



***Atta cephalotes* (Hymenoptera: Myrmicinae) is colonizing urban areas in Cali, Colombia**

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Abstract

Numerous studies have examined the effect of invasive species on biodiversity in urban environments, however, few of them have investigated the role of native species while turning into invasive pests. In Colombia, *Atta cephalotes*, a native leaf-cutting ant (LCA), has responded successfully to the conversion of natural ecosystems to agricultural-rural environments and, most recently, to residential and urban development. In this study, we illustrate the incidence and distribution of this native ant species in an environment where animal life must face urban disturbances in the physical environment, resource availability, and ecosystem processes associated with human urbanization in Cali, the third most important city in Colombia. For this, *A. cephalotes* nests were georeferenced in public green areas located in 12 communes across the city of Cali, southern Colombia. Vegetation and soil cover, urban settings, foraging trails and plants foraged by the ants were recorded. *A. cephalotes* nests were present in all green areas and, even in human dwellings; the ants harvested both native and introduced plant species. Despite being well adapted to strongly modified urban environments, this ant species appears to be dependent on human-subsidized resources. Given the wide distribution of leaf-cutting ants in Latin America, it is plausible to expect that similar processes are underway in other countries where these ants are found. Hence, this study also proposes to alert the academic and social communities to direct future research towards evaluating both the responses and impacts of these ants in relation to changes in the urban landscape.

Keywords Urbanization · Leaf cutting ants · Biotic homogenization · Ecological adapters

Introduction

Worldwide, urbanization is a primary driver of environmental change. It generates several forms of disturbance including loss, alteration, fragmentation and isolation of the original habitats (McKinney 2006; Simkin et al. 2022). Expansion of cities across the planet leads to widely documented, unstoppable biological homogenization, i.e. the

replacement of the original biota by a small set of expanding species that thrive in human-altered environments (Olden and Poff 2015). Some generalist insect species, among them some hundreds of ant species, profit from the drastic alterations carried out by humans in urban areas (Buczkowski and Douglas 2012). Urbanization determines a wide variety of land use and management practices that benefit the so-called adapters (species making use of both natural and human resources) and exploiters (entirely dependent on human subsidies; sensu Blair 2001) to different degrees. Traditionally, a majority of the studies on ant urbanization have been carried out in temperate zones, usually reporting displacement of native species by the same few adaptable species (Klotz et al. 2007; Vonshak and Gordon 2015; Angulo et al. 2016). However, urban conglomerates with projection to expand, engulf and destroy biodiversity are located in South and Mesoamerica (Simkin et al. 2022).

Our understanding of this process in urban and suburban tropical environments is still incipient since relatively few studies have been carried out in tropical zones (Vital 2007;

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Rocha-Ortega and Castaño-Meneses 2015; Pérez-Sánchez et al. 2018). This lack of understanding is especially worst in those scenarios occupied by native species, such as the leaf-cutter ants (LCA) (Hymenoptera: Formicidae: Myrmicinae) when they behave as “invaders”. Studies on these ant species are typically focused on its ecology specially in highlighting their negative impacts on agricultural systems. However, relatively few information is gathered from its effects on urban ecosystems including urban forests (sensu Kotze et al. 2022), residential yards and gardens, recreational parks and civil and industrial buildings.

Urbanization promotes biotic homogenization at different spatial scales. To the extent that the habitat of native species is destroyed, a new one is created for relatively few species that are adapting to urban and suburban conditions (McKinney and Lockwood 1999; Olden and Poff 2015). For LCA, a broad analysis of the importance of LCA in Neotropical Forest areas modified by human activities has been provided, especially those resulting from the progressive process of deforestation (Leal et al. 2014). In many cities, small fragments of vegetation are associated to urbanization generating changes in local climate, pollution, habitat loss and fragmentation (Pyle et al. 1981). Usually, the fragments are not connected to each other; making them green islands in the middle of a concrete matrix where ant nesting sites availability are constantly altered (see Angilletta Jr et al. 2007). Under this scenario it is plausible to expect drastic distortions and consequences on the LCA biology (i.e. reproductive success, dispersal, nesting biology, genetic variability) (Leal et al. 2014). In parallel, a range of factors, such as loss of key natural enemies, changes in microclimate, and alterations in landscape configuration and assembly (Leal et al. 2014) may drive and modify the eco-functional roles of the LCA. While in one hand it is possible to expect some ecological benefits on the nutrient cycles (i.e., drop of the accumulation of dead material and return of nutrients to the soil), on the other hand, negative interactions, or consequences (considered “disservices”) are produced due to increase of their herbivory. LCA species may develop different adaptive strategies aiming to avoid natural enemies (Rao 2000) and nesting in opportunistic sites, for instance in proximity to roads (Vieira-Neto et al. 2016). These factors are identified as indicators of *Atta* proliferation in the tropical dry forest in north-eastern Brazil (Tabarelli et al. 2010). However, the driving forces for LCA proliferation in urban habitats are still obscure and require detailed studies.

LCA of the genus *Atta* represents 20 recognised species inhabiting different habitats in both Neotropical dry and wet forests (AntWiki 2020). While some *Atta* species may have a wide geographic distribution (e.g. *A. sexdens* in Brazil) (Forti et al. 2020), a few species may be considered endemic or habitat specialists with very reduced or limited geographical distribution (e.g., *A. robusta* Borgmeier and *A. insularis* (Guérin-Méneville) (Leal et al. 2014). According to Brener and

Ruggiero (1994), the vegetational characteristics of the environment plays an important role in the distribution of the LCA nests. These authors point out that a complex vegetational pattern provides a variety of microsites for nesting and offers a diverse range of resources for foraging. LCA are recognised as generalist herbivores with a high degree of polyphagia, with the ability to ingest a rich diversity of plant matter: leaves, flowers, seeds, and plant sap (Farji-Brener 2001; Leal et al. 2014). While neighbouring plant species composition has been considered the most important environmental factor regulating LCA nest distribution/density (Farji-Brener 2001), canopy cover is likewise an indicator of micro-climate soil favouring heterogeneous LCA distribution (Van Gils et al. 2011). In every habitat, LCA is characterized by their herbivory that includes a wide range and number of plant species. In urban areas, proliferation of ant nests and ant herbivory affect the development of ornamental plants which, in many cases, die during early stages of development (per. Obs.). In this manner, the ant activities become an important limiting factor for the establishment of new plants in the city and for defining vegetation types and complexity, aspects that remain basically neglected. Furthermore, ant nest excavation generates instability of the terrain, putting urban infrastructure (platforms, roads, dikes and walls) at risk (Montoya-Lerma et al. 2006). On the other hand, these ants represent ideal systems for the study of species proliferation in human-modified landscapes (Siqueira et al. 2017). At present, the status of several of these ants as pests with economic impact has evolved as humans simplify biodiversity in forests and natural environments, generally giving way to extensive monocultures. However, there is a lack of understanding of the human-controlled processes that alter and affect urban biodiversity, thus promoting emergence and increase of some pests. Based on this information, the effects of LCA in urban areas need to be assessed (Montoya-Lerma et al. 2011).

Surprisingly, while the transition of some LCA species from natural habitats to rural, agricultural and semi-urban environments has been evaluated (de Carvalho-Cabral 2015), the potential threat posed by certain species in urban environments remains largely unexplored. In Brazil, Mariconi (1970) was a pioneer in emphasizing the importance of LCA as potential urban pests after observing their interference in several civil constructions. Years later, (Campos-Farinha and Zorzenon 2008) and latter de Carvalho-Campos (2011) recognized several LCA species as urban pests. Recently, Bueno et al. (2017) echoed this perception by pointing out that a similar situation occurs in several urban areas of Brazilian cities. In Colombia, warned of the potential threat of the dominant LCA species, *A. cephalotes* (L.), as a response to urbanization in some areas previously occupied by tropical dry forest (Montoya-Lerma et al. 2006; Montoya-Lerma et al. 2011). At present, this ecological zone is transformed in urban areas harbouring the largest human populations

with the greatest growth rates in the country. It also includes the fertile lands in the Department of Valle del Cauca where, after undergoing a continuous process of deforestation since 1550, few forest fragments remain standing (Cardona-Arcila et al. 2012). Before today's extensive monoculture of sugar cane, intense processes of agricultural transformation were dominated by coffee, tobacco, indigo and cotton. Although we do not have records of LCA species composition at that time, Mutis, the Spanish-Colombian naturalist of 18-19th centuries, reported at least two LCA species, *A. cephalotes* and *A. colombica* Guérin-Méneville, cohabiting in this once extensive dry forest (Wilson and Gómez-Durán 2010). Although it is plausible to suppose still the current coexistence of these two LCA species, Mackay and Mackay (1986), and more recently, Fernández et al. (2015), pointed out that *A. cephalotes* is today the dominant leaf-cutting ant species in the Valle del Cauca Department, even in forest remnants. Despite strongly contrasting environmental conditions, we have observed that *A. cephalotes* retains high colony densities in several Colombian cities, indicating its predisposition to become a dominant urban species. Notwithstanding its ecological and economic importance, the issue has apparently never been systematically explored.

It is important to keep in mind that, although relatively few LCA species are adapted to urban environments (Supplementary Table 1), the species listed are widely distributed in tropical America and some of them are recognized as the most successful in terms of abundance in human simplified and modified areas (Leal et al. 2014). These LCA species have been recorded attacking plants in places such as street separators, lawns, gardens, urban forests, and recreational green zones (Supplementary Table 1). Motivated by the above observations we were aimed to evaluate the distribution and abundance of *A. cephalotes* nests in an urban environment in Cali (Colombia). In order to accomplish this, we (1) surveyed and mapped the number of *A. cephalotes* nest quantifying and describing its abundance and degree of colonization in the urban environment studied. In addition, we intended to show its impact on ornamental and paved urban settings, thus determining its status as an urban pest. Our final goal is aimed at contributing to understanding the ecological factors that favour the success of *A. cephalotes* as a dominant urban species.

Methods

Areas of study

The search for ant nests was restricted to the public green areas of 12 communes (political divisions of the city, equivalent to districts) in the urban landscape of Santiago de Cali, Colombia (3°24'56" N, 76°30'10" W). The human population is close

to 1.8 million inhabitants (Departamento Administrativo Nacional de Estadística- DANE- 2018) but has increased in recent years due to a high rate of migration from rural areas of southwestern Colombia. The city is located at the foothills of the western cordillera of the Andean mountains at 900 m.a.s.l. Annual average temperature is 29.3 C and relative humidity about 70–75%. The annual precipitation pattern is higher in the south (1474 mm) than in the north of the city (908 mm), distributed into two well-defined rainy periods (March–May and September–December) (Aerocali 2017). Ecologically, the area corresponds to Tropical dry forest and tropical dry premontane forest (sensu Holdridge 1982) connected to the biogeographic Chocó area. The city is irrigated by six rivers that go down from the Farallones Mountains, all of them tributaries of the Cauca River that flows from the south to the north.

Historically, this eco-zone represents a deciduous dry forest, mixed with evergreen dry forest, and a gallery forest along the Cauca River. On either side of the valley, the dry forests give access to another eco-zone or biome (moist montane forest) along the slopes of the Central and Western Andean ranges. According to the botanical census of Cali region made by the Departamento Administrativo de Gestión del Medio Ambiente (DAGMA 2006), there were 193,000 trees (ratio: one tree for 11.5 people), including introduced and native species. In the green areas of the communes studied, typical introduced ornamental species were interspersed with remnants of native plants. The displacement of the native species by the introduced ones is estimated at 59% (Vargas 2012).

Field activities

Six groups of five people were formed. Each group had a biologist (usually entomologist) as the leader who supervised the surveying and mapping of LCA nests in each visited area. Daily (08:00–17:00), Monday to Friday, from February to August 2015, each group was assigned an area to geo-locate any LCA nest found while comprehensively combing the whole area step by step. Prior to data collection, personnel were trained to find any conspicuous or hidden LCA nest (incipient and mature), as well as differentiate *Atta* and *Acromyrmex* nests. Each group received a map with the green areas of the commune that will be explored during the week. The nests were geo-referenced using a hand-held global positioning system (Garmin™ 62sc).

Species, ant nest area, density, and distribution of LCA nests

Specimens of major LCA workers (soldiers when available) were collected and identified according to Fernández et al. (2015). These were deposited in the entomological collection at the Universidad del Valle Museum (Cali, Colombia).

The superficial ant nest area was estimated by multiplication of superficial nest length and width dimensions (Montoya-Lerma et al. 2006). The density of the nests in each commune was obtained by dividing the number of nests found in each commune by the surface (ha) of public green areas explored in the commune. The areas of the communes and their urban green zones were respectively gathered from Departamento de Planeación Municipal (2021) and Departamento Administrativo de Gestión del Medio Ambiente DAGMA (2006). LCA nests were found and mapped as follows: All data were imported into a geographic information system (GIS) database (ArcGIS 2016). This geo-referenced database was created for spatial analysis. All ant nest GPS coordinates from the communes were matched to the corresponding city structures using the official Valle del Cauca environmental geographic information (CVC-DAGMA). Ant nest maps were produced for the different communes with their surrounding urban green areas. Green areas were defined using vegetal cover shape-file (CVC Geodatabase landcover) and direct field observation.

Urban settings of leaf-cutter nest

The study areas were categorized according to the following urban settings: (i) Ornamental, including parks/yards (i.e., open recreational areas with the presence of grass and/or sparse native or introduced trees) and (ii) impervious or hardscape: predominately cemented areas with variable scattered pockets of trimmed grass containing shrubs and/or garden flowers. The latter may include the occasional presence of buildings, pedestrian pathways, rainwater channels and riverbanks with strips of land (dikes) built to avoid overflow; pedestrian or vehicular bridges; and road separators restricted to small green areas surrounded by cement. Overall, the landscape was dominated by flat land although nests were eventually observed in inclined or rugged areas. Private residential areas and commercial and recreational complexes were not evaluated.

Vegetal and soil nest cover

The vegetal cover was estimated as canopy cover (%) using a spherical densitometer (Forestry Suppliers Inc., Jackson, MS, USA). One of the members of each group oversaw the measuring of the vegetation cover of the nests. For this, he took position in the centre of the nest and made four measurements of the vegetation cover. After each measurement, the person rotated 90° clockwise to take the next measurement, completing a 360° view of the vegetation cover on the nest. Vegetation cover was the average of the 4 measurements.

It is well known that some LCA species behave as nest clearing species in forest areas, removing the scrub vegetation from their mounds (Meyer et al. 2011; Stephan et al. 2015), yet

little is known about this behaviour in city areas. Hence, to test whether the ants covered their nests, or not, the soil cover was determined and categorized visually as littered or bare. Soil cover was classified: bare ground cover (without plants growing on the surface of the nest), leaf litter (when there was died vegetal material covering more than 50% of the nest surface) and vegetation (when more than 50% of the nest surface was covered by living plants). This information was taken from the superficial area of each nest.

Vegetation attacked and foraging trails

Vegetation attacked by the ants was recorded. Nest trails were followed to the plants used as a foraging resource, and foraging action by the ants was observed and recorded on site. The level of herbivory or attack was classified as dense (trees), medium (shrubs and herbs) and scarce (pasture), regardless of whether they were native or introduced. Plants that could not be classified in the field were collected and brought to the university to be identified by a specialist. The number of events that LCA attacked a vegetal species was quantified. In addition, foraging trails information was taken on each nest. Trails number, length and bifurcations were recorded.

Data analysis

Numerical data was subjected to basic descriptive statistical analysis. The spatial behaviour of the nests was evaluated. ARC-GIS' nearest neighbour analysis was used to determine their distribution pattern (see supplementary Table 2). To evaluate whether vegetation cover, soil cover type (bare; semi-littered and littered) and, urban setting (green area and build area) as explanatory variables, had effects on nest density, linear mixed models (LMM) were adjusted with communes as random effect and different structure of variances (homo and heterogeneous variances) and data that failed to conform to the symmetric residuals were log transformed (Barlett 1947). We select the best model using the Akaike information criteria (AIC) and Bayesian information criteria (BIC). A similar procedure was carried out to test the effect of the vegetal fragments on nest density using a GLMM model previous checking for overdispersion using a negative binomial model if found. The analyses were complemented using Tukey post hoc tests to assess pairwise statistical differences across groups. We used "nlme" (v. 1.1–3.1-163; Pinheiro, Bates and R Core Team 2023) and "lme4" (v. 1.1–34; Bates et al. 2015) packages in R (v. 4.2.3; R Core Team 2023) to build the LMM and GLMM models, respectively, determining statistical differences at a 5% level of significance. Mean values of the percentage of average vegetation per commune were used to evaluate the relationship between the nest density and vegetation cover variables using the Spearman correlation coefficient (r_s).

Results

Field activities

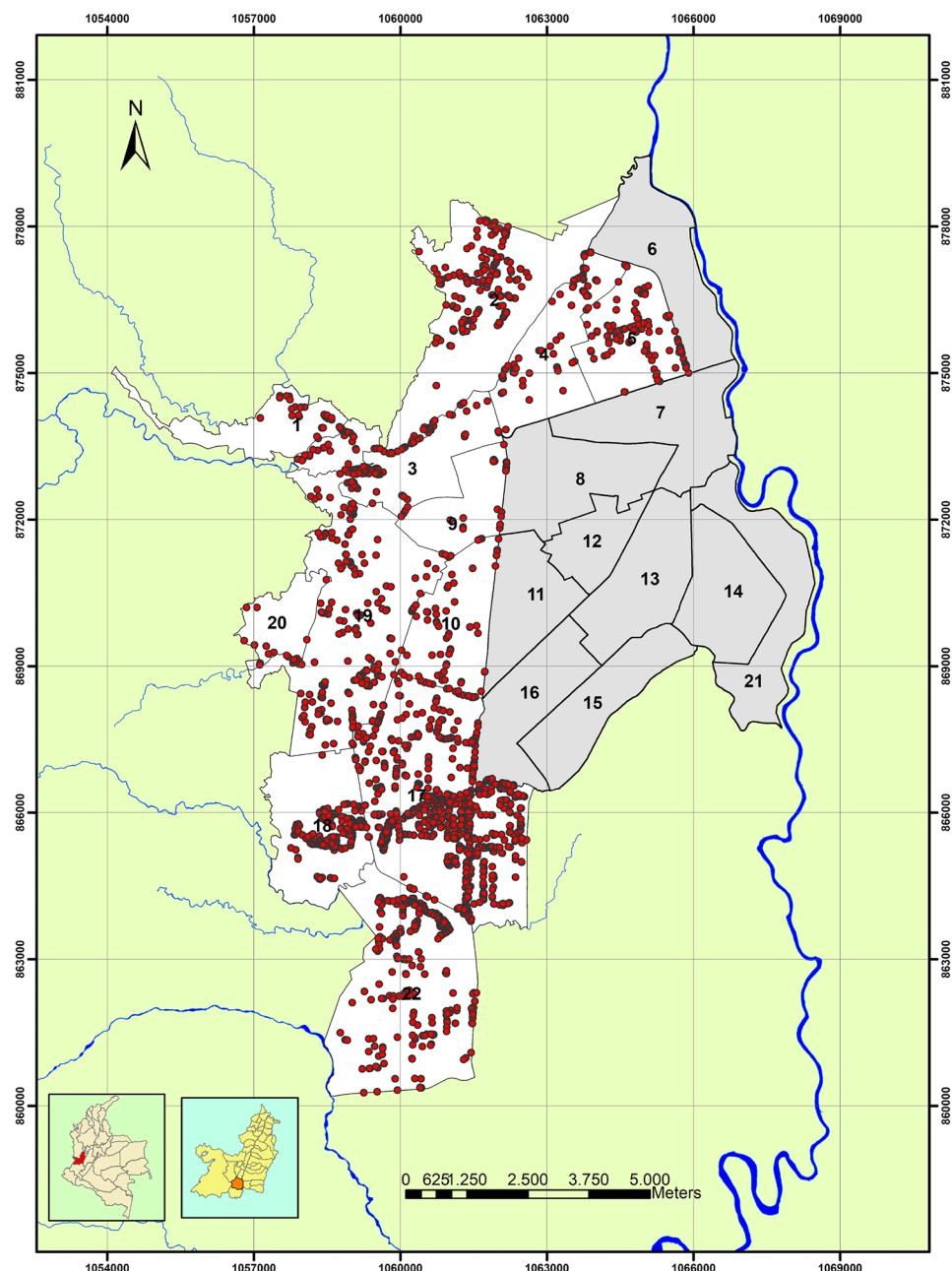
Species, ant nest area, density, and distribution of LCA nests

Atta cephalotes was the only LCA found in all the communes studied. A total of 2323 nests of this species were distributed throughout the 12 communes, occupying a total area of 139,807.36 m², displaying a clustered nest pattern in all communes, except in commune 20 (see Fig. 1

Fig. 1 Spatial distribution of *Atta cephalotes* nest in the communes studied (clear area). Dots indicate active nests. The numbers represent the different communes of the city (only the white areas were studied). Blue lines represent the rivers of the city

and Supplementary Table 2). Nest number, size as well as colony densities were variable among the communes (Table 1). For instance, the highest density, but with the second smallest area, was found in Commune 9 which corresponds to the north-centre of the city, an area with the least number of trees in the city (Table 1).

The statistical analysis of nest numbers and their densities in the 12 communes revealed a great influence of the amount of the green area available in each commune. This was true for the number of nests and their total surface area, both of which strongly and significantly depended on the amount of green area (Fig. 2; $r_s = 0.89$, $p = 1.07e^{-4}$ and



$r_s = 0.92$, $p < 2.2e^{-16}$, respectively). Likewise, the overall density of nests per communal land surface was sufficiently explained by the amount of green area available in the respective commune. The analyses as a whole reveal that nest density significantly increased as the density of plants increased per green area (ha) ($r_s = 0.72$, $p = 0.011$).

The areas most affected by the presence of ants were C17 and C22, which in turn are the largest public green spaces in the city. C17 had the largest number of nests (915 in total) and more than 55% of these are young nests (less than 1 year old). The largest nest was found in the Cañasgordas wetland (C22) reaching 1150 m². On the other hand, in communes 1, 3, 9 and 20, the green areas were scarce representing minimal food resources and reduced chance for ant nesting and limited space for development of large colonies. However, the highest number of nests per hectare was recorded in C9, meaning that the few green areas available had always *A. cephalotes* anthills. Although the nests do not reach sizes

larger than 500 m², in areas with a high number of buildings, the actual size of the anthills may be underestimated, as a large part of it may be under roads, pavements or other structures.

Urban settings of leaf-cutter nest

The predominance of *A. cephalotes* nests in ornamental areas was evident. Table 2 shows that, on average, 63% of the *A. cephalotes* nests were found in ornamental areas, including parks and green areas. 36.3% of the nests were located in areas with some type of urban infrastructure, such as: sidewalks, buildings, dykes or road dividers. The ant nest area in ornamental areas was, on average, three times larger than occupied in paved areas (hardscape). In addition, 27.9% of the nests were found in sloping areas (inclination between 10 and 60°) including mainly river-banks and water channels (Fig. 3B).

Table 1 Main characteristics of the communes (C) studied indicating the total area, and the corresponding number, area and densities of ant nests. As comparative parameters an estimation of the green areas and the total number of trees per commune are included

Commune	Commune area (Ha)*	Number green areas*	Number recorded trees*	Number of nests	Mean area nests (m ²)	Total area nests (m ²)	Green areas (Ha)*	Density (nests/ha)
C1	384.2	14	5837	70	71.92	5034.55	24.63	2.84
C2	1131.3	43	29,175	247	57.65	14,240.63	101.14	2.44
C3	370.4	16	5881	76	65.05	4944.13	37.49	2.03
C4	452.5	33	12,376	76	57.57	4375.29	19.11	3.98
C5	419.8	36	5881	113	95.5	11,424.46	71.36	1.58
C9	289.9	9	5339	29	80.09	2322.54	3.16	9.18
C10	429.8	41	13,178	55	66.67	3666.8	23.4	2.35
C17	1255.6	26	51,551	915	54.59	49,945.7	205	4.46
C18	542.9	13	11,935	188	75.58	14,209.62	33	5.70
C19	1136.7	38	27,760	200	73.46	14,692.71	72.41	2.76
C20	243.9	7	1013	27	61.02	1647.67	15	1.8
C22	1058.9	4	13,863	383	39.94	13,059.05	55	5.95
				2323	60.18	139,807.36	660.7	3.75 ± 2.25

C1: Western Cordillera between the Cali and Aguacatal river basins and 1 ecopark

C2: This sector has an ecopark

C3: Northwest of Cali, main center of the city

C4: Northeast of the city, bordered on the west by the main center of the city. 4 sports areas and paved parks

C5: Eastern center of the city, some parts have recreational and sport areas. The green area indicator per inhabitant is 9 m² per inhabitant

C9: North-centre of the city.

C10: Intermediate sector in the southeast of the city

C17: South of the city. This commune is part of the lower part of the Melendez and Lili river basins. 50.07 ha in addition to a green area park, and a zone scale park

C18: South of the city in the foothills of the Western Cordillera between the Melendez and Cañaveralejo river basins

C19: Southwest of the city, it forms a central peripheral area between the centre and the south of the city

C20: Southwest covering the foothill and hillside areas

C22: Southwest covering the foothill and hillside areas. Public green areas and there is also the Lago de las Garzas 6.13 (hectare) Ecopark

* Data on the area of the communes and data of the green zones and number of trees** of the communes were obtained by Departamento Administrativo de Planeación (2021) and DAGMA (2021), respectively

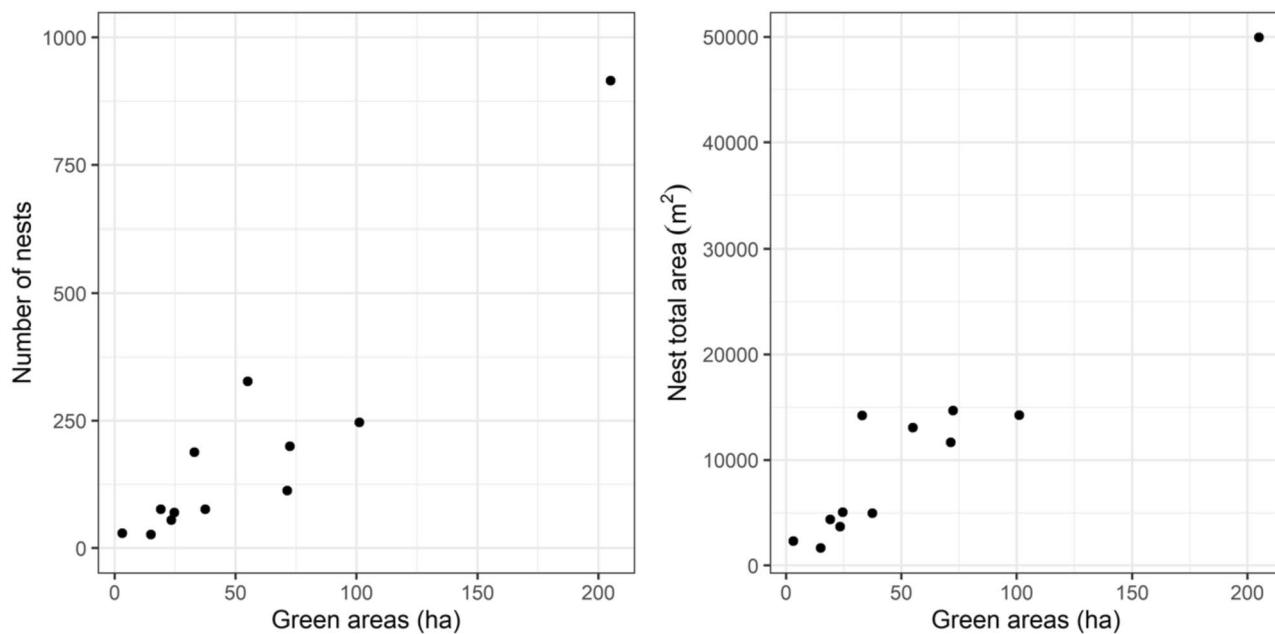


Fig. 2 Left: Total number of *Atta cephalotes* nests in green areas of Cali. Right: Graph showing the relationship between ant density (nest/ha of total land) and green area (ha)

Vegetal and soil nest cover

Supplementary Table 3 shown the information criteria for the adjusted models. The best model was obtained assuming homogeneity of variances, where is evident a significant effect of the vegetal cover ($\chi^2=16.7635$, $df=1$, $p<4.2\text{ e-}5$) (Fig. 4) and soil cover ($\chi^2=25.7106$, $df=2$, $p<2.6\text{ e-}6$). Regarding littering activity, the results of Tukey's multiple comparison test, suggest that the density of nests with total cover (Littered) differs from the density of semi-covered (Semi-littered) and open nests (Bared) (Fig. 5; Supplementary Table 4). It was estimated that 75.40% of the nests were littered or covered by grass remains and only 15.3% had a

fully exposed external area (bare soil). However, no statistical effects were detected when setting (i.e., ornamental vs. hardscape) areas were compared.

Vegetation attacked and foraging trails

False laurel (*Ficus benjamina*), an introduced plant, was the tree species most frequently foraged by the ants, which took advantage of its leaves and synconia. Other species were also foraged (Table 3). GLMM results suggest a significant effect of the source of the fragments ($\chi^2=143.99$, $df=2$, $p<2.2\text{ e-}16$, independent variable=Category of the plants: native or introduced or cultured).

Table 2 Total number of *Atta cephalotes* nests, their means and relative percentage distributed in public green areas in 12 communes of Cali showing the comparison of the percentage sum of nests in ornamental (63.8) vs. hardscape (36.3) settings

Sites	Total number of nests	Mean area (m ²)	Percentage (%)
<i>Ornamental</i>			
Parks	365	134.3	15.3
Green areas	1156	64.5	48.5
Total	1521	198.8	63.8
<i>Paved area</i>			
Roads, channel walls	52	26.5	2.2
Buildings (Houses, walls or buildings)	3	12	0.1
Pedestrian pathways	160	32.6	6.7
Rainwater channels	139	34.4	5.8
Pedestrian or vehicular bridges	12	15.6	0.5
Road separators	499	50.9	20.9
Total	865	172.0	36.3



Fig. 3 *Atta cephalotes* nests in different areas of Cali: A. On green area. B. On slope of a rainwater channel. C. On vial divider. D. Below a sidewalk. E. On a park. F. At the base of a building

According to the Tukey test, total ant “leaf herbivory” varied between native/cultured species and introduced species in both settings. There were more nests number with fragments of herbivory (i.e., leaf-cutting signals) coming from introduced plants (mean = 66.9; ES = 88.34) compared to nests number from fragments of native (mean = 18.83; ES = 27.95) and cultured (mean = 23.36; ES = 44.99) plants.

Positive and significant correlations were found between the proportion of ant nests and the availability of both the native and introduced species.

No relationship between distance to plant resource (m) and density of active nests ($r_s = -0.1398, p = 0.6672$) was found. Similarly, the length of the main trail to nests from paved areas was greater than those located in green

Fig. 4 Density of *Atta cephalotes* nests/ha according to the percentage of average vegetation cover in the communes of the city of Cali

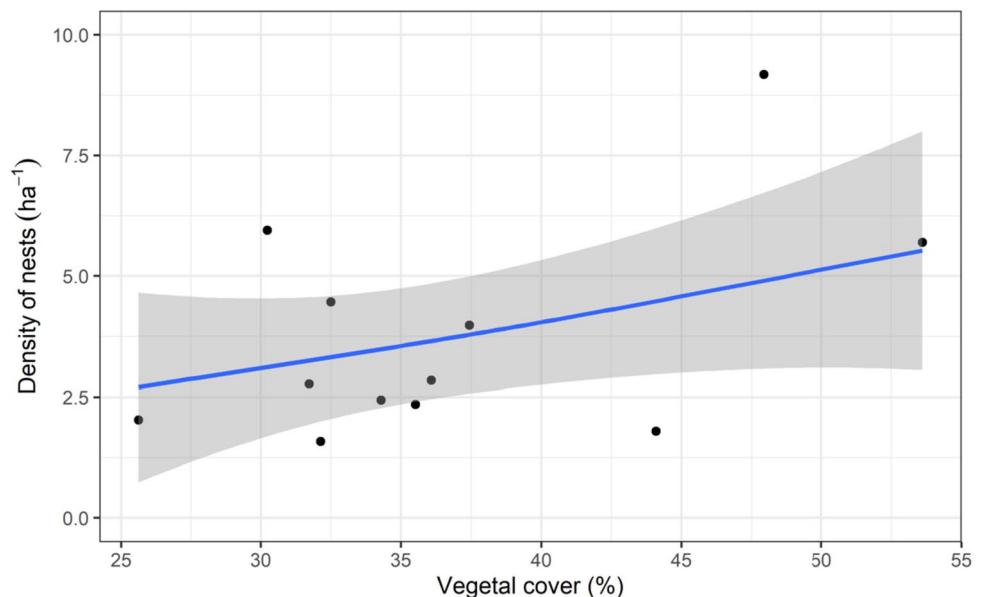
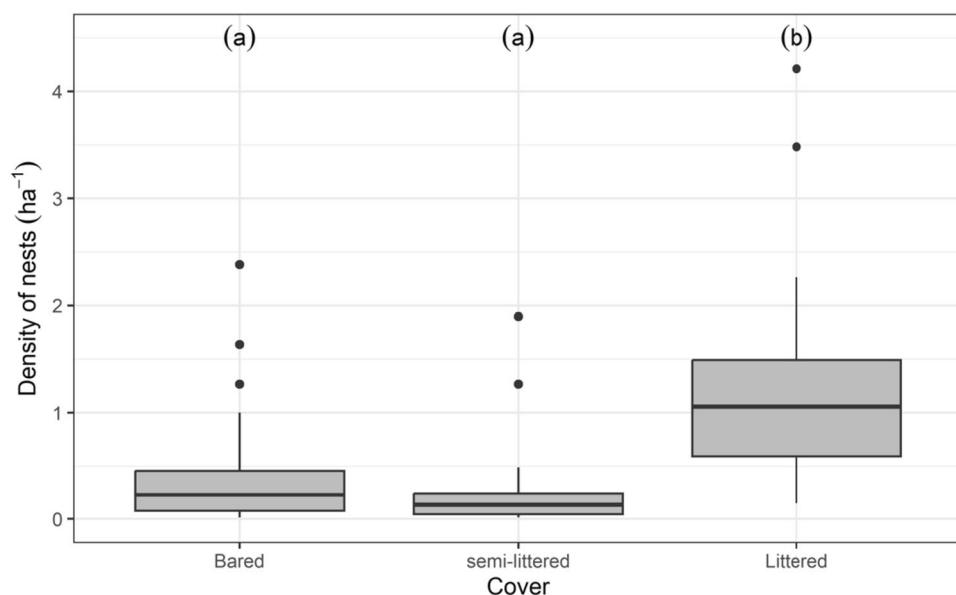


Fig. 5 Tukey's multiple comparison test of *Atta cephalotes* nest density with its littering activity



areas. Average number of mounds and littering was similar between paved and unpaved zones (data not shown). The longest track observed at a nest exceeded 150 m from the nest to the plant resource. An important observation made during this work was the carrying of grass and leaf litter by the workers.

Discussion

In this study we evaluated the distribution, abundance and density of *A. cephalotes* nests in an urban environment in the city of Santiago de Cali. Our findings are striking and surprising. Although no allowing a meaningful comparison, there are no data from Colombian natural areas, it may result interesting for the sake of the discussion to compare some of our results with some data obtained from other places where LCA are present.

Ant nest density in the public green areas of the sampled communes was remarkably higher than that reported for *Atta* species in mature primary rain forests, ranging from 0.03 ha^{-1} to 0.6 ha^{-1} (see Cherret 1968; Vasconcelos 1988; Jaffe and Vilela 1989; Wirth et al. 2003; Wirth et al. 2007) and 0.97 ha^{-1} in agricultural areas (Montoya-Lerma et al. 2012). Significantly, along the edge of Caatinga, the proliferation of *A. opaciceps* reached a density of 2.45 ha^{-1} (Siqueira et al. 2017), a density closer to our results (3.85 ha^{-1}). Hence, we wonder whether a similar mechanism of ant urbanization is under process. It would also be important to note that $1.8 \text{ A. cephalotes}$ nests ha^{-1} were recorded on a recovered patch of secondary forest in the Cali Botanical Garden (Sánchez and Urcuquí 2006), result similar to that reported in old growth forests in Costa Rica (Perfecto and Vandermeer 1993). In absence of published information on equal coverage in urban areas elsewhere, it is acceptable to compare the long-term changes in the

Table 3 List and order of the vegetal species most foraged by *Atta cephalotes* in 12 communes of Cali-Colombia

Commune	Order of foraged in each commune			
1	<i>Leucaena leucocephala</i>	<i>Swinglea glutinosa</i>	<i>Clitoria fairchildiana</i>	
2	<i>Ficus benjamina</i>	<i>Mangifera indica</i>	<i>M. indica</i>	
3	Unidentified Grass	<i>Phithecellobium dulce</i>	<i>Calliandra</i> sp.	
4	Unidentified Grass	<i>F. benjamina</i>	<i>L. leucocephala</i>	
5	<i>F. benjamina</i>	<i>Calliandra</i> sp.	Unidentified Grass	
9	Unidentified Grass	<i>F. benjamina</i>	<i>Caesalpinia peltophoroides</i>	
10	<i>C. peltophoroides</i>	<i>S. glutinosa</i>	<i>M. indica</i>	
17	<i>F. benjamina</i>	<i>M. indica</i>	Unidentified Grass	
18	<i>M. indica</i>	<i>Duranta repens</i>	Unidentified Grass	
19	<i>F. benjamina</i>	<i>M. indica</i>	<i>L. leucocephala</i>	
20	<i>Samanea saman</i>	<i>S. glutinosa</i>	Unidentified Grass	
22	Unidentified Grass	<i>F. benjamina</i>	<i>Jacaranda mimosifolia</i>	

number of nests previously recorded (Montoya-Lerma et al. 2006). In 9 years, the average colony densities in the green areas of three communes (17–18 and 19) increased 11.15, 14.5 and 4.2 times, respectively. This indicates that the urban proliferation of *A. cephalotes* is an on-going process and provides key evidence for the capacity of this species to expand and become a “successful invader” in urban and sub-urban environments (Leal et al. 2014) and, as its colony densities increase, they gradually become a peri-domiciliary pest.

A glance at our results, it is tempting to suggest an obvious, logical assertion: ant abundance is related to the presence of green areas. Both palatable forage (Farji-Brener 2001) and suitable soil hypotheses (Van Gils et al. 2011) which include canopy cover are measures of resource availability. However, ants appear to be opportunists, benefitting from high-ranked, non-tree leaf availability and ornamental plants which may also represent productive, fast growing, and high-quality sources. It is likely that the available green resources from domestic gardens and lawns in confluence with the soil micro-climate conditions favour survival rate of *A. cephalotes* colonies over time.

The fact that the mean nest size is smaller in hardscape structures such as pathways, road separators, dikes, etc. is an additional but relevant finding. Besides supporting the idea that *A. cephalotes* proliferates and benefits from these mixed plant-cemented habitats, they might be interpreted as areas where both bottom-up and top-down forces are altered compared to natural environments (Wirth et al. 2008; Falcão et al. 2011; Leal et al. 2014). It is important to note that although ant nests did not reach sizes greater than 500 m² in areas with a large number of buildings, the visible size of an ant mound could not be indicative of its colony size. Its actual size might be underestimated because much of it is under paved asphalt ground, platforms, or other structures.

Arborisation and urban gardens provide appropriate vegetal availability for its dominance. In the first place, this ant is a generalist herbivore species, and the Colombian dry forest is its native range of distribution. Hence, it is plausible that, besides exploiting the native vegetal species, it can also benefit from the introduced and cultured ornamental species that, with few exceptions, are highly palatable and might have scarce defences against its herbivory (Coley et al. 1985; Howard 1988; Nichols-Orians and Schultz 1989; Farji-Brener 2001; Wirth et al. 2003). In Brazil, it was estimated that LCA attacked and damaged at least 40 plant ornamental species, showing preference for introduced ones (Campos-Farinha and Zorzenon 2008; de Carvalho-Campos 2011). Secondly, ornamental plants, as well native plants, are frequently submitted in urban areas to artificial fertilization (Blanton and Ewel 1985; Vasconcelos and Cherrett 1996; Meyer et al. 2006) and fumigation that protect them from certain pests. However, they ultimately constitute nitrogen

deposits and other easily accessible nutrients exploited by ant foragers as well as representing an excellent fungus garden fodder bank (Dukes and Mooney 1999).

In our study, *A. cephalotes*, in its condition as a native generalist herbivore species, appears to be adapted to exploit Old World cultivars and introduced ornamental plants brought to city areas where may fail their natural defences against New World pests, including leaf-cutter ants (Rockwood 1976; Howard 1987; Howard 1988; Nichols-Orians and Schultz 1990; Urbas et al. 2007; Mundim et al. 2009; Falcão et al. 2011; Leal et al. 2014). A good example is *Dypsis lutescens* Beentje & J. Dransf (Arecaceae), a palm imported from Madagascar. A positive correlation indicates that the larger the number of palms, the higher the proportion of ant attacks. However, it is not possible to generalise as some introduced species appear to be unaffected regardless of their number. Most noticeable was *Ficus benjamina* (Moraceae), a large, long-living tree with ornamental use, native to Asia and Australia and very abundant in Cali (a total of 7169 trees in the communes studied, DAGMA 2006). It represented a continuous supply of fresh leaves and fruits available to the *A. cephalotes* colonies. This double use may be the reason why this plant is the one most attacked by ants. Other attacked tree species were commonly observed in the urban area. There is not a clear explanation for the carry of grass and leaf litter by workers. Many fragments of grass and dry plant material surrounded many mound nests; hence we cannot rule out that these resources were used as substrate to cultivate the symbiont fungus.

As stated before, urbanization determines a variety of land use and management practices that directly and indirectly benefit the so-called adapters and exploiters (de Carvalho-Campos 2011). In this sense, human habitats might facilitate the rapid transition of native species into the invader state as occurred with *Tapinoma sessile* (Buczkowski 2010; Alberti et al. 2017) and *Linepithema humile* (Holway and Suarez 2006; Klotz et al. 2007). In the case of *A. cephalotes*, changes in the physical environment, availability ecosystem resources and other processes of a biogeochemical type that trigger its population growth are unveiled. Hence, the present study represents a first effort at approaching them. However, it is important to recognize the need of intervention of the common citizen and the urban planner in order to reach a successful management in the urban system. As a whole, a chain or cascade reaction is generated with multiple effects including alterations in inter-specific interactions and food dynamics (Shochat et al. 2010). In our case, it is clear that what is recorded is only a snapshot of a series of historical (poorly documented) processes of land use and other developments in Cali. However, we are providing some biological, spatial (urbanistic) and physical elements that favour the dominance of *A. cephalotes*, a native species that strongly profits from the forest edge (Leal et al. 2014) and should be considered an urban adapter sensu Blair (2001).

Potential implications

Urbanization of LCA may have socio-economic and biological implications but human perception of the ecological role of the LCA in nature might be misleading. In our case, *A. cephalotes* nests in urban settings have been found affecting urban buildings and walls but its special importance is represented by the potential subsidence of engineering works on riverbanks designed to prevent flooding of areas, such as the Cauca Riverbank where 700,000 people live. Hence, since most people would perceive LCA as serious pests, they would promote using insecticides as a first option to combat and eliminate them. Under these circumstances, *A. cephalotes* proliferation requires a budget for its control. The national government invested more than 800 million dollars in works directed at recovering the dike that regulates the waters of the Cauca River. The filling of the ant nests (up to 4 m depth) with concrete was one of the main activities carried out (Ramírez 2016). To this budget must be added the costs that DAGMA (the environmental entity) must allocate for the control of this ant in the maintenance of streets, parks, buildings, etc. A rough estimate was \$ 66,000US for 5 months in 2012 (data not shown). This money is primarily intended for chemical control without considering the fact that the littered nests might be skipped by city scouter in charge of nest control. Besides, most important, there is not awareness that insecticides used (mainly commercial products based on Sulfluramid and Chlorpyrifos) may lead to a health risk for citizens and cause environmental damages. The active ingredients or metabolites in formicide products may be carried by air and water and may eventually affect the inhabitants causing morphological changes in the brain with irreversible effects extending into early school years (Rauh et al. 2012) or damage to the respiratory, nervous and cardiovascular systems in adults (Sinha et al. 2006). Although the hazards of these insecticides for human health and the environment are well known (Sinha et al. 2006; Rauh et al. 2012; Deb and Das 2013; Simon-Delso et al. 2015), the regulation of their use is weak and, therefore, continue to be used without adequate precautions in both agricultural and urban areas. In addition to the damage to human health, the potential effects, and disturbances that these insecticides can cause to the urban fauna associated with parks must be addressed.

Urban adapters have frequently been identified as edge-species (McKinney 2006) and this applies perfectly to LCAs which Leal et al. (2014) have characterized as native species that strongly profit from the forest edge. In this paper, we propose to classify *A. cephalotes* as urban adapters for the first time. The results of this study have shown that this leaf-cutter ant is best suited to urban environments in Cali. A central question arising here is whether the phenomenon of the high incidence and density of *A. cephalotes* in Cali would before a definite time or, conversely, a persistent event, as was shown in the LCA populations in the Brazilian

Atlantic Forest (Meyer et al. 2009). Hence, as many of these patterns based on elements of the gradual changes are copied or occurring in other Neotropical countries, it is plausible to formulate a hypothetical scheme of a similar invasive pattern in those cities where some leaf-cutting ant species with stable populations are reported affecting urban premises (see Supplementary Table 1) and hence expected to disperse and persist as hyper-abundant populations of LCA.

Conclusions

This study provides evidence of the severe proliferation of *A. cephalotes* populations in urban settings. Distribution maps of the nests of this native leafcutter ant revealed that is widely distributed affecting ornamental and paved areas such as urban buildings and walls. There are several conditions that favour the dominance of *A. cephalotes* in Cali. Among them, the transformation of the forests, the inadequate habitat management, the poor agricultural and control practices favour the ability of this species to tolerate high levels of human disturbance. The findings of this research provide insights related to the poor or medium vegetal coverage, the abundance of introduced plants species, and the available ornamental resources from gardens. All these aspects contribute to an ecological disbalance that favour the success of *A. cephalotes* as a dominant urban species in Cali. Our main goal is to generate an alert to other cities of Colombia and, by extension, to other Latin American countries where leaf cutting ants are also present in urban areas (Supplementary Table 1).

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11252-023-01469-y>.

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Declarations

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