

Ants associated with dry forest fragments and urban environments in Santa Marta, Colombia

Lina María Ramos Ortega^{*}, Hubert Sierra, Johan D. Roncallo, Roberto J. Guerrero

Universidad del Magdalena Santa Marta, Magdalena 470004, Colombia * **Corresponding author:** Lina María Ramos Ortega, linamariaramosortega@gmail.com

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https://creativecommons.org/licenses/by/4.0/ **Abstract:** A publicly accessible database of ants associated with dry forest fragments and urban environments in Santa Marta, Colombia, is presented through the Colombian Biodiversity Information System (SIB). Capture methods included the installation of pitfall traps, protein and carbohydrate baits, extraction by the Winkler method of ants associated with leaf litter and manual collection of ants foraging on tree vegetation. The dataset contains 54,323 records, distributed in seven subfamilies, 42 genera, 88 species and nine morphospecies. This list is a tool to encourage the study and conservation of ants in urban areas.

Keywords: biodiversity conservation; urban ecology; exotic species; Formicidae; ecological patterns

1. Introduction

Due to the accelerated expansion of urban areas, one of the main environmental challenges is to understand how this process affects biodiversity [1]. Although urbanization is one of the main causes of loss of native species, the high spatial heterogeneity in urban habitat, produced by different land uses, can result in some cases in increases in diversity at the local level [2]. Cities, with their high degree of landscape transformation can host a considerable amount of a region's species, as well as promote conservation scenarios and spaces for environmental education [3].

Ants constitute one of the most conspicuous insect groups in terrestrial ecosystems and are commonly associated with urban environments where they successfully inhabit, being found in a wide variety of sites, ranging from green areas, to household spaces (e.g., kitchens) and hospitals [4]. Among the reasons for the success of ants in cities are the wide variety of food resources they use [5], the ability to nest in compact soils and surfaces with gray cover [6], and a high tolerance to heat stress [7].

In general, cities are highly heterogeneous spaces, where gradients can be generated between urbanized sites and the set of green areas (e.g., forest fragments, parks, vacant lots, among others). Thus, the effect of urbanization on the ant community seems to be the result of the spatial context and the ability of native species to adapt to the new habitat conditions imposed by the urban environment. The city of Santa Marta is no stranger to this heterogeneity, being immersed in a context of tropical dry forest, which is considered one of the most threatened ecosystems and with a high degree of degradation in Colombia, whose distribution in most cases is in the form of fragments or patches [8]. Studies of the myrmecofauna of the dry forest in Colombia have focused mainly on natural areas [9], leaving information gaps in urban areas.

The research that resulted in the data set presented here aimed to understand the

spatial and temporal dynamics of the taxonomic diversity of ants in the urban environment of Santa Marta, as well as the impact of the transformation of the natural landscape on the diversity of this group of insects [10]. This study covers a broad spatial and temporal scale at the urban level. In addition, the use of different methods of capturing ants is maximized to obtain a reliable estimate of the inventory of this group. Therefore, potentially relevant information is made available for the identification of ecological patterns associated with urban areas of the city of Santa Marta, as well as to promote the conservation of ants in these environments.

2. Project data

Title. Diversity of ants in urban environments of the city of Santa Marta (Colombia).

Name. Lina María Ramos Ortega

Funding sources. The project was financed with resources from installed capacity through the Vice Rector's Office for Research of the Universidad del Magdalena.

Description of the study area. The collection of information was developed in three types of environments within the urban and peri-urban area of the city of Santa Marta: district parks, theme parks and natural areas (dry forest fragments). Four samplings were carried out between the months of October-December 2019 and January 2020, trying to cover months of high and low precipitation.

Description of the project. The project was oriented to know the spatial and temporal dynamics of ant diversity in the urban environment of the city of Santa Marta, as well as the impact of the transformation of the landscape on the diversity of this group of insects. Another important aspect of this evaluation was to establish whether the green areas of the city (district and theme parks) are spaces that favor the maintenance and conservation of local diversity.

2.1. Taxonomic coverage

Description. The data set contains 54,323 records of the family Formicidae (Insecta: Hymenoptera) corresponding to 52,946 specimens, distributed in seven subfamilies, 42 genera, 88 species and nine morphospecies, from the samplings carried out during the development of the project "Diversity of ants in urban environments of the city of Santa Marta".

2.2. Categories

Subfamily. Dolichoderinae, Dorylinae, Ectatomminae, Formicinae, Myrmicinae, Ponerinae, Pseudomyrmecinae.

Genus. Acromyrmex Anochetus, Azteca, Brachymyrmex Camponotus, Cardiocondyla, Cephalotes, Crematogaster, Cyphomyrmex, Dolichoderus, Dorymyrmex, Ectatomma, Forelius, Hypoponera, Kalathomyrmex, Labidus, Leptogenys, Megalomyrmex, Monomorium, Mycetomoellerius, Myrmicocrypta, Neivamyrmex, Nesomyrmex, Nylanderia, Odontomachus, Pachycondyla, Paratrachymyrmex, Paratrechina, Pheidole, Platythyrea, Pogonomyrmex, Pseudomyrmex, Rogeria, Sericomyrmex, Solenopsis, Strumigenys, Tapinoma, Temnothorax, Tetramorium, Thaumatomyrmex, Trichomyrmex, Wasmannia.

Species. Acromyrmex octospinosus, Acromyrmex santschii, Anochetus inermis, Brachymyrmex cordemoyi, Brachymyrmex minutus, Camponotus blandus pronotalis, Camponotus zonatus, Camponotus coruscus, Camponotus lindigi, Cardiocondyla emery, Cephalotes femoralis, Cephalotes minutus, Cephalotes pellans, Cephalotes pusillus, Crematogaster abstinens, Crematogaster crinosa, Crematogaster distans, Crematogaster limata, Crematogaster obscurata, Crematogaster rochai, Crematogaster torosa, Cyphomyrmex flavidus, Cyphomyrmex rimosus, Dolichoderus diversus, Dorymyrmex biconis, Dorymyrmex tuberosus, Ectatomma ruidum, Ectatomma tuberculatum, Forelius damiani, Hypoponera clavatula, Hypoponera opacior, Kalathomyrmex emery, Labidus coecus, Leptogenys pubiceps, Leptogenys ritae, Megalomyrmex silvestrii, Monomorium pharaonis, Mycetomoellerius urichii, Mycetomoellerius zeteki, Myrmicocrypta buenzlii, Neivamyrmex iridescens, Nylanderia nodifera, Odontomachus bauri, Odontomachus ruginodis, Pachycondyla harpax, Paratrachymyrmex cornetzi, Paratrachymyrmex irmgardae, Paratrechina longicornis, Pheidole distorta, Pheidole fallax, Pheidole guajirana, Pheidole impressa, Pheidole indica, Pheidole inversa, Pheidole leptina, Pheidole praeusta, Pheidole radowszkowskii, Pheidole subarmata, Pheidole urbana, Platythyrea pilosula, Pogonomyrmex mayri, Pseudomyrmex boopis, Pseudomyrmex curacaensis, Pseudomyrmex eduardi, Pseudomyrmex elongatus, Pseudomyrmex gracilis, Pseudomyrmex simplex, Pseudomyrmex urbanus, Pseudomyrmex venustus, Rogeria curvipubens, Rogeria foreli, Sericomyrmex bondari, Solenopsis altinodis, Solenopsis bicolor, Solenopsis geminata, Solenopsis picea, Solenopsis whitfordi, Strumigenys dyseides, Strumigenys eggersi, Strumigenys elongata, Strumigenys spatula, Strumigenys tanimastax, Tapinoma melanocephalum, Temnothorax subditivus, Tetramorium lanuginosum, Tetramorium simillimum, Trichomyrmex destructor, Wasmannia auropunctata.

2.3. Geographical coverage

Description. The records come from the sampling of eight district parks (P. Simón Bolívar, P. Avenida del Río, P. Gaira, P. de la Vida, P. Manzanares, P. Equidad, P. Los Almendros and P. Los Trupillos), four theme parks (Universidad del Magdalena Campus, Quinta de San Pedro Alejandrino Botanical Garden, Teyuna Recreational Center and Parque del Agua) and four natural areas (Parcela Bosque Seco Universidad del Magdalena, Fragmento de Bosque Seco Quinta de San Pedro Alejandrino, Reserva La Iguana Verde and Quebrada Seca).

Coordinates. 11°10'11.17" N and 11°14'45.17" N latitude; 74°8'32.1" W and 74°13'22.12" W longitude. The records cover an altitudinal range between 1 and 100 m asl.

2.4. Temporary coverage

9 October, 2019, 23 January 2020.

2.5. Collection data

Name of the collection. Biological Collections Center of the University of Magdalena.

Collection Identifier. National Registry of Collections: 207

Parental collection identifier. CBUMAG: ENT Method of preservation of specimens. Complete specimen in Ethanol

3. Materials and methods

Study area the city of Santa Marta, in northern Colombia, has a total area of 2393.35 km², of which 55.10 km² correspond to the urban area [11]. The average annual temperature is 27 °C and the average annual precipitation is 608.8 mm, with a unimodal rainfall regime [12]. The predominant vegetation cover in these areas is characterized by forests and scrublands of isomegathermal floor (high and constant temperatures throughout the year), with pronounced xeromorphic characters due to the longer rainless season, reaching nine months per year [13,14]. According to the physiognomic and floristic characteristics, these plant formations are defined as those of a tropical subxerophytic zonobiome [14]. The data collection sites and some of their main characteristics are presented in **Table 1**.

Table 1. Description of the urban environments monitored for the study of ants associated with dry forest fragments and urban environments in Santa Marta, Colombia.

| Environment | Coordinates | Area (ha) | Features |
|-----------------------------------------------------------|------------------------------------|-----------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| P. Simon Bolivar | 11°14741.8567/N 74°12'48.959" W | 1.0 | The district parks are characterized by their open access and variable sur- face area. The plant species present there are a combination of native spe- cies (Tabebuia rosea, Prosopis juliflora, Ceiba pentandra, Enterolobium cyclocarpum, among others) and introduced species (Mangifera indica, Azadirachta indica, Terminalia cata-ppa, Tamarindus indica, among oth- ers); generally exhibiting a low plant richness (10 species on average). They also have large concrete surfaces around them (benches, planters, etc.). |
| P. Avenida del Rio | 11°13′52.68" N 74°1Г8.843" W | 0.1 | |
| WP. of Gaira | 11°11′23.28" N 74°13'22.115" W | 0.4 | |
| P. de la Vida | 11°12/43.2" N 74°1Г20.615" W | 0.8 | |
| P. de Manzanares | 11°13755.8847/N 74°12′38.123″ W | 0.9 | |
| Equity P. | 11°13/27.408///N 74°1Г50.82″ | 0.9 | |
| P. Los Almendros | 11°14745.1687/N 74°11′42.827″ W | 0.1 | |
| P. Los Trupillos | 11°13742.9967/N 74°10'15.959" W | 1.3 | |
| Campus Unimagdalena | 11°13735.47/N 74°m0.824″ W | 11 | Access to the theme parks is more restricted, with a larger area than in the district parks. The plant species are also a combination of native species (Prosopis juliflora, Ceiba pentandra, Quadrella odoratissima, Enterolo- bium cyclocarpum, among others) and introduced species (Mangifera in- dica, Azadirachta indica, Delonix regia, Spathodea campanulata, among others), although with a greater number of species (18 species on average). They have less concrete surface around them, since they promote positive interaction with the surrounding nature. These parks have recreational, cultural, and environmental education purposes. |
| Quinta de San Pedro Alejandrino Botanical Garden | 11°13741.6287/N 74°10'41.376" W | 13 | |
| Center Recreational Teyuna | 11°10757.6487/N 74°13'0.191" W | 11.5 | |
| Water P. | 11°13723.5927/N 74°10'28.523" W | 3.3 | |
| Parcela Bosque Seco Unimagdalena | 11°13716.0687/N 74°1Γ10.967″ W | 2.8 | They correspond to fragments of dry forest located within the urban and peri-urban areas of the city and in all cases, these areas are subject to con- |
| Parcela Bosque Seco Quinta de San Pedro Alejandrino | 11°13'42.06" N 74°10'31.259" W | 22.0 | servation, research and environmental education. The plant species present there are characteristic of the dry forest with a plant richness between 20– 50 species (Albizia niopoides, Cordia alba, Acacia polyphylla, Pereskia guamacho, among others) [15]. |
| La Iguana Reserve Green | 11°10'11.172" N 74°10'29.639" W | 19.0 | |
| Quebrada Seca | 11°13′9.624″ N 74°8′32.1″ | 6.0 | |

Sampling description. Four samplings were conducted between the months of October-November 2019 (rainy season) and December 2019–January 2020 (dry season). The choice of capture methods and number of sampling units was made based on the recommendations established in [16]. In the city parks, the collection of ants was done through two types of baits: tuna (protein source; BaP) and a mixture of cookie and condensed milk (carbohydrate source; BaC). Additionally, manual collection of ants foraging or inhabiting mainly arboreal vegetation (C) was performed. In the natural areas, in addition to the methods described above, pitfall traps (Pf) were installed and leaf litter was collected for ant separation using Winkler bags (mW).

4. Quality control

Due to the variety of urban environments monitored, as well as the methods used to capture the ants, codes and collection labels were established to clearly differentiate the environment (PD, PT, ZN) and method (BaC, BaP, Pf, mW, C); in this way, the probability of confusion of the samples in the field and during the process of separation, mounting and identification in the laboratory was minimized. Taxonomic identification was done to the lowest possible level, for which specialized taxonomic keys were used. Similarly, comparisons were made with reference collections deposited at CBUMAG. The geographic information of each record was associated with each trap or sampling point where the specimens were collected, which were georeferenced with a Garmin[®] 62 GPSmap. Each sample is deposited in CBUMAG with its respective catalog number.

Step-by-step description of the methodology

- Each site was georeferenced before the start of field activities. In the natural environments, the delimitation of the three 100 m transects was done with the help of a plastic rope, which was marked every 10 m and in each of these marks a pitfall trap (7 oz or 207 mL plastic cups) was placed, filling them up to 1/3 of their volume with 96% alcohol; 30 traps were installed in each natural zone, which were left to act for 72 h.
- 2) Leaf litter was collected within the area delimited by the transects. Quadrants of 1 m² were established and the plant material contained therein was passed through a sifter to discard the coarser fractions. The fine material was deposited in cloth bags and taken to the laboratory for the final extraction process in Winkler bags. The action time of the traps was 48 h.
- 3) The installation of the baits was done in the three urban environments considered in the study. Protein (tuna) and carbohydrate (cookie + condensed milk) baits were placed on pieces of cardboard (10 × 10 cm) and left on the ground surface with an action time of 30 min. In the district and theme parks, the baits were placed in the planter areas. While, in the natural areas, the baits were installed along the delimited transects, covering them proportionally. At each site, 15 protein baits and 15 carbohydrate baits were installed. The ants present in the baits were deposited in Whirl-Pak bags or plastic vials, each labeled considering the number and type of bait. All samples were preserved in 96% alcohol and transported to the laboratory for cleaning and separation.

- 4) The collection of ants that foraged mainly on the arboreal vegetation was done manually. At each site, the vegetation was visually inspected for one hour and all the collected material was deposited in plastic vials previously labeled and filled with 96% alcohol.
- 5) The material collected in the field was subjected to a cleaning process to eliminate plant material and sediments in the case of samples obtained by pitfall and Winkler bag methods, and tuna and cracker remains in the case of baits. The samples were transferred to plastic vials and preserved in 96% alcohol, maintaining in all cases the labels designated in the field.
- 6) To facilitate the taxonomic identification of the ants, dry mounts of the specimens were made using a Nikon SMZ745 stereoscope. The taxonomic keys used corresponded to the works of [17–19] and the electronic resource AntWeb Version 8.56. The specimens were deposited in the Biological Collections of the Universidad del Magdalena-CBUMAG.

5. Results

Description of the data set

The myrmecofauna collected in the urban environments of Santa Marta represent about 64% of the subfamilies recorded for the Neotropics and Colombia, as well as 40% of the genera in Colombia [20]. Of the 97 taxa determined, 88 were identified to species level, corresponding to 8% of the current records for the country [20,21]. The subfamilies Myrmicinae, Ponerinae, Formicinae and Pseudomyrmecinae contributed about 88% of the ant richness, a trend that remained relatively constant among the urban environments evaluated (**Figure 1**). The genera Pheidole, Cephalotes, Crematogaster, Pseudomyrmex, Camponotus, Solenopsis and Strumygenys contributed about 50% of the species recorded. Dorymyrmex, Ectatomma, Odontomachus, among other genera, had between 2 and 3 species (**Figure 2**); while a total of 12 genera recorded only one species. The species with the highest capture frequencies corresponded to Ectatomma ruidum (44%), Dorymyrmex biconis (19%), Pheidole indica (13%), Pheidole fallax (12%) and Trichomyrmex destructor (10%).



Figure 1. Number of ant species by subfamily in dry forest fragments and urban environments of Santa Marta, Colombia.



Figure 2. Number of ant species by genus in dry forest fragments and urban environments of Santa Marta, Colombia. The category "Other genera" contains all those generic taxa with only one species.

In this study, more than 90% of the taxa were identified at a specific level, allowing the recognition of new ant records for the country within the genera Hypoponera, Myrmicocrypta, Solenopsis and Strumigenys. Similarly, the presence of exotic ants was identified, some of which are widely distributed in Colombia, such as Paratrechina longicornis, Monomorium pharaonis and Tapinoma melanocephalum; while the species Pheidole indica, Trichomyrmex destructor, Tetramorium lanuginosum, Tetramorium simillimum and Cardiocondyla emeryi have been recorded in a few localities in the country [22].

Because of the variety of microhabitats in which ants can establish themselves, the choice of trapping methods is a critical aspect of diversity studies and ecology in general. For the data set presented here, the three trapping methods employed provided both unique and complementary information on the inventory of ants associated with the urban environment. The pitfall (Pf) and manual collection (CM) methods yielded the highest number of species, followed by the method for leaf litter ants (mW) (**Table 2**). Regarding the baits, the protein bait was the one that captured the highest richness. On the other hand, the number of species that were collected with only one of the methods corresponds to 24% of the total richness of the study, which highlights the importance of using varied capture methods that cover different microhabitats in the evaluated environments. The most frequent species among the methods correspond to Ectatomma ruidum, Crematogaster crinosa, Acromyrmex santschii, Solenopsis bicolor, Pheidole guajirana, among others (**Table 2**).

| Capture method | Wealth | No. exclusive species | Frequent species |
|----------------------------|--------|------------------------------------------|------------------------------------------------------------------------------------------------------------------------------|
| Bait carbohydrate (BaC) | rate 0 | | Ectatomma ruidum, Dorymyrmex biconis, |
| Bait protein (BaP) | | Pheidole indica, Irichomyrmex destructor | |
| Manual collection (CM) | | | Crematogaster crinosa, Brachymyrmex minutus, Camponotus lindi- gi, Paratrechina longicornis |
| Drop traps (Pf) | | | Ectatomma ruidum, Acromyrmex santschii, Pheidole fallax, Campo-notus zonatus, Pogo- nomyrmex mayri, Pheidole guajirana |
| Winkler extraction (mW) | | | Solenopsis bicolor, Pheidole guajirana, So- lenopsis picea, Anochetus inermis, Hypo- ponera opacior |

Table 2. Richness, number of exclusive and frequent species according to capture method, of ants inhabiting urban environments in Santa Marta, Colombia.

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References

- Turrini T, Knop E. A landscape ecology approach identifies important drivers of urban biodiversity. Global Change Biology. 2015; 21(4): 1652-1667. doi: 10.1111/gcb.12825
- McKinney ML. Urbanization, Biodiversity, and Conservation. BioScience. 2002; 52(10): 883-890. doi: 10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO; 2
- 3. MacGregor-Fors I, Zuria I. Living cities: Biodiversity in urban environments. Universidad Autónoma del Estado de Hidalgo; 2019. pp. 113–127.
- 4. Chacón de Ulloa P, Montoya-Lerma J, Abadía JC, et al. Urban ants. National University of Colombia; 2019. pp. 1171–1185.
- Blüthgen N, & Feldhaar H. Food and shelter: How resources influence ant ecology. Oxford University Press; 2010. pp. 115– 136.
- Dáttilo W, MacGregor-Fors I. Ant social foraging strategies along a Neotropical gradient of urbanization. Scientific Reports. 2021; 11(1). doi: 10.1038/s41598-021-85538-2
- Angilletta MJ, Wilson RS, Niehaus AC, et al. Urban Physiology: City Ants Possess High Heat Tolerance. Chown S, ed. PLoS ONE. 2007; 2(2): e258. doi: 10.1371/journal.pone.0000258
- 8. García H, González R. Dry forest Colombia: Biodiversity and management. Alexander von Humboldt Biological Resources Research Institute; 2019.
- 9. Fontalvo-Rodríguez L, Solís-Medina C. Ant (Hymenoptera: Formicidae) assemblage in dry forest fragments in the El Cerrejón carboniferous complex (La Guajira, Colombia). Revista Intropica. 2009; 4: 5-15.
- 10. Ramos LM. Diversity of ants in urban environments of the city of Santa Marta (Technical report). Vice-rectorate of Research, Universidad del Magdalena; 2021.
- 11. Urban Geography. Plan de ordenamiento territorial Santa Marta formulation document. Mayor's Office of Santa Marta; 2020.
- Rangel JO, Carvajal-Cogollo JE. Climate of the Colombian Caribbean region. National University of Colombia; 2012. pp. 67–129.

- Carbonó-Delahoz E, Barros-Barraza A, Jiménez-Vergara J. Cactaceae from Santa Marta, Magdalena, Colombia (Spanish). Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales. 2014; 37(143): 177. doi: 10.18257/raccefyn.2
- Hernández-Camacho J, Sánchez H. Terrestrial biomes of Colombia. Instituto de Ecología, A.C., Secretaría de Desarrollo Social; 1992. pp. 153–173.
- 15. Barranco Pérez W, Castellanos Barliza J, León Peláez JD. Ecological Evaluation of an Urban Fragment of Dry Forest (Spanish). Universidad del Magdalena; 2019.
- Guerrero R, Delsinne T, Dekoninck W. Collection methods and curation. In Ants of Colom-bia. National University of Colombia; 2019. pp. 319–369.
- 17. Fernández F, Guerrero R, & Delsinne T. Ants of Colombia. National University of Co-lombia; 2019.
- Hoenle P, Lattke J, Donoso D, et al. Odontomachus davidsoni sp. nov. (Hymenoptera, Formicidae), a new conspicuous trapjaw ant from Ecuador. ZooKeys. 2020; 948: 75-105. doi: 10.3897/zookeys.948.48701
- Camargo-Vanegas JJ, Guerrero RJ. Pheidole ants (Formicidae: Myrmicinae) in the tropical dry forest of Santa Marta, Colombia (Spanish). Revista Colombiana de Entomología. 2020; 46(2): 1-22. doi: 10.25100/socolen.v46i2.8433
- 20. Fernández F, Guerrero R, & Delsinne T. Phylogeny and systematics of neotropical ants. National University of Colombia; 2019. pp. 57–89.
- García EI, Tocora MC, Fiorentino G, et al. New records of ants (Hymenoptera: Formicidae) for Colombia. Biota Neotropica. 2020; 20(4). doi: 10.1590/1676-0611-bn-2020-1088
- 22. Dekoninck W, Wauters N, Delsinne T. Invasive ants in Colombia. National University of Colombia; 2019. pp. 1149–1169.