* sp., *Solenopsis* sp., *Strumigenys* sp., *Tapinoma* sp., *Tranopelta gilva* Mayr, 1866, *Wasmannia auropunctata* (Roger, 1863)	An, Cal, Cas, Cau, Hu, Na, Q, Ri, Sa, To	An, B, Cal, NS, VC	3, 11, 13, 15	An, Cal, Cun, NS, Q, Ri, Sa, To, VC
Rhizoecidae					
Capitisetella migrans (Green, 1933)				8, 9, 11	¿?
Coccidella ecuadorina Konczné Benedicty & Foldi, 2004[1, 2]		Cau	Na		

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(Continuation of table 1)

Taxon	Collection		Ent. Col.	Literature information	
	Associated ants	Distribution	Distribution	Author(s)	Distribution
Rhizoecidae					
Geococcus coffeae Green, 1933	*Acropyga exsanguis* (Wheeler, 1909), *Acropyga* pos. *guianensis*, *Acropyga smithii* Forel, 1893, *Acropyga* sp., *Azteca* sp., *Brachymyrmex aphidicola* Forel, 1909, *Brachymyrmex pictus* Mayr, 1887, *Brachymyrmex* sp., *Carebara* sp., *Hypoponera* sp., *Leptanilloides caracola* Donoso, Vieira y Wild, 2006, *Linepithema* sp., *Odontomachus* sp., *Pheidole radoszkowskii* Mayr, 1884, *Pheidole* sp., *Prionopelta* sp., *Pseudomyrmex* sp., *Solenopsis geminata* (Fabricius, 1804), *Solenopsis* sp., *Strumigenys* sp., *Tapinoma* sp., *Tranopelta gilva* Mayr, 1866, *Wasmannia auropunctata* (Roger, 1863)	An, Cal, Cau, Q, Ri, To	NS, VC	3, 9, 11, 15, 16	Cau, NS, To, VC
Neochavesia caldasiae (Balachowsky, 1957)	*Acropyga exsanguis* (Wheeler, 1909), *Acropyga smithii* Forel, 1893, *Brachymyrmex aphidicola* Forel, 1909, *Brachymyrmex patagonicus* Mayr, 1868, *Pheidole radoszkowskii* Mayr, 1884, *Solenopsis* sp.	An, Cal, Ri	VC	1, 3, 4, 9, 11, 13, 15, 16	VC
Neochavesia eversi (Beardsley, 1970)				2, 11, 15, 16	¿?
Neochavesia trinidadensis (Beardsley, 1970)				11, 16	¿?

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(Continuation of table 1)

Taxon	Collection		Ent. Col.	Literature information	
	Associated ants	Distribution	Distribution	Author(s)	Distribution
Rhizoecidae					
Pseudorhizoecus bari Caballero & Ramos-Portilla 2018			NS	3	NS
Pseudorhizoecus proximus Green, 1933				8, 11, 16	¿?
Rhizoecus americanus (Hambleton, 1946)	*Acropyga smithii* Forel, 1893, *Pheidole* sp.	An, Cau, Q, Ri	NS, VC	3, 11, 15, 16	VC
Rhizoecus arabicus (Hambleton, 1976)	*Acropyga smithii* Forel, 1893, *Acropyga* sp., *Azteca* sp., *Brachymyrmex aphidicola* Forel, 1909, *Brachymyrmex pictus* Mayr, 1887, *Linepithema* sp., *Pheidole biconstricta* Mayr, 1870, *Pheidole* sp., *Pseudomyrmex* sp., *Solenopsis* sp.	An, Cal, Cau, Q, Ri, To		7, 11, 16	Cal
Rhizoecus atlanticus (Hambleton, 1946)[1, 2]		Ri			
Rhizoecus cacticans (Hambleton, 1946)	*Brachymyrmex pictus* Mayr, 1887, *Carebara* sp., *Linepithema* sp., *Pheidole* sp., *Pseudomyrmex* sp., *Tranopelta gilva* Mayr, 1866	An, Cal, Cau, Ri, To	Na		
Rhizoecus caladii Green, 1933		An	Cal		
Rhizoecus coffeae Laing, 1925			NS	3, 4, 6, 11, 13	NS

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(Continuation of table 1)

Taxon	Collection		Ent. Col.	Literature information	
	Associated ants	Distribution	Distribution	Author(s)	Distribution
Rhizoecidae					
Rhizoecus colombiensis Ramos & Caballero, 2016	*Acropyga exsanguis* (Wheeler, 1909), *Azteca* sp., *Brachymyrmex aphidicola* Forel, 1909, *Brachymyrmex patagonicus* Mayr, 1868, *Brachymyrmex pictus* Mayr, 1887, *Brachymyrmex* sp., *Hypoponera* sp., *Linepithema* sp., *Odontomachus* sp., *Pheidole biconstricta* Mayr, 1870, *Pheidole radoszkowskii* Mayr, 1884, *Pheidole* sp., *Prionopelta* sp., *Solenopsis* sp., *Tranopelta gilva* Mayr, 1866, *Wasmannia auropunctata* (Roger, 1863)	An, Cal, Cau, Q, Ri, To	VC	3, 14	Cal, VC
Rhizoecus compotor Williams & Granara de Willink, 1992		Ri		16	Cal
Rhizoecus mayanus (Hambleton, 1946)	*Acropyga* sp., *Azteca* sp., *Solenopsis* sp.	Cal		11	Cal
Rhizoecus setosus (Hambleton, 1946)	*Solenopsis* sp., *Wasmannia auropunctata* (Roger, 1863)	Cau, Ri, To	Cun	11, 13	To
Rhizoecus spinipes (Hambleton, 1946)[1,2]	*Acropyga exsanguis* (Wheeler, 1909), *Acropyga smithii* Forel, 1893, *Acropyga* sp., *Brachymyrmex* sp., *Hypoponera* sp., *Odontomachus* sp., *Pheidole radoszkowskii* Mayr, 1884, *Pheidole* sp., *Solenopsis* sp., *Wasmannia auropunctata* (Roger, 1863)	An, Cau, Q, Ri, To			

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(Continuation of table 1)

Taxon	Collection		Ent. Col.	Literature information	
	Associated ants	Distribution	Distribution	Author(s)	Distribution
Rhizoecidae					
Rhizoecus stangei McKenzie, 1962[1, 2]		To			
Rhizoecus variabilis Hambleton, 1978[1]		An, Q, To			
Ripersiella andensis (Hambleton, 1946)	*Acropyga exsanguis* (Wheeler, 1909), *Acropyga smithii* Forel, 1893, *Brachymyrmex patagonicus* Mayr, 1868, *Brachymyrmex pictus* Mayr, 1887, *Brachymyrmex* sp., *Hypoponera* sp., *Odontomachus* sp., *Pheidole radoszkowskii* Mayr, 1884, *Pheidole* sp., *Solenopsis* sp., *Wasmannia auropunctata* (Roger, 1863)	An, Cal, Q, Ri, To	Cal, VC	3, 6, 13	An, Cun, VC

Note: Information is presented discriminated by taxon and the source of the specimen collection (field collection, entomological collection and literature). For those specimens collected, the associated species and the distribution by departments are indicated. For the samples found in entomological collections, the departments where they were collected are shown. For the species listed from the literature, the references and geographical location indicated in the publication are cited.
Abbreviations: (Ent. Col.) entomological collections; Colombian departments: (An) Antioquia, (B) Boyacá, (Cal) Caldas, (Cas) Casanare, (Cau) Cauca, (Cun) Cundinamarca, (Hu) Huila, (Na) Nariño, (NS) Norte de Santander, (Q) Quindío, (Ri) Risaralda, (Sa) Santander, (To) Tolima, (VC) Valle del Cauca. Cited authors: (1) Balachowsky (1957); (2) Beardsley (1970); (3) Caballero et al. (2018); (4) Gallego & Vélez (1992); (5) Granara de Willink (2009); (6) Hambleton (1946); (7) Hambleton (1976); (8) Hambleton (1977); (9) Kondo (2001); (10) Kondo (2013); (11) Kondo et al. (2008); (12) Murillo (1931); (13) Posada (1989); (14) Ramos-Portilla and Caballero (2016); (15) Villegas et al. (2009); (16) Williams and Granara de Willink (1992). Superscript 1 = New record for *Coffea arabica* and 2 = New record for Colombia
Source: Elaborated by the authors

On the other hand, the coccids *Coccus viridis* (Green, 1889) and *Saissetia coffeae* (Walker, 1852), and the ortheziids *Insignorthezia insignis* (Browne, 1887) and *Praelongorthezia praelonga* (Douglas, 1891) have been previously recorded on coffee in Colombia, but only in the aerial parts of the plant (Ben-Dov, 1994; Kondo, 2001; Posada, 1989). This is the first record of these ortheziids on the roots of its hosts in Colombia. Further, De Lotto (1965) recorded *S. coffeae* associated with coffee roots in Kenya.

Regarding the family Diaspididae, specimens belonging to the genera *Odonaspis* (Leonardi, 1897) and *Hemiberlesia* (Cockerell, 1897) were found. Specimens of the genus *Odonaspis* are recorded exclusively associated with roots of host plants distributed in ten families (mainly Poaceae), in which Rubiaceae is not included (Aono, 2009; Ben-Dov, 1988). This is the first record of *Odonaspis* in association with *Coffeae arabica*, specifically with the Geisha variety. In contrast, *Hemiberlesia* is a genus of which there is no record of hypogeal habit and with the information reported in this study, knowledge on the biology of the genus is broadened.

Correction of previous identifications

Specimens identified by Caballero et al. (2018) such as *Dysmicoccus radicis* (Green, 1933), were corrected to *Dysmicoccus grassii* (Leonardi, 1913); for this reason, the distribution of *D. radicis* is restricted to Quindío and Risaralda, meanwhile the distribution of *D. grassii* includes the Departments of Cauca and Norte de Santander. Also, specimens identified as *Dysmicoccus mackenziei* Beardsley, 1959, by these same authors, were corrected to *D. varius*; in this sense, the distribution of *D. mackenziei* is restricted to the department of Caldas.

Scale insect-ant relation

Trophobiosis between ants and scale insects is a phenomenon in which the ant feeds on the sugar excretion of the scale or of the flake itself (Gullan, 1997; Ramos & Serna, 2004). Given the food potential of a population of scale insects for an ant colony, it is understandable that for millions of years this last group of insects increased the survival probabilities of scale insects, transporting them and protecting them from natural enemies (Johnson et al., 2001).

This study shows an important advance in terms of records of new associations between scale insects and ants, recording 170 associations for Colombia (table 1). In Colombia, *Acropyga fuhrmanni* (formerly *Rhyzomyrma fuhrmanni*) is recorded as the "Ant of Amagá" or *Hormiga de Amagá* (in Spanish), associated with the scale insect *Neochavesia caldasiae* (formerly *Eumyrmococcus* sp.) (Serna, Mera-Rodríguez, Ramírez, & Gaigl, in press; Villegas et al., 2009). *Acropyga fuhrmanni* was not found in any of the 32 morphospecies of ants collected in the nine departments visited. In contrast, the ants, *A. exhanguis* and *A.* nr. *guianensis*, were found. Considering the volume of samples (541), these results allow us to conclude that the "Ant of Amagá" could correspond to one of these species and not to *A. fuhrmanni*. There are also two records of *P. proximus* and *R. caladii* with "*Acropyga parameibensis*" (sic) according to Williams (1998), but this species is a junior synonym of *A. exsanguis*.

Agronomic context

Figure 1 shows the distribution of the scale insects associated with coffee roots, based on the study of specimens from field collections, review of materials preserved in entomological collections and a literature review.

Gil et al. (2015), Villegas et al. (2009) and Villegas-García & Benavides-Machado (2011) mention that the most important species for Colombian coffee farming, due to the economic damage they cause, are *D. brevipes*, *D. texensis*/*D. neobrevipes* (in this study referenced as the *Dysmicoccus* complex *texensis*), *G. coffeae*, *N. caldasiae*, *P. jackbeardsleyi* and *Pu. barberi*. Of these species, those with the greatest geographic distribution are *Pu. barberi* (14 departments), *G. coffeae* (9 departments), *D. brevipes* and *D.* complex *texensis* (7 departments each).

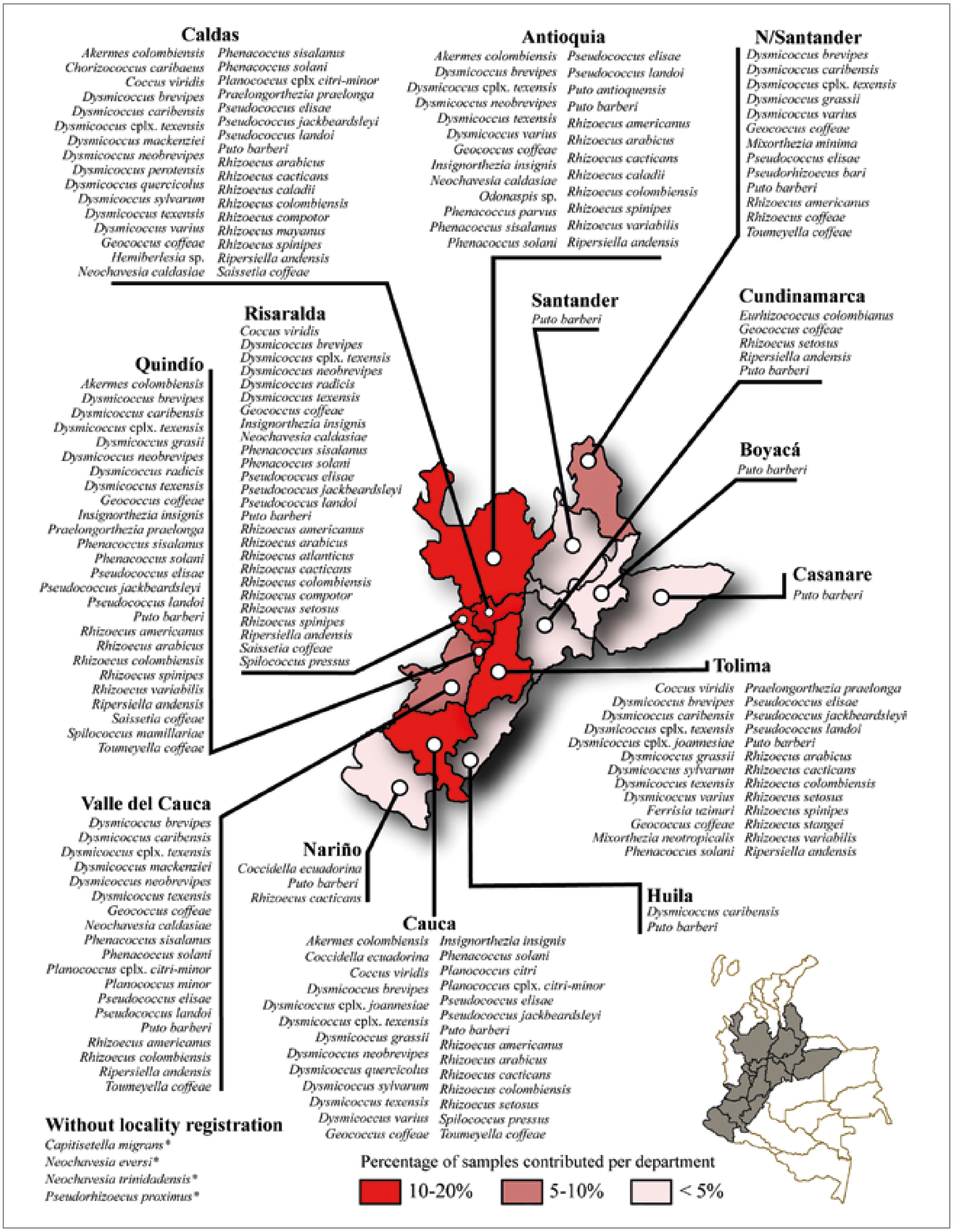

Figure 1. Map of Colombia showing the distribution of scale insects associated with coffee roots and percentage of samples contributed by each of the 14 studied departments. Names with an asterisk (*) indicate that there is only a literature record.
Source: Elaborated by the authors

Neochavesia caldasiae and *Ps. jackbeardsleyi* were collected only in three departments. *Geococcus coffeae* is the species most frequently found in the 541 samples analyzed, appearing in 37.9 % of the samples, followed by *Pu. barberi* (33.3 %) and *D.* complex *texensis* (24 %). *Dysmicoccus brevipes* (5.9 %), *N. caldasiae* (2.4 %) and *P. jackbeardsleyi* (0.7 %) show low occurrence.

In contrast, there is a high occurrence of species not mentioned in the literature as harmful to coffee, such as *R. colombiensis* (15.2 %), *P. elisae* (9.6 %) and *R. arabicus* (8.9 %); these three species, in terms of distribution, are found in six, seven and five departments respectively.

In this context, according to the distribution and frequency of occurrence, data provided in this study, the potentially most important species are *Puto barberi*, *Geococcus coffeae*, *Dysmicoccus* complex *texensis*, *Rhizoecus colombiensis* and *Pseudococcus elisae*.

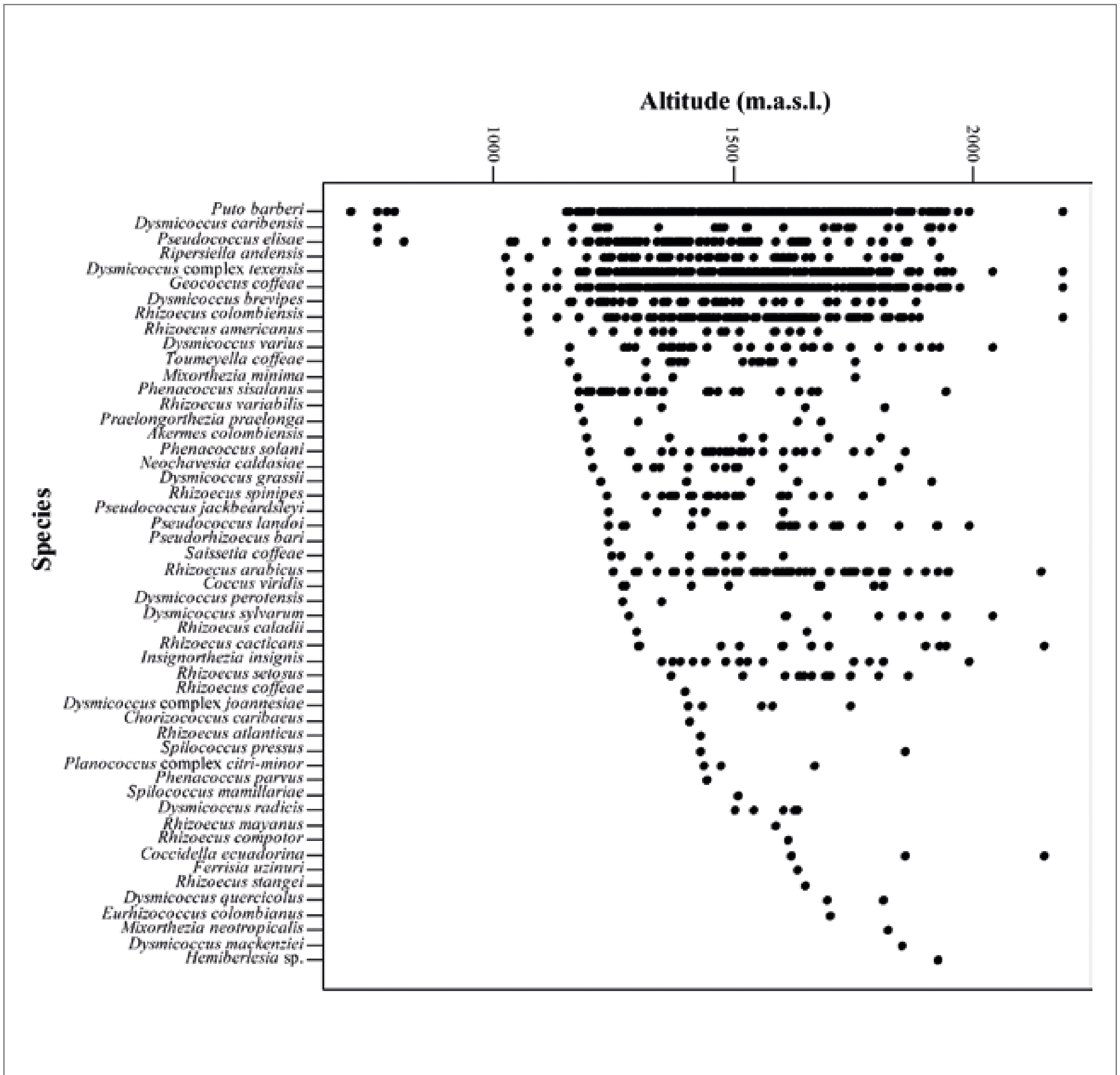

Figure 2. Altimetry height interval of scale insect species associated with coffee roots in Colombia.
Source: Elaborated by the authors

This is supported by the altitudinal distribution for each species (figure 2). The five species mentioned above have the highest altitudinal range of the entire group of species found, covering about 1,200 m of elevation. *Puto barberi* has the largest distribution range (from 700 to 2.185 m), *P. elisae* occurs between 760 and 1,900 m.a.s.l., meanwhile *D.* complex *texensis*, *G. coffeae* and *R. colombiensis* occur between 1,000 and 2,200 m.a.s.l. Thus, three groups are then presented: the first is *Puto barberi* that is the species with the highest altitudinal adaptation capacity, allowing it to colonize coffee crops in warm, temperate and cold climates. The second is *P. elisae* that colonizes established crops in warm and temperate climates. In the third group, *Dysmicoccus* complex *texensis*, *G. coffeae* and *R. colombiensis* show the opposite behavior, as they colonize established crops in temperate and cold climates. It is worth noting that *D. caribensis*, although it is not a species with high recurrence in samples (0.7 %), has an altitudinal range as wide as *P. elisae*, and therefore, it must be a species that should be considered within the monitoring of scale insects in coffee roots.

Another ecological criterion that is valuable in the agronomical aspect is the scale insect-ant relationship, given that it is the most common and effective non-anthropogenic form of dispersion of scale insects (Gullan, 1997; Johnson et al., 2001). The five scale insect species proposed here as a focus of attention and phytosanitary surveillance have multiple trophobiotic associations, i.e. *Puto barberi* is associated, at least, with 24 ant species; *Geococcus coffeae* with 23; *Dysmicoccus* complex *texensis* with 19; *Rhizoecus colombiensis* with 16, and *Pseudococcus* elisae with 12 (table 1, column 2 "Associated ants"). In this regard, it should be noted that *D. brevipes* is associated with at least 13 ant species.

Conclusions

This is the first study focused exclusively on the diversity of Coccomorpha associated with coffee roots in Colombia, in addition to considering its trophobiosis with ants. An advance in the taxonomic knowledge of scale insects is generated through new geographic and host records. The new information presented in this manuscript increases the records of species associated with coffee roots from 32 to 61 species, and the scale insects associated with coffee in Colombia in general (45 species). It is important, however, to extend the sampling to biogeographical provinces where research has not been carried out, such as in the north and in the south of the country. Considering the diversity of agroecosystems in the regions where no samples were taken and of which there is no material conserved in entomological collections, the diversity of scale insect species that remains to be recorded associated with coffee may be much higher. In this sense, it is recommended to continue with the sample collection process throughout the country to deepen the knowledge of the diversity of scale insects and their associated ants.

It was observed that the group of scale insects associated with roots have been little studied and lack physical material (curated specimens conserved in entomological collections), that can be used in morphology, taxonomy and biodiversity studies. The contribution of cured material generated by this study aims at contributing with physical evidence of the fauna "megadiversity" that the country harbors.

The taxonomic results of this study have a future impact on the phytosanitary management of coffee crops. On one hand, *Dysmicoccus* complex *texensis*, *Geococcus coffeae*, *Pseudococcus elisae*, *Puto barberi* and *Rhizoecus colombiensis* are defined as the species with the greatest potential to become pests. Therefore, it is recommended to carry out studies in which it should be stated if these are real pests, and if they are, define the levels of damage and the corresponding economic thresholds.

In this same line and from a chemical control perspective, updating the list of species associated with coffee requires reevaluating the options that exist for the chemical management of these species. Currently, there are only three molecules approved by ICA to control mealybugs (Pseudococcidae and Putoidae) on coffee: Thiamethoxam (neonicotinoid), Lambdacialotrine (pyrethroid) and Chlorpyrifos (organophosphate) (Instituto Colombiano Agropecuario [ICA], 2018). It is also recommended to begin with insecticide efficacy trials to expand the record of target species that include a larger part of the group of species and families that were listed in this study.

On the other hand, it has been verified that the occurrence and frequency of occurrence of the scale insect species is dynamic and changing, for which continuous sampling and taxonomic identification are necessary to make viable the integrated management plans of scale insects, and additionally, it is shown that within the population dynamics of scale insects, many more species than were expected just 10 years ago were involved.

In the current investigation no ants of the species *Acropyga fuhrmanni* and *A. goeldii* were found. Taking into account the extensive sampling carried out in the coffee growing areas of Colombia, it can be considered that the presence of these two species for coffee in Colombia is doubtful. On the other hand, the species *A. exsanguis*, *A. smithii* and *A*. close to *guianensis* show a wide distribution in the coffee growing areas of Colombia. Likewise, the species *Linepithema angulatum* (Emery, 1894), *Brachymyrmex aphidicola* Forel, 1909, *B. patagonicus* Mayr, 1868, *B. pictus* Mayr, 1887, *Pheidole biconstricta* Mayr, 1870 and *P. radoszkowskii* Mayr, 1884, are widely distributed in Colombia, with facultative associations with Hemiptera (Serna et al., in press). The information obtained in the current study could be considered as a starting point for the agronomic management of ants and provides basic information for further investigations aimed at the insect scale-ant interaction.

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