



Urban patches of dry forest as refuges for ants and carabid beetles in a neotropical overcrowded city

Nataly Forero-Chavez¹ · Anderson Arenas-Clavijo¹ · Inge Armbrrecht¹ · James Montoya-Lerma¹

Accepted: 28 December 2023
© The Author(s) 2024

Abstract

Cali is the third most prominent, and one of the most crowded, Colombian cities. It still harbours some tropical dry forest patches that can mitigate the impacts of the urban transformation; however, there is an almost total absence of information on the biological importance of these sites and their potential for future ecological restoration processes. To assess if they serve as important refuges for insect bioindicator species, we sampled five urban patches of tropical dry forest in the city, plus one nearby rural patch, using specific trapping procedures for ants and carabid beetles. Patch areas were variable, from 1 to 50 ha. We found that the smallest patch presented the highest ant richness, with a tendency towards generalists and a few unique species. Meanwhile, some specialist species were found in the rural patch. A total of 109 ant and 13 carabid species were recorded, including four new records of ants for Colombia. Results suggest that environmental variables favour the presence of generalist and opportunistic ants. Despite this, the high ant richness demonstrates that. Urban forest patches are important refuges for biodiversity. The low richness observed for carabids could be a sign of the challenges that urban forests face considering the ecological importance of beetles. The possible dangers of intensive internal use of these forests is discussed to prevent local extinctions, since the biggest forests are not necessarily conserving a higher richness. This work represents an important contribution to urban ecology in the region, with possibilities of further restoration in urban environments.

Keywords Colombia · Insect biodiversity · Database · Endangered areas · Conservation

Introduction

Biodiversity is declining at global level due to several social and cultural factors. Among these, urbanization is expected to rapidly expand between 30% and 180% from 2020 to 2100 (Chen et al. 2020). Globally, urban growth in tropical cities has been associated with effects on biodiversity hotspots (Miller and Hobbs 2002; McDonald et al. 2008; Seto et al. 2012). In the tropical Americas, dry forests have been highlighted as one of the most threatened ecosystems due to a high rate of deforestation driven mainly by agriculture and cattle ranching (Hoekstra et al. 2005; Armenteras et al. 2013; Sánchez-Cuervo and Aide 2013). It is also estimated that 66% of these ecosystems have been converted

to these land uses (Portillo-Quintero and Sánchez-Azofeifa 2010). Furthermore, processes of rapid habitat transformation, deterioration, and fragmentation are exacerbated by mining, tourism, and urban development (Portillo-Quintero and Sánchez-Azofeifa 2010).

Colombian tropical dry forests provide irrefutable proof of the land transformation effects: a critically endangered ecosystem facing soil degradation via erosion, conflagrations, and the high pressure due to proximity to urban areas and infrastructure projects (Etter et al. 2017). Furthermore, these forests have very little or poor representation in conservation policies (Pizano et al. 2017). This incipient level of knowledge, coupled with a history of transformation, places species, ecological processes, and ecosystem services at risk (Gómez et al. 2016).

In Colombia, the remnants of dry forests are confined to five regions: Catatumbo, the peri-Caribbean belt, the Norandean province, the Magdalena River valley, and the Cauca River valley (García et al. 2014). According to Alvarado-Solano and Otero-Ospina (2015), the dramatic degradation

✉ James Montoya-Lerma
james.montoya@correounivalle.edu.co

¹ Department of Biology, Universidad del Valle, Avenida Pasoancho No 100-00 Cali- Valle, Cali, Colombia

and consequential fragmentation of forests in the Cauca River valley has been accelerated by the region's favourable climate, the fertility of its soils, and a lack of control from the authorities, which have allowed massive deforestation that has provided pathways for agricultural development with pastures and croplands (particularly sugar cane). Additionally, irregular settlements have allowed people to occupy most of the forested areas that remain in the city. These surviving patches of urban forests within cities often serve as refuges of biodiversity (Ives et al. 2016; Luna et al. 2018), potentially supporting viable populations of native, and possibly threatened, species.

As such, urban patches (or urban environments) can prevent biodiversity loss and thus play an essential role in reaching the objective of the Convention on Biological Diversity (CBD) (Müller et al. 2013). For this reason, a growing interest has focused on including biodiversity in urban planning (UN Secretariat of the Convention on Biological Diversity 2012) as an effective tool to reduce the negative impacts of urbanization on ecosystem services (Haase et al. 2014). There is an urgent need to develop strategies that promote biodiversity and urban forest patches, strategies that are aimed at sustainable development, liveability, and resilience in the urban environment (Gómez-Baggethun et al. 2013; Soanes and Lentini 2019). Further, there is a need to develop biodiversity monitoring baselines in these areas through rapid species inventories (McKinney 2002).

The present study widely adheres to McKinney's (2002) suggestions and to the proposal of Pizano et al. (2017) for the advancement of knowledge and conservation of tropical dry forests, taking ants (Hymenoptera: Formicidae) and ground beetles (Coleoptera: Carabidae) as study models. Both of these taxonomic groups have been proposed as ecological bioindicators at a global level. They quickly respond to habitat transformation, are highly diverse and abundant in almost all types of environments, perform a variety of functions within ecosystems, are relatively easy to sample, and have relatively good taxonomic resolution (Ribas et al. 2012; Gerlach et al. 2013; Aranda et al. 2022; Makwela et al. 2023). Specifically, ants have largely been used as a target group to assess diversity in highly transformed scenarios, suggested as indicators of environmental changes. For example, their competitive interactions are modified by anthropogenic habitat alterations (Achury et al. 2020), habitat loss has shown to eliminate ant-plant mutualistic networks (Emer et al. 2013), and changes in the richness and composition of species in urban fragments have been indicated (Santos et al. 2019), among other studies. Meanwhile, studies on ground beetles have shown that more urbanized sites have significantly fewer forest specialists and more generalist species (Gaublomme et al. 2008), the group clearly responds to agricultural management practices

(Kotze and O'hara 2003), and beetle diversity composition and traits change along an urbanization gradient (Koivula and Vermeulen 2005).

Various other studies have indicated that abiotic variables influence the diversity and composition of species. Temperature and humidity, for example, are known to be determinants of ant species richness (Vasconcelos et al. 2018; Werenkraut et al. 2015; Dantas and Fonseca 2023) and plant diversity (Leal et al. 2012), which influences other variables such as leaf litter depth, forest cover, and proportion of bare soil. These factors regulate food resources and shelters as microhabitats that support biodiversity (Brandão et al. 2009; Ahuatzin et al. 2019; Fernandes et al. 2019).

The present research aims to establish a baseline inventory of ant and ground beetle diversity within five tropical dry forest patches located throughout an urban matrix in southwestern Colombia, and compare this diversity with a rural tropical dry forest patch surrounded by sugarcane. To date, little relation has been found between ant and beetle richness with the exception that both groups are known to be more diverse in forests than in other anthropogenic land uses in southwestern Colombian Andes (Arenas et al. 2015; Arenas-Clavijo and Armbrrecht 2018). In addition, given the potential of these forest patches as biodiversity refuges for other insects, we include ground beetles (Coleoptera: Carabidae) in our study because most of these species are second-order consumers (predators), and therefore are more susceptible to human disturbances (Eyre et al. 2016; Jacobsen et al. 2022). Furthermore, no previous works have reported the ground beetle diversity from urban forests in the country. As assessing biodiversity is one of the very first steps to propose conservation strategies, we intend to set a baseline for ground beetles for future studies on biodiversity.

The following hypotheses were proposed in this study: (i) ant and carabid beetle assemblages differ among urban tropical dry forest patches in the city of Santiago de Cali, with species richness showing reductions as patch sizes decrease, and all urban patches will be less diverse than the rural forest patch; and (ii) ant and carabid beetle species richness are related to abiotic and biotic conditions such as temperature, humidity, plant diversity, canopy cover, leaf litter percentage, and/or bare soil percentage.

Materials and methods

Study sites

The study was conducted in the city of Santiago de Cali (hereafter "Cali"), southwestern Colombia. Among the natural areas comprising the city, a topographically flat alluvial valley spans approximately 3,000 km², with an average

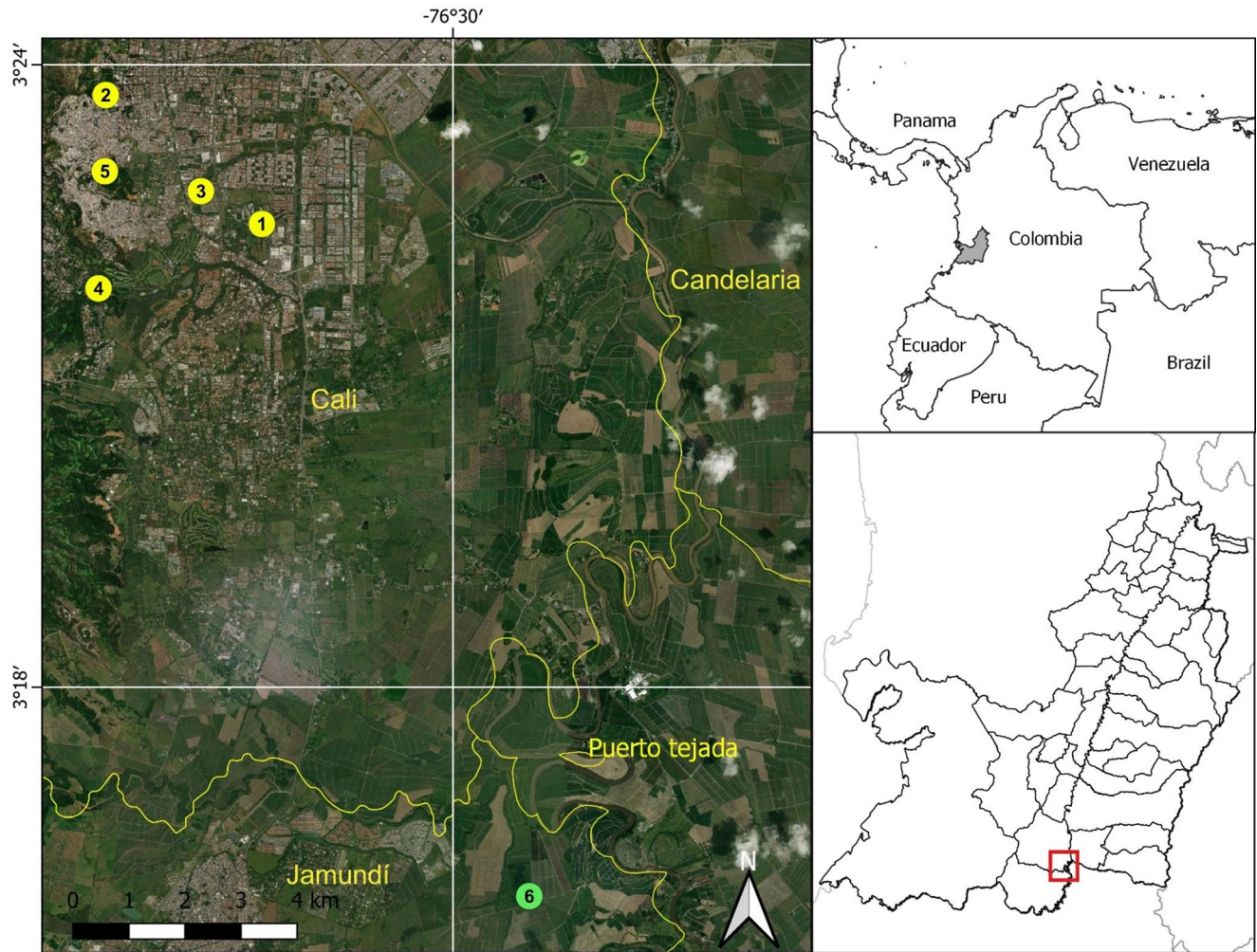


Fig. 1 Location of study sites in the urban area south of Santiago de Cali. 1: UP1 “Microestación”, 2: UP2 “Fundación El Refugio” Cali, 3: UP3 “Meléndez”, 4: UP4 “Club Campestre de Cali”, and 5: UP5 “Cantón Militar Pichincha”

Table 1 Characteristics of the five urban patches (UP in Santiago de Cali) and one rural patch (RP Colindres in Jamundi) of tropical dry forest studied. Altitude: meters above sea level (m.a.s.l.)

Forest patch	Coordinates	Altitude (m.a.s.l.)	Area (ha)
UP1: Microestación	3° 23' 42.59"N 76° 33' 21.01"W	989	1
UP2: Fundación El Refugio	3° 23' 42.79"N 76° 33' 21.08"W	989	1
UP3: Meléndez	3° 22' 47.89"N 76° 32' 25.74"W	986	1
UP4: Club Campestre de Cali	3° 21' 50.87"N 76° 33' 24.14"W	1087	36
UP5: Cantón Militar Pichincha	3° 22' 50.87"N 76° 33' 24.14"W	1040	50
RP: Colindres	3° 15' 59.23"N 76° 29' 16.46"W	970	40

altitude of around 1000 m above sea level (m.a.s.l.), where tropical dry forest has historically existed. Nowadays, however, about 98% of the forest cover has been lost in this valley (Arcila et al. 2012). The area is characterised by temperatures above 24 °C, rainfall between 700 and 2000 mm per year, and usually two marked periods of drought per year (García Martínez et al. 2019). The city has an urban area of 11,570 ha and approximately 2,250,000 inhabitants (DANE 2023). Due to the progressive urbanisation and establishment of agricultural systems, the forest cover has been losing its extension, with only relictual stands remaining amongst an urban matrix. Five of these patches were sampled for this study, with an average separation of 2.4 km between each site (Fig. 1; Table 1 and Supplementary Table S1 online). To account for disturbances other than urban, one closely rural forest patch was also sampled, with an average distance of 14 km from the other sites (Supplementary Table S1 online). This forest fragment, located 21 km south of Cali, is immersed in an agricultural matrix of sugar cane,

the most widespread crop in the region, although its borders are buffered by pastures in ecological succession. This forest patch, located in the vicinal municipality of Jamundí, is called Colindres (hereafter “RP-Colindres”) and belongs to the network of Civil Society Nature Reserves (Table 1).

Sampling design and environmental variables

Each urban forest patch was sampled twice during 2021, between February–April and October–December. The climate pattern La Niña/Southern Oscillation occurred throughout this sampling period, resulting in an atypical meteorological season characterized by unusually high amounts of rain across an extended range of months.

In each forest patch, three starting points were selected at random (considering a minimum distance of 20 m), from which three 50 m long transects were established. Each transect was composed of six stations separated 10 m apart from each other (Supplementary Figure S1 online). Two sampling techniques were carried out at each station: a pitfall trap and visual/hand picking. The first method consisted of 16 oz plastic cups buried flush to the ground with a plastic roof over them (protection against rainfall) and filled 2/3 full with a preservative solution consisting of ethyl alcohol and water. Pitfall traps were arranged in three transects with one trap every 10 m up to 50 m. Transects started 5 m from the forest edge (defined as the outermost line connecting the trunks of mature trees, *sensu* Kotze et al. 2012) into the forest. An additional trap was placed 5 m outside the forest

border. The pitfall traps operated for a week. Each trap and its surrounding area within five meters were considered as a sampling station.

Hand picking was conducted between 06:00 and 09:00 h considering that the activity of ants and carabid beetles decreases around noon in tropical dry forests. The method consisted in actively searching for five minutes per sampling station under rocks, fallen logs, leaf litter, and around each pitfall trap. Several habitat variables were measured at each sampling station, specifically: canopy cover, bare soil, litter depth, vegetal diversity, temperature, and humidity (Table 2).

Laboratory phase

Specimens were preserved in 96% ethanol and later identified to species and/or morphospecies level using taxonomic keys in Fernández et al. (2019) for ants and Reichardt (1977) and Martínez (2005) for carabid beetles. Collected specimens were authorized in the collection permit stated in the resolution 1070 of August 28, 2015 (modified in the resolution 01255 of June 28, 2019) of the Colombian “Autoridad Nacional de Licencias Ambientales” (ANLA). The identified material was deposited into the Entomological Museum of Universidad del Valle (MUSENUV, code: 77), in accordance with the curatorial regulations of the museum and the national biodiversity system (SiB Colombia).

Data analyses

Estimates and comparisons were made for ant diversity and composition. To reduce statistical bias in the ant taxonomic group from the aggregation of workers in colonies, species incidence data were used as a surrogate of abundance (Hölldobler and Wilson 2009). Data on carabid beetles was excluded from the statistical analyses due to their low abundance; however, invaluable biological information was obtained from this data.

Alpha diversity

Non-parametric estimates were used to construct rarefaction curves, and the theoretical species richness was determined. A rarefaction curve was plotted based on the progression of species richness with sampling effort. Sampling completeness was found to determine the percentage of detected species with respect to estimated richness, using the iNEXT package version 3.0.0 (Hsieh et al. 2016) in RStudio 4.2.2 (RStudio Team 2022).

Ant richness was estimated using rarefaction cover (Chao et al. 2014) for three orders of diversity (Hill numbers $q=0$, 1 and 2): (1) $q=0$, or effective species richness (0D), which

Table 2 Selected environmental variables in the urban and rural patches of tropical dry forest in Santiago de Cali, Valle del Cauca, and the rural patch Colindres in Jamundí, Valle del Cauca

Variable	Description
Canopy cover	This measurement was carried out according to the recommendations of Lemmon (1956) and Baudry et al. (2014) with a spherical vegetation densitometer in the centre of each sampling point.
Bare soil (%)	This percentage was estimated from the average of ten measurements around each pitfall trap, taken with a GRS densitometer, according to guidelines of FAO (2015).
Litter depth	A ruler was inserted into the litter until it reached the ground, and the depth was read (in centimetres). The measurement was repeated four times around each pitfall trap, and the values were averaged.
Plant diversity	An inventory of vegetal diversity was carried out in a 5 m radius around each sampling point, considering trees and shrubs.
Temperature and humidity	These measurements were taken between 09:00 and 10:00 h with a digital thermo-hygrometer, allocating the sensor as close as possible to the pitfall trap site.
Patch area	The size of the area for each urban and rural patch of tropical dry forest in the city of Santiago de Cali.

gives greater weight to rare species; (2) $q=1$, or Shannon exponential (1D), in which species are assigned in relation to their incidence; and (3) $q=2$, or inverse Simpson (2D), which gives greater weight to the dominant species.

Using the data from the rarefaction curves, diversity comparisons were performed according to the effective number of species, $q=0$ (Chao and Jost 2012), with inter and extrapolations. The diversity between urban and rural patches of tropical dry forest was compared in four proposed scenarios: (1) effective number of species, (2) interpolation with respect to the lowest sampling coverage, (3) extrapolation with respect to the forest patch with the greatest sampling coverage, and (4) average between the site with the highest coverage and the site with the lowest coverage.

Beta diversity

In order to determine species shared across forest patches, and the turnover of ant species among them, a non-metric multidimensional scaling (NMDS) was performed using the incidence frequency data with the Jaccard similarity measurement. This analysis was run for k values (number of dimensions) ranging from one to two dimensions, and the optimal number of dimensions was determined by examining a scree plot of stress vs. k dimensions. In addition to NMDS, a similarity analysis (ANOSIM) was performed to test if there are similarities between ant communities across different patches of tropical dry forest. These tests were performed with the *vegan* package in R (Oksanen et al. 2019). To determine which species contribute to the dissimilarity between locations (Clarke and Warwick 2001), a SIMPER test (percentage of similarity-contribution by species) was performed with the *vegan* R package (Oksanen et al. 2019). Furthermore, to discard any potential effect of the geographic location on ant communities and their diversity, a Mantel spatial autocorrelation test was performed. This analysis was based on the Spearman rank correlation of a geographic distance matrix (sites) with a Bray-Curtis similarity matrix (composition of communities), with 999 permutations.

Effect of environmental factors on biodiversity attributes

To assess the impact of abiotic factors on species richness in urban and rural tropical dry forest patches, a generalized linear model with a Conway-Maxwell-Poisson (GLM-CMP) distribution was performed. Variable selection was carried out using the Akaike Information Criteria (AIC), identifying relevant variables that explain ant richness behavior. An analysis of variance determined the significance of the final variables in the model, and model fit was indicated by

a pseudo- R^2 . We used the *glmmTMB* package to perform the modeling of generalized linear mixed models (Brooks et al. 2017).

Results

Diversity of ant and carabid beetle species

During the two sampling seasons, 6273 ants were obtained, belonging to 38 genera and 109 morphospecies (hereafter: species, Supplementary Table S2 online). Species identification led to 86 spp.; *Nesomyrmex vicinus* (Mayr, 1887), *Pheidole alacris* Santschi, 1923, *Ph. alpestris* Wilson, 2003, and *Ph. tobini* Wilson, 2003 represent new country records for Colombia (Supplementary Figure S2 online). *Wasmania auropunctata* (Roger, 1863) was the most abundant species in all the urban patches (1835 individuals), followed by *Solenopsis azteca* Forel, 1893 and *Pachycondyla harpax* (Fabricius, 1804) with 348 and 304 individuals, respectively.

For carabid beetles, a total of 39 individuals representing 13 morphospecies from ten genera were collected (Supplementary Table S3 online). The invasive carabid *Mochtherus tetraspilotus* (Macleay, 1825), which was collected only at RP, was the most abundant species. In general, a low abundance of carabids was observed in the different urban patches. All the recorded genera are ground dwellers, and they are commonly reported in soil samples from other tropical dry forests. This is the first known record of *Athrostictus chlaenioides*, *Galerita aequinoctialis*, and *Notiobia umbrifera*, associated with processes of urbanization in Colombia. Further, *Mochtherus tetraspilotus* and the genera *Selenophorus*, *Notiobia*, and *Pentagonica* are reported for the first time in the rural patch of RN.

Alpha diversity

For ants, the most species were present at UP2 (${}^0D=55$), followed by RP (${}^0D=49$), then UP3 (${}^0D=48$), UP5 (${}^0D=46$), UP1 (${}^0D=45$), and finally, UP4 (${}^0D=37$) (Fig. 2).

Regarding common species (1D), UP2 again showed the highest number (${}^1D=36.82$), followed by UP5 (${}^1D=33.01$), UP1 (${}^1D=31.57$), RP (${}^1D=31.15$), UP3 (${}^1D=32.62$), and UP4 (${}^1D=23.91$). However, for the diversity order (2D), UP2 represented the patch with the largest number of very abundant species (${}^2D=28.81$), followed by UP3 and UP5 (${}^2D=25.93$ and ${}^2D=25.09$, respectively), then UP1 (${}^2D=24.87$), RP (${}^2D=22.45$), and finally, UP4 (${}^2D=16.59$) (Fig. 2).

For ants, the sampling coverage was different between the urban and rural patches (Fig. 2). Even so, sampling coverage was above 84.6% in all sites (Fig. 3), which means very few additional species would be expected if the sampling

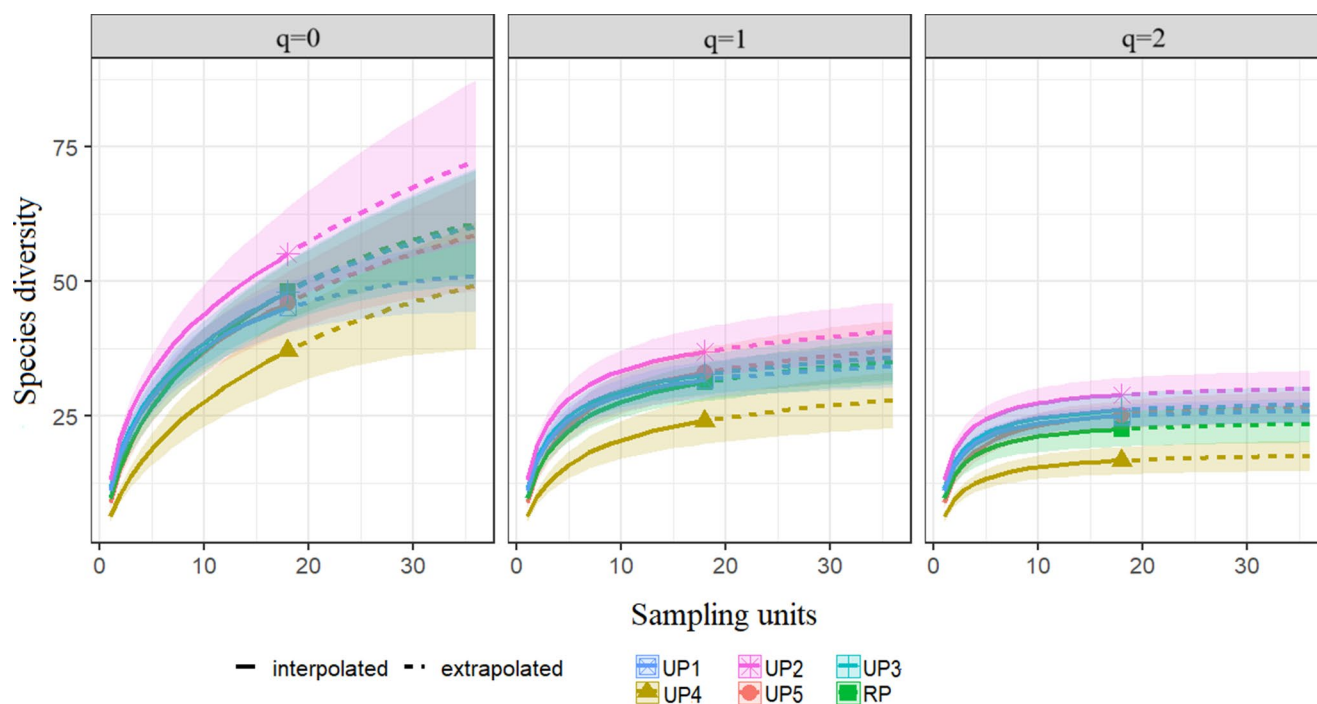


Fig. 2 Rarefaction curves based on ant species richness for each urban tropical dry forest patch; $q=0$ or effective species richness (0D), $q=1$ or Shannon exponential (1D), and $q=2$ or inverse Simpson (2D)

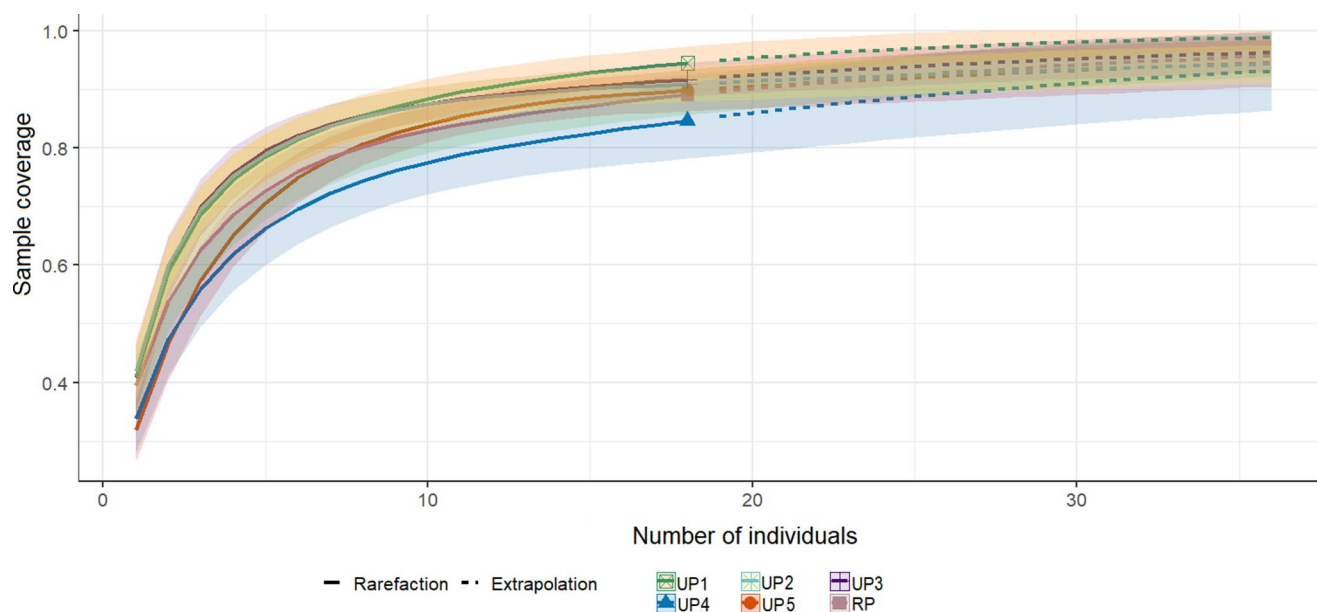


Fig. 3 Rarefaction curves constructed based on the completeness of the sample of each urban and rural patch

effort were larger (Fig. 3). As the 95% CIs overlap between urban patches, the estimates are not considered different from each other.

Comparison of diversity of ants

Four scenarios are proposed (Fig. 4, Supplementary Table S4 online):

Scenario 1 (effective species richness): UP2 presented the highest values for diversity indices measuring richness (${}^0D=55$), common species (${}^1D=36.82$), and dominant species (${}^2D=28.81$), followed by UP5 for common and dominant species (${}^1D=33.01$ and ${}^2D=25.09$), but not in richness.

Scenario 2 (interpolation with respect to the lowest sampling coverage UP4=84.6%): this scenario varied with respect to scenario 1: RP had the highest observed richness

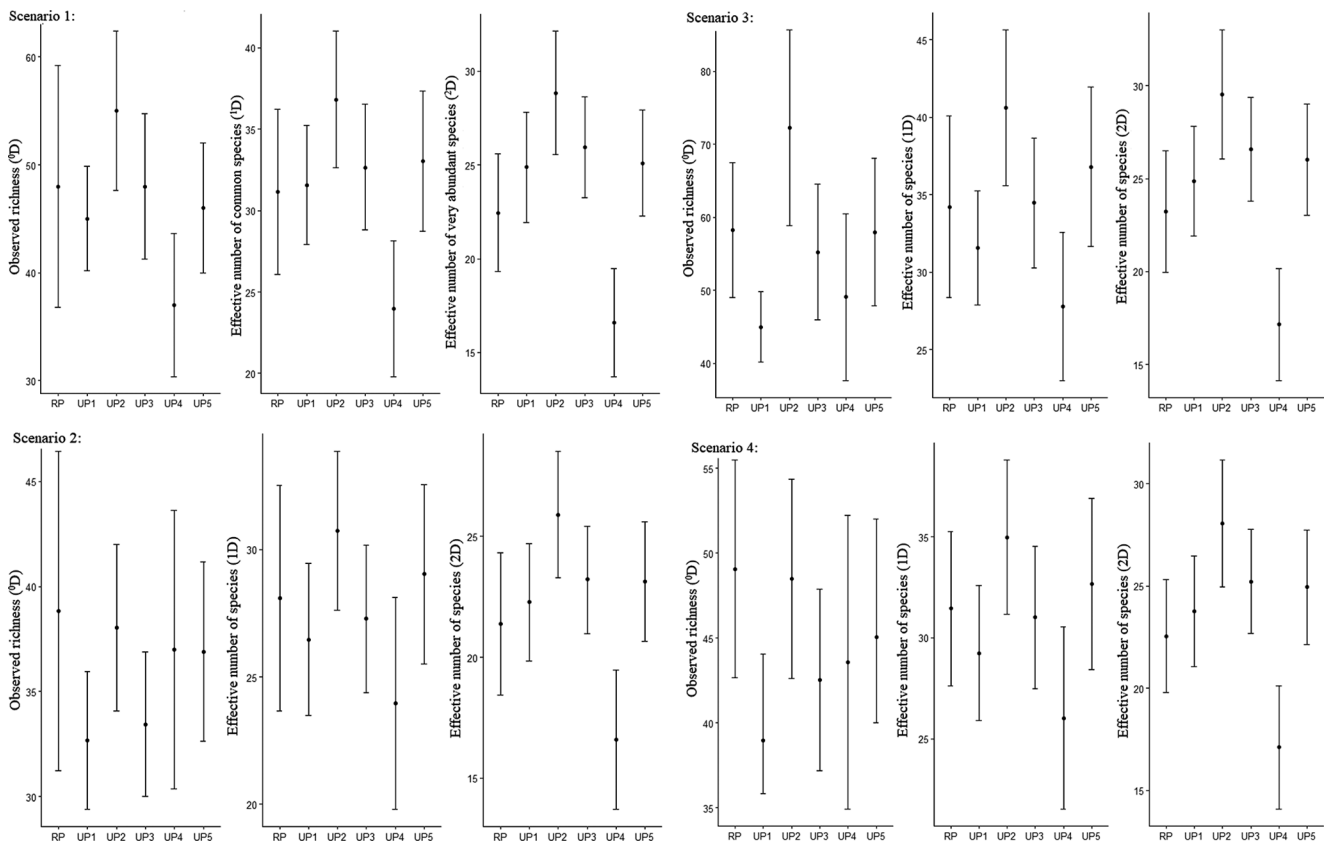


Fig. 4 Scenarios for comparing ant diversity in urban (UP1 to UP5) and rural (RP) patches of tropical dry forest. Scenario 1: effective species richness, Scenario 2: interpolation with respect to the lowest sampling coverage, Scenario 3: extrapolation with respect to the for-

est patch with the greatest sampling coverage and Scenario 4: average between the site with the highest coverage and the site with the lowest coverage

(${}^0D = 38.83$), followed by UP2 (${}^0D = 38.04$), which also presented the highest values for common and dominant species (${}^1D = 30.74$ and ${}^2D = 25.90$, as in scenario 1).

Scenario 3 (extrapolation with respect to the forest patch with the greatest sampling coverage UP1 = 94.4%): results in this scenario were similar to the first and second scenario, with UP2 and RP having the greatest richness of effective species (${}^0D = 72.28$ and ${}^0D = 58.25$ respectively), while UP2 again had the highest number of common and dominant species (${}^1D = 40.60$ and ${}^2D = 29.52$).

Scenario 4 (average between the sites with the highest and lowest coverage): RP and UP2 presented the highest values for effective species richness (${}^0D = 49.05$ and ${}^0D = 48.49$ respectively), and UP2 had the highest values for the other two indices (${}^1D = 34.97$ and ${}^2D = 28.04$).

The results of UP2 and the RP presenting the greatest richness of effective species (0D) are consistent across all comparison scenarios.

For carabid beetles, RP showed the highest effective species richness (${}^0D = 7$ species), followed by UP5 and UP1 presenting the same effective species richness (${}^0D = 3$ species), then UP2 (${}^0D = 2$ species), and finally, UP3 (${}^0D = 1$

species). In general, low abundances were observed for this taxonomic group.

Beta diversity: ant communities

The NMDS grouping analysis with ants (stress = 0.1533) showed that the urban patches UP1, UP2, and UP5 show similarities, and they are different from UP3 and UP4. Likewise, all urban patches separate from the rural patch. The urban patches show overlap, specifically between UP1, UP2, and UP5. The observed stress value indicates that the observed ordering was a fair representation of the dissimilarity matrix between the ant communities (Fig. 5).

The analysis of similarities showed significant differences between urban patches and the rural patch (global R ANOSIM = 0.9379, $p = 0.001$; 999 permutations). The NMDS and ANOSIM similarity analyses (Fig. 5) reveal a separation of species composition between urban patches. The spatial autocorrelation test showed correlation between geographic distance and Jaccard dissimilarity matrix (Mantel statistic $r = 0.5857$; p -value: 0.077), suggesting dependence

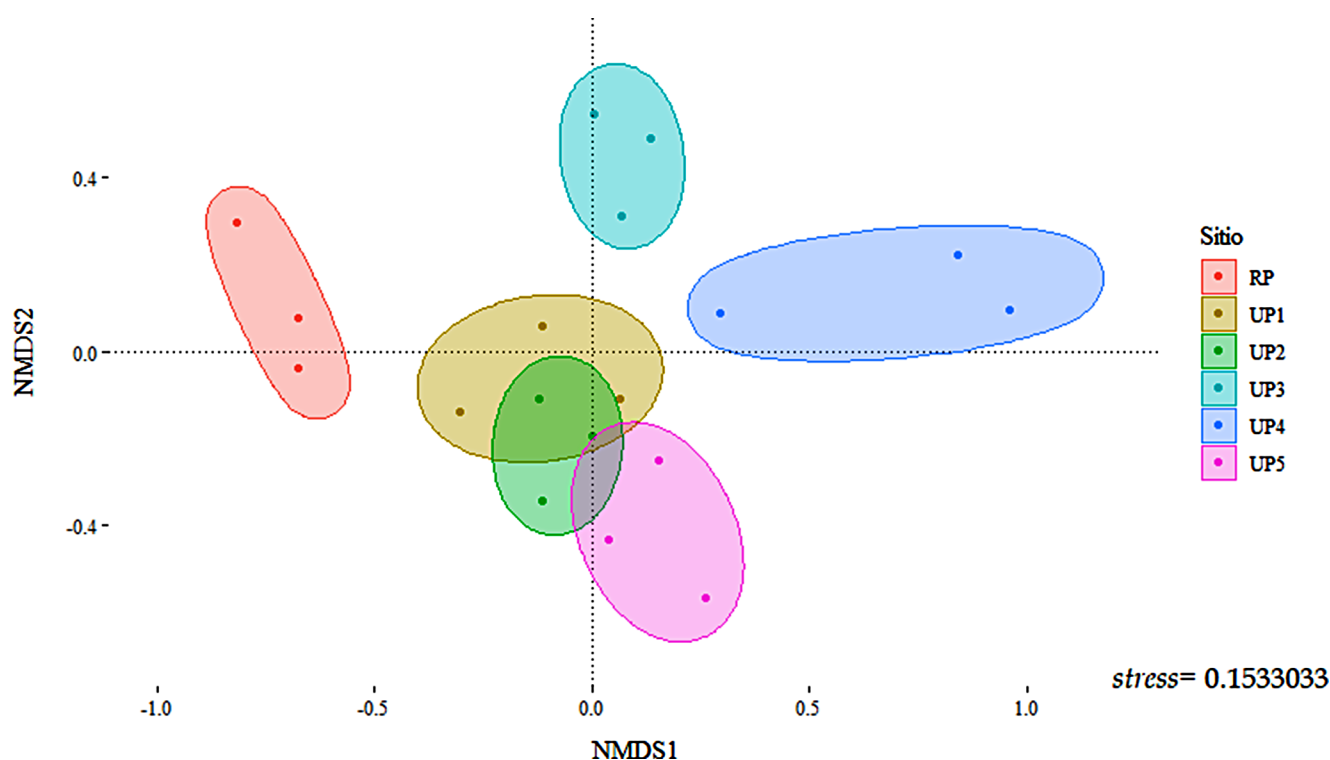


Fig. 5 Ordering of ant communities in the urban and rural patches of dry forest by means of non-metric multidimensional scaling (NMDS) using ant incidence data

Table 3 Contribution to the dissimilarity of urban and rural tropical dry forests for each pair of patches: values represent the sum of the percentages of dissimilarity

	UP1	UP2	UP3	UP4	UP5	RP
UP1	-	68.29	70.10	77.60	77.34	72.94
UP2	68.29	-	69.38	79.56	78.59	77.29
UP3	70.10	69.38	-	81.26	82.75	81.11
UP4	77.60	79.56	81.26	-	80.99	85.25
UP5	77.34	78.59	82.75	80.99	-	83.75
RP	72.94	77.29	81.11	85.25	83.75	-

of the composition of ant communities and sites on geographic distance.

The SIMPER analysis showed a dissimilarity in ant species composition between the different urban and rural patches (Table 3). *Odontomachus bauri*, *Solenopsis azteca*, *Crematogaster curvispinosa* and the exotic ant *Monomorium floricola* contributed strongly to the dissimilarity of UP1, while for UP2 only *Pheidole sussanna* Forel, 1886 was distinct; *Holcaponera striatula*, *Nylanderia steinhelli*, and *Crematogaster carinata* stood out for UP5, while for UP4 the species *Pachycondyla harpax*, *Ph. simonsi*, and *Ph. synarmata* were most dissimilar to other sites. In RP *Pheidole* cf. *calimana* contributed to the dissimilarity (Supplementary Table S5 online). *Wasmannia auropunctata* stands out as one of the species with the greatest contribution to the average dissimilarity between groups. This can be explained due to the most abundant species tending to have highest

variances and contributions in SIMPER analyses even when they do not differ between groups (Supplementary Table S5 online).

Effect of environmental factors on biodiversity attributes

The GLM-CMP revealed that five of the seven assessed variables (Table 2) were significant in explaining ant richness in urban and rural patches of tropical dry forest in the city of Santiago de Cali. Humidity, canopy cover, and plant diversity positively influenced ant species richness, while bare soil and patch area were negatively associated with species richness (Table 4).

Discussion

Alpha diversity

Despite the hydrological anomaly of La Niña/Southern Oscillation (ENSO) event (2020–2022), an efficient sample coverage was obtained (Figs. 2 and 3) in ants. The ENSO occurs in the South American tropics (Poveda and Mesa 1996) and directly affects the conditions of the rural and urban patches of tropical dry forest. In 2021, Cali city experienced acute and abundant rains. As stated by Fuentes and Campusano (1985), the response of natural populations to climatic fluctuations is dependent on the density-dependent structure, which is the consequence of the food web architecture in which the population is embedded. Although studies on terrestrial arthropods are scarce, the emergence of some arthropod species (ants in our case) may be expected to be favoured by the increases in plant growth, fruit, and seed production associated with the excess rainfall, as documented in Galapagos Islands (Dueñas et al. 2021) and in arid areas in Chile (Fuentes and Campusano 1995). In contrast, carabid beetles were scarce, both in terms of abundance and richness, which we discuss below.

Considering these climatic conditions and the resulting diversity response (${}^0D=55$ species), a noteworthy result was that the UP2 patch was the most diverse in all the biodiversity comparison scenarios despite being the smallest in area (together with UP3). This pattern is contrary to what is expected from island biogeography theory (MacArthur and Wilson 1967), which states that richness increases with fragment area. Despite this, this observed phenomenon has been documented in other urban studies with ants (Gibb and Hochuli 2002; Clarke et al. 2008; Ješovnik and Bujan 2021). One possible explanation is that this fragment this fragment has remained isolated from human actions such that internal degradation has not permeated the interior of the patch. Other patches, such as UP4 and UP5, are internally affected by intense management such as walking paths, which are sometimes paved to favour continuous passage of people and gardening practices. In other words, the biggest forest fragments are being constantly disturbed. The 50-ha forest is used by the battalion military for their exercises (although the internal roads are not paved), and

the 36-ha forest is used for recreation by the club members, with several internal roads that are constantly pruned (possibly also fumigated against mosquitoes). However, we did not evaluate perturbation variables, so this explanation must be further tested in future studies.

One plausible explanation for the unexpected, high richness of UP2, the 1-ha “El Refugio,” is that this urban patch is very close to a piedmont transition zone. This geographical situation might facilitate the colonization of ant species in this patch as opposed to the other patches. Indeed, the other patches (with the exception of UP4) are surrounded by an accentuated urban matrix that probably isolates them from the city’s closest natural areas. This isolation could cause a negative effect on the richness of ant species that has been documented in other investigations (Vasconcelos et al. 2006; Emer et al. 2013). However, the fact that the UP4 patch also shows connectivity to the foothills and the Pance River basin hinders this explanation of ant richness due only to this geographical factor.

We expected a relatively greater richness of species in RP due to the surrounding matrix, a combination of agriculture and pasture in regeneration that acts as a buffer towards surrounding cane monocultures. This factor does not seem to have a strong negative effect on the loss of ant richness, and seems to be more “friendly” than the urban matrix (Rivera-Pedroza et al. 2019). While this forest has been conserved for at least three human generations, so have the urban ones. The intensification of usage inside and outside the forests probably affect insect richness, a phenomenon that has been evidenced in studies on ant richness along a land-use gradient, where less degraded environments present greater richness (Armbrecht et al. 2005; Santos et al. 2019; Aranda et al. 2022). Finally, the smallest urban patches may be concentrating biodiversity that has nowhere else to seek refuge, possibly resulting in population stresses for fauna in these last refuges. In this case, community diversity could be expected to decrease in the future, but this hypothesis was not tested in the present study.

Beta diversity: ant communities

The similarity in species composition between urban patches UP1, UP2, and UP3 of dry forest may be explained in terms of their geographic proximity (an average separation of 2.5 km, Supplementary Table S1 online) and the presence of generalist species that can move through the urban matrix that divides these patches. In fact, our results reveal that the distances between transects are statistically correlated with species diversity. That is, the differences in the richness of ant species show correlation or covariation with the geographical distances between the transects in the urban and rural patches. The results also found that the biggest patches

Table 4 Variables explaining ant richness in urban and rural patches of tropical dry forest through the generalized linear model with Conway-Maxwell-Poisson distribution

Variable	Estimate	p-value
Humidity	0.033	5.82e-07
Canopy cover	0.01	<2e-16
Bare soil	-0.003	2.55e-15
Plant diversity	0.001	0.000506
Patch area	-0.006	<2e-16

appear to be distinct from the smallest patches and the rural one. In the NMDS, the urban and rural patches are separated from each other, with the urban patches more closely related amongst themselves (Fig. 5). Agudelo-Martínez and Pérez-Buitrago (2020) found a similar grouping when comparing locations near and far from an urban centre in Arauca Department and suggested that proximity to the urban centre might influence the composition of ant communities by acting as a centre of disturbance that “simplifies” the structure of nearby environments, producing a decrease in species richness.

The presence of dominant South American native species such as *Wasmannia auropunctata*, *Cyphomyrmex rimosus*, and *Atta cephalotes* in urban patches corroborates the fact that some species benefit from disturbances (Tabarelli et al. 2010), as was found by Achury et al. (2020) and Montoya-Lerma et al. (2023) in ants. *Wasmannia auropunctata* stands out for its wide distribution and abundance, and is known for its invasive potential outside of its native distribution range, from Argentina to Mexico (Passera 1994). Similarly, the leaf cutting ant *Atta cephalotes* is commonly found in urban areas of southwestern Colombia, such as Cali (de Chacón de Ulloa et al. 2019).

The observed ant richness was similar than that reported by Ramos-Ortega et al. (2022) from fragments of dry forest and urban environments in Santa Marta (Colombia). These authors found 97 species and/or morphospecies of ants, compared to the 109 found in our study. The richness of the RP rural patch (49 morphospecies) is higher than that obtained from sites close to the urban area of Arauca (23 and 32 species; Agudelo-Martínez et al. 2020).

According to Holway and Suarez (2006), biotic homogenization is the pattern of increasing species similarity between urban areas. The urban patches of dry forest share 14 species, making them highly similar to each other (Supplementary Table S2 online). Most of these species are common (*A. cephalotes*, *B. pictus*, *C. ager*, *Ce. manni*, *N. steinhelli*, *O. bauri*, *P. harpax*, *Ph. alacris*, *Ph. boruca*, *Ph. boruca*, *So. azteca*, *St. louisianae*, and *W. auropunctata*) and have a broad geographic range (Supplementary Table S2 online). Some are classified as “tramp ants” (Passera 1994) with great potential for domiciliation (Olaya-Masmela et al. 2005). Some of these species, such as *W. auropunctata* native to the Americas, even represents one of the most complex invaders to other regions. This species has been classified as dominant and highly competitive (Achury et al. 2020) and could contribute to the homogenization of ant communities (Sanders et al. 2007). As such, the urban matrix likely increased similarities of the species composition among the urban patches, but caused differentiation between the urban patches compared to the rural patch (RP). In this rural patch, a greater number of exclusive species

with specialized habits was found, such as *Acanthognathus ocellatus* Mayr, 1887, *Crematogaster rochai* Forel, 1903, *Neivamyrmex humilis* (Borgmeier, 1939), *Neoponera crenata* (Roger, 1861), and *Nesomyrmex vicinus* (Mayr, 1887).

Invasive ant species are expected to negatively affect native species (Holway et al. 2002), and the proportion of invasive species is expected to be higher in the city than in rural or natural areas (Mack et al. 2000). While this has been observed in ants (see Vonshak and Gordon 2015), only two exotic species were found in the urban patches in Cali: *Monomorium floricola* (Jerdon, 1851) and *Strumigenys rogeri* Emery, 1890; and the rural patch did not present any invasive ant species. One possible explanation for this could be the recent time elapsed since the forests became urban. Just four decades ago, these now remnant urban forests were rural, but have increasingly been engulfed by intensive development towards the south of Cali.

Our results contrast with those reported by Roncallo et al. (2022) from urban environments in the city of Santa Marta, where they found eight exotic species (*Cardyocondila emery*, *Monomorium pharaonis*, *Paratrechina longicornis*, *Pheidole indica*, *Tapinoma melanocephalum*, *Tetramorium lanuginosum*, *Te. simillimum*, and *Trichomyrmex destructor*). The overall perception of these species is negative, as they often display aggressive behaviour and high plasticity to colonise and establish in new areas with high chances of becoming domestic pests (Jaramillo and Chacón de Ulloa 2003; Chacón de Ulloa et al. 2006). More importantly, however, these exotic species might affect the local diversity by inducing the displacement (or even extinction) of native species (Grimm et al. 2008; Faeth et al. 2011; Falcão et al. 2017).

Another important but underestimated threat stems from the native species, such as the leaf cutting ant *A. cephalotes*. This species has been observed to create favourable ecological communities by exploiting urban patches and successfully outcompeting other native ant species, a process favoured by the absence of control measures in such areas (Montoya-Lerma et al. preprint). In Cali, increasing the environmental heterogeneity and connectivity is advisable to avoid McKinney’s predictions (2006) that such biological homogenization and elimination of native species from an area will lead to the establishment of non-native species. Unfortunately, according to its property owners (pers. comm. 2023), the RP is for sale, and its future is uncertain against a fastly growing trend of urbanization in the area. Likely in a few decades, this forest patch will be surrounded by large condominiums.

The NMDS, ANOSIM, and SIMPER analyses found that the urban patches are represented by generalist species like other patches in the middle basin of the Cauca River. With this high percentage of generalist species, the compositional

differences in ant communities are similar (Table 3, Supplementary Table S5 online). Species in genera such as *Solenopsis*, *Crematogaster*, and *Pheidole* are tolerant to a wide range of environmental conditions (Silva et al. 2007; García-Martínez et al. 2015). Fortunately, in the rural patch of tropical dry forest, specialist species such as *Acanthognathus ocellatus*, *Gnamptogenys alfaroi*, *Nesomyrmex humilis*, *Neoponera crenata*, *Neivamyrmex vecinus*, and *Procryptocerus* sp.1 are still present, possibly due to the heterogeneity of microhabitats (Silva et al. 2007).

Effect of environmental factors on ant biodiversity attributes

According to the GLM-CMP, ant richness is positively influenced by humidity, canopy cover, and plant diversity. These variables have been associated with heterogeneous habitats, where an increase in tree richness may represent greater resource availability for generalist ant species (Ribas et al. 2003), a pattern also observed in urban patches (Ahuatzin et al. 2019). The combination of fragment area and habitat structure has been found to be a significant predictor of species richness (Leal et al. 2012; De Queiroz et al. 2013). Our results emphasize that the size of both urban and rural patches negatively affects ant species composition and richness. Larger patch sizes exhibit lower species diversity and share a higher proportion of species, mostly generalists. It is possible that larger urban patches are more exposed to other pressures, such as anthropogenic influences.

Although several studies have reported that ants are positively influenced by temperature (Gibb et al. 2015; Grevé et al. 2018; Parr and Bishop 2022; Almeida et al. 2023), this variable was not detected as significant in our GLM-CMP model. We were also unable to detect the effect of leaf-litter depth on ant richness. It has been largely reported that leaf-litter serves as habitat and for supplying prey (McGlynn et al. 2009); several studies (Pacheco et al. 2009; Silva et al. 2011; Liu et al. 2019) have suggested that the heterogeneity of the litter depth is a determinant factor for ant feeding on the tropical forest soils. Other abiotic and/or biotic factors should be considered for potentially influencing the richness of ants, for example, the availability of light and nesting sites, among others.

Diversity of carabid beetles

This study is the first to report the diversity of ground beetles within tropical dry forest patches inside an urban matrix. Although the number of individuals seems very low when compared to ants, this pattern is not unusual. A standardized sampling effort within a rural area of tropical dry forests in the same inter-Andean valley found only 67 individuals of

25 species (Arenas and Chacón de Ulloa 2016). In another tropical dry forest within the same valley (El Vínculo Regional Park), sampling involving 30 days of pitfall trapping (30 traps), hand picking (3 h of nocturnal searches) and leaf-litter sifting (6 samples of 1 m²) yielded only 59 individuals of 21 species (Arenas-Clavijo, unpublished data).

Overall, carabid abundance and richness in both the urban and rural forest patches were comparatively low. *Mochtherus tetraspilotus* (Macleay, 1825), collected only at RP, was the most abundant species, which is remarkable considering that this is an exotic species to Colombia (Torres-Domínguez et al. 2020). It is likely that the local scarab species are surviving at very low populations, potentially indicating that these populations are under high pressures (i.e., competition, habitat transformation, incidence of invasive species, low quality matrix, etc.), but this requires further studies. A possible explanation for the low number carabids collected may be the relatively scarce sampling effort. In forested areas, Uribe and Vallejo (2013) collected 313 carabids representing four subfamilies, eight tribes, and ten genera using complementary capture methods such as black light traps and interception plus manual sampling. However, their study was performed outside of urban matrices, inside a relatively conserved dry forest in central Colombia. While previous studies have assessed carabid beetle diversity in other tropical dry forest areas (Uribe and Vallejo 2013; Arenas et al. 2015; Arenas-Clavijo and Chacón de Ulloa 2016; Ariza et al. 2021), but this is the first study intended to report such diversity within an urban matrix.

Since our sampling effort was adjusted to the sampling protocols for carabids (Lövei 2008), we consider this to be adequate in our urban patches. Moreover, it seems that the dominance of ants at lowlands (i.e., ~900–1000 m. asl) is high, so much so that other ground dwelling organisms (such as ground beetles) are not likely to be readily found. In contrast, at higher altitudes ant incidence decreases, and ground beetle abundance seems to be higher with the same sampling effort (Arenas and Armbrrecht, unpublished data).

The sampling representativeness for carabid beetles was very low compared to that of ants (Supplementary Table S3 online); therefore, the rarefaction curves for this group did not reach an asymptote. Because of the low representativeness in this family, it was excluded from the biodiversity analyses proposed for this work. However, the findings from this study using a standard sampling method for all patches are very important to report. These insects have been relatively well studied in temperate urban environments (Lövei and Sunderland 1996; Niemelä et al. 2000. Magura et al. 2010), and display the following patterns: (i) their species richness declines as urbanization increases (Gibbs and Stanton 2001; Niemelä et al. 2002; Ishitani et al. 2003; Venn et al. 2003; Weller and Ganzhorn 2004), (ii) urbanization

negatively impacts their abundance even for the most abundant species, (iii) the forest specialists do not thrive in areas affected by urbanization (Venn et al. 2003, 2013; Mitchell et al. 2023), and (iv) these effects are even manifested in morphological characteristics (Magura and Lövei 2021). Studies sampling carabid diversity in those zones and other tropical areas report between three and 28 days of sampling with pitfall traps per unit (Antvogel and Bonn 2001; Ariza et al. 2021). Despite the highly transformed environments surrounding the urban tropical dry forests, they still hold some proportion of ground beetle diversity (even if the abundance is low due by natural dynamics), making these patches important biodiversity reservoirs within urban planning. Considerations regarding their natural history should be considered for contributing to urban ecology knowledge.

Species of *Apenes*, *Loxandrus*, *Notiobia*, and *Selenophorus* are typically found in the leaf litter of forests at various degrees of conservation (Arenas et al. 2015; Arenas-Clavijo and Chacón de Ulloa 2016). The first two genera are considered generalist predators, while the latter two feed on seeds (Paarmann et al. 2001; Arndt and Kirmse 2002). Although their abundances recorded in urban forests were very low in this study, the presence of these genera shows that, even in such a densely populated city, resources still exist to sustain viable small populations. In the geographic region where this study was conducted, both *Athrostictus chlaenioides* (Dejean, 1829) and *Galerita aequinoctialis* Chaudoir, 1852 are typically found in open, rural areas (AAC, pers. obs.). Their presence within the forests could be due to external pressures exerted by the surrounding ecosystems on increasingly smaller and isolated forests, where generalist species can enter and move through forest fragments as well as some areas in early succession (Ariza et al. 2021).

A remarkable observation was the detection of *Notiobia umbrifera* Bates, 1884 within an urban forest, as this species had previously only been recorded in well-preserved habitats both in the same region (Arenas et al. 2015) and in the Amazon (Paarmann et al. 2001). This may be attributed to the presence of a certain key resource, such as *Ficus* spp. commonly found in urban patches in Cali, which is a crucial resource for maintaining populations of several *Notiobia* species, apparently independent of the size of the forest patch. This suggests that while the patch sizes in urban areas may not be as large as in natural habitats, maintaining key elements of plant-animal interactions can favour the preservation of at least a small portion of carabid populations.

This study highlights the feasibility of using ants in urban ecology studies. It shows that urbanization negatively affects species composition, with generalist and wide-ranging species being more present in urban patches of tropical dry forest. In the city of Santiago de Cali, the largest patches do not necessarily have the greatest diversity of ants, but

rather contain mostly generalist native species with a low proportion of exotic species. The type of matrix surrounding the study areas may influence the diversity and composition of ant species, as well as environmental variables such as canopy cover, bare soil, litter depth, plant diversity, and patch area. Although ground beetles presented low richness and abundance in urban patches of tropical dry forest, this study provides preliminary information on species within matrices of anthropogenic change. This study furthers our knowledge on the ant and carabid fauna of the urban forests within the city of Cali.

As stated by Soanes and Lentini (2019), “people cannot protect what they are not aware of.” The present study gives additional data and tools for citizens and land managers to make decisions in a more scientific way. In general, this study demonstrates the biological value of urban forest fragments in a ~2,5 million people neotropical city, habitat that lots of organisms depend on for survival. Therefore, the conservation, diversification, and expansion of these patches is a recommend policy for future urban planning. This study also cautions against the intensive management within the interior of such forest patches, as the largest urban patches were internally fragmented by linear elements (walking roads) and military practices, possibly causing a decrease in their species richness. The urban forest fragments still harbour unique ant species whose populations might be decreasing, but this hypothesis requires further testing.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11252-023-01504-y>.

Acknowledgements This research was funded by the Ministry of Sciences and Technology (MinCiencias-Colombia) within the collaborative Program 70306: Multiscale relationships of biodiversity in altitudinal gradients of the tropical forest, in the frame of the project 70721: “The dry forest in context. Twenty-five years later: spatiotemporal relationships of ant biodiversity” (contract number CT 491–2020) and the research vice-rectory office of the Universidad del Valle, Cali, Colombia. We thank myrmecologist specialists Roberto José Guerrero and Fernando Fernández for their invaluable time in the taxonomic resolution of ant species, and the anonymous reviewers for their valuable comments and suggestions.

Author contributions IA, JML, AAC and NFC conceived ideas and designed experimental design. JML and IA, supervised the study. NFC set up the plot network and collected the data, performed the statistical analysis and wrote initial draft of the manuscript. All authors critically contributed to the final version and gave their approval for publication.

Funding Open Access funding provided by Colombia Consortium

Declarations

Conflict of interest The authors declare no conflict of interest.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing,

adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Achury R, Chacón de Ulloa P, Arcila Á, Suarez AV (2020) Habitat disturbance modifies dominance, coexistence, and competitive interactions in tropical ant communities. *Ecol Entomol* 45(6):1247–1262. <https://doi.org/10.1111/een.12908>
- Agudelo-Martínez JC, Pérez-Buitrago N (2020) Riqueza estacional y estructura de la comunidad de hormigas epígeas en fragmentos de bosque de sabanas inundables, Orinoquia Colombiana. *Rev Biol Trop* 68(3):947–958
- Ahuatzin D, Corro E, Jaimes A, Valenzuela Gonzalez J, Feitosa R, Ribeiro M, Dáttilo W (2019) Forest cover drives leaf litter ant diversity in primary rainforest remnants within human-modified tropical landscapes. *Biodivers and Conserv* 28:1091–1107. <https://doi.org/10.1007/s10531-019-01712-z>
- Almeida R, Silva R, da Costa A, Ferreira L, Meir P, Ellison A (2023) Induced drought strongly affects richness and composition of ground-dwelling ants in the eastern Amazon. *Oecol* 1–11. <https://doi.org/10.1007/s00442-023-05316-x>
- Alvarado-Solano DP, Otero-Ospina JT (2015) Distribución espacial del bosque seco tropical en El Valle Del Cauca, Colombia. *Acta Biol Col* 20(3):141–153. <https://doi.org/10.15446/abc.v20n2.46703>
- Antvogel H, Bonn A (2001) Environmental parameters and microspatial distribution of insects: a case study of carabids in an alluvial forest. *Ecography* 24(4):470–482. <https://doi.org/10.1111/j.1600-0587.2001.tb00482.x>
- Aranda R, Tibcherani M, Nacagava VAF, de Carvalho SS, de Souza PR (2022) The role of urban savannah fragments and their characteristics for the conservation of ants (Hymenoptera: Formicidae) in central Brazil. *Commun Ecol* 23(1):115–127. <https://doi.org/10.1007/s42974-022-00078-7>
- Arcila AM, Valderrama Ardila C, Chacón de Ulloa P (2012) Estado de fragmentación del bosque seco de la cuenca alta del río Cauca, Colombia. *Biota Col* 13(2):86–101
- Arenas A, Corredor G, Armbrrecht I (2015) Hormigas y carábidos en cuatro ambientes del piedemonte del PNN Farallones de Cali, Colombia. *Rev Col Entomol* 41(1):120–125
- Arenas-Clavijo A, Armbrrecht I (2018) Gremios y diversidad de hormigas (Hymenoptera: Formicidae) en tres usos del suelo de un paisaje cafetero del Cauca-Colombia. *Rev Biol Trop* 66(1):48–57. <https://doi.org/10.15517/rbt.v66i1.30269>
- Arenas-Clavijo A, Chacón de Ulloa P (2016) Escarabajos terrestres (Coleoptera: Carabidae) de fragmentos de bosque seco en El valle geográfico del río Cauca, Colombia. *Bol Mus Entomol Universidad del Valle* 16(2):18–25
- Ariza GM, Jácome J, Esquivel HE, Kotze DJ (2021) Early successional dynamics of ground beetles (Coleoptera, Carabidae) in the tropical dry forest ecosystem in Colombia. *ZooKeys* 1044:877. <https://doi.org/10.3897/zookeys.1044.59475>
- Armbrrecht I, Rivera L, Perfecto I (2005) Reduced diversity and complexity in the leaf-litter ant assemblage of Colombian coffee plantations. *Conserv Biol* 19(3):897–907. <https://doi.org/10.1111/j.1523-1739.2005.00062.x>
- Armenteras D, Cabrera E, Rodríguez N, Retana J (2013) National and regional determinants of tropical deforestation in Colombia. *Reg Environ Change* 13(2):1181–1193. <https://doi.org/10.1007/s10113-013-0433-7>
- Arndt E, Kirmse S (2002) Adaptation to seed-feeding in ground beetles (Coleoptera: Carabidae: Harpalini) of South Venezuela. *Stud on Neotrop Fauna and Environ* 37:151–157. <https://doi.org/10.1076/snfe.37.2.151.8581>
- Baudry O, Charmetant C, Collet C, Ponette Q (2014) Estimating light climate in forest with the convex densiometer: operator effect, geometry and relation to diffuse light. *Eur J for Res* 133(1):101–110. <https://doi.org/10.1007/s10342-013-0746-6>
- Brandão CR, Silva RRD, Delabie JHC (2009) Formigas (Hymenoptera). In: Panizzi AR, Parra JRRR (Eds). *Bioecología e nutrição de insetos: Base para o manejo integrado de pragas*. Brasília: Embrapa Informação Tecnológica; 2009
- Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized Linear mixed modeling. *R J* 9(2):378–400. <https://doi.org/10.32614/RJ-2017-066>
- Chacón de Ulloa P, Jaramillo G, Lozano M (2006) Hormigas urbanas en el departamento del Valle del Cauca, Colombia. *Rev Acad Col Cienc* 30(116):435–431
- Chao A, Jost L (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecol* 93(12):2533–2547. <https://doi.org/10.1890/11-1952.1>
- Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK, Ellison AM (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecol Monogr* 84(1):45–67. <https://doi.org/10.1890/13-0133.1>
- Chen G, Li X, Liu X, Chen Y, Liang X, Leng J, Xu X, Liao W, Qiu Y, Wu Q, Huang K (2020) Global projections of future urban land expansion under shared socioeconomic pathways. *Nat Commun* 11:537. <https://doi.org/10.1038/s41467-020-14386-x>
- Clarke KR, Warwick RM (2001) Change in marine communities. An approach to statistical analysis and interpretation. Plymouth, Primer-E Ltd, p 256
- Clarke KM, Fisher BL, LeBuhn G (2008) The influence of urban park characteristics on ant (Hymenoptera, Formicidae) communities. *Urban Ecosyst*. 11:317–334. <https://doi.org/10.1007/s11252-008-0065-8>
- Dantas A, Fonseca CR (2023) Global biogeographical patterns of ants and their abiotic determinants. *Perspect in Ecol and Conserv* 21(3):237–246. <https://doi.org/10.1016/j.pecon.2023.07.003>
- de Chacón P, Montoya-Lerma J, Abadía JC, Castaño-Quintana K (2019) Hormigas urbanas. In: Fernández F, Guerrero RJ, Delsinne T (eds) *Hormigas de Colombia*. Univ. Nacional de Colombia, Bogotá
- De Queiroz ACM, Ribas CR, França FM (2013) Microhabitat characteristics that regulate ant richness patterns: the importance of leaf litter for epigeic ants. *Sociobiol* 60(4):367–373. <https://doi.org/10.13102/sociobiology.v60i4.367-373>
- Departamento Administrativo Nacional de Estadística DANE. http://www.dane.gov.co/files/censo2005/resultados_am_municipios.pdf Accessed 15 February 2023
- Dueñas A, Jiménez-Uzcátegui G, Bosker T (2021) The effects of climate change on wildlife biodiversity of the Galapagos Islands. *Clim Change Ecol* 2. <https://doi.org/10.1016/j.ecochg.2021.100026>
- Emer C, Venticinque EM, Fonseca CR (2013) Effects of dam-induced landscape fragmentation on amazonian ant-plant mutualistic networks. *Conserv Biol* 27(4):763–773. <https://doi.org/10.1111/cobi.12045>

- Etter A, Andrade A, Saavedra K, Cortés J (2017) Actualización de la lista roja de los ecosistemas terrestres de Colombia [electronic source]. <http://reporte.humboldt.org.co/biodiversidad/2017/cap2/204/#seccion1>. Accessed 4th April 2023
- Eyre MD, Sanderson RA, McMillan SD, Critchley CNR (2016) Crop cover the principal influence on non-crop ground beetle (Coleoptera, Carabidae) activity and assemblages at the farm scale in a long-term assessment. *Bull Entomol Res* 106(2):242–248. <https://doi.org/10.1017/S0007485315001054>
- Faeth S, Bang, Saari S (2011) Urban biodiversity: patterns and mechanisms. *Ann NY Acad Sci* 1223:69–81. <https://doi.org/10.1111/j.1749-2066.2010.05925.x>
- Falcão J, Dáttilo W, Díaz-Castelazo C, Rico-Gray V (2017) Assessing the impacts of tramp and invasive species on the structure and dynamic of ant-plant interaction networks. *Biol Conserv* 209:517–523. <https://doi.org/10.1016/j.biocon.2017.03.023>
- Fernandes TT, Dáttilo W, Silva RR, Luna P, Oliveira CM, Morini MS (2019) Ant occupation of twigs in the leaf litter of the Atlantic Forest: influence of the environment and external twig structure. *Trop Conserv Sci* 12:1940082919852943. <https://doi.org/10.1177/1940082919852943>
- Fernández F, Guerrero RJ, Delsinne T (2019) Hormigas de Colombia. F. Fernández (Ed.). Universidad Nacional de Colombia, Bogotá. Entre Textos, 2, 135–138
- Food and Agriculture Organisation of the United Nations (FAO) (2015) Field guide for rapid assessment of forest protective function for soil and water. A scientifically sound, cost effective and easy-to-apply method for collecting data to promote forest management for protection of soil and water. Prepared in the framework of the Global Forest Resources Assessment 2015. <https://www.fao.org/publications/sofi/2015/en/>. Accessed February 28 2023
- Fuentes ER, Campusano C (1985) Pest outbreaks and rainfall in the semi-arid region of Chile. *J Arid Environ* 8:67–72. [https://doi.org/10.1016/S0140-1963\(18\)31338-7](https://doi.org/10.1016/S0140-1963(18)31338-7)
- García Martínez H, Corzo G, Isaacs P, Etter E (2014) Distribución y estado actual de los remanentes del bioma de bosque seco tropical en Colombia: insumos para su gestión: 229–251. In: Pizano C, García Martínez H (eds) *El Bosque Seco tropical en Colombia*. Instituto Alexander von Humboldt, Bogotá
- García-Martínez MÁ, Martínez-Tlapa DL, Pérez-Toledo GR, Quiroz-Robledo LN, Castaño-Meneses G, Laborde J, Valenzuela-González JE (2015) Taxonomic, species and functional group diversity of ants in a tropical anthropogenic landscape. *Trop Conserv Sci* 8(4):1017–1032. <https://doi.org/10.1177/194008291500800412>
- García-Martínez H, Pizano C, López R, Jurado RD, Cuadros H, Castaño-Naranjo A, Mogollón A (2019) Bosque seco Colombia: biodiversidad y gestión. In: García H, González-M R. (Eds). *Bosque seco Colombia: biodiversidad y gestión*. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt. Bogotá, DC, Colombia. 32 p
- Gaublomme E, Hendrickx F, Dhuyvetter H, Desender K (2008) The effects of forest patch size and matrix type on changes in carabid beetle assemblages in an urbanized landscape. *Biol Conserv* 141(10):2585–2596. <https://doi.org/10.1016/j.biocon.2008.07.022>
- Gerlach J, Samways M, Pryke J (2013) Terrestrial invertebrates as bio-indicators: an overview of available taxonomic groups. *J of Ins Conserv* 17:831–850. <https://doi.org/10.1007/s10841-013-9565-9>
- Gibb H, Hochuli DF (2002) Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. *Biol Conserv* 106(1):91–100. [https://doi.org/10.1016/S0006-3207\(01\)00232-4](https://doi.org/10.1016/S0006-3207(01)00232-4)
- Gibb H, Sanders N, Dunn R, Watson S, Photakis M, Abril S, Parr C (2015) Climate mediates the effects of disturbance on ant assemblage structure. *Proc R Soc B: Biol Sci* 282(1808):20150418. <https://doi.org/10.1098/rspb.2015.0418>
- Gibbs JP, Stanton EJ (2001) Habitat fragmentation and arthropod community change: carrion beetles, phoretic mites, and flies. *Ecol Appl* 11:79–85. [https://doi.org/10.1890/1051-0761\(2001\)011\[0079:HFAACC\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2001)011[0079:HFAACC]2.0.CO;2)
- Gómez MF, Moreno LA, Andrade GI, Rueda C (2016) Biodiversidad 2015 Estado y tendencias de la biodiversidad continental de Colombia. Instituto Alexander von Humboldt. Bogotá, D.C., Colombia
- Gómez-Baggeth E, Gren A, Barton DN, Langemeyer J, McPhearson T, O'Farrell P, Andersson E, Hamstead Z, Kremer P (2013) Urban Ecosystem Services (175–251). In: Elmquist T, Fragkias M, Goodness J, Güneralp B, Marcotullio PJ, McDonald RI, Parnell S, Schewenius M, Sendstad M, Seto KC, Wilkinson C (eds) *Urbanization, biodiversity and ecosystem services: challenges and opportunities: a global assessment*. Springer Nature, p 755
- Grevé ME, Hager J, Weisser WW, Schall P, Gossner MM, Feldhaar H (2018) Effect of forest management on temperate ant communities. *Ecosphere* 9(6):e02303. <https://doi.org/10.1002/ecs2.2303>
- Grimm N, Faeth S, Golubiewski N, Redman C, Wu J, Bai X, Briggs J (2008) Global change and the ecology of cities. *Science* 319(5864):756–760. <https://doi.org/10.1126/science.1150195>
- Haase D, Larondelle N, Andersson E, Artmann M, Borgström S, Breuste J, Gomez-Baggeth E, Gren A, Hamstead Z, Hansen R, Kabisch N, Kremer P, Langemeyer J, Rall EL, McPhearson T, Pauleit S, Qureshi S, Schwarz N, Voigt A, Wurster D, Elmquist T (2014) A quantitative review of urban ecosystem service assessments: concepts, models, and implementation. *Ambio* 43(4):413–433. <https://doi.org/10.1007/s13280-014-0504-0>
- Hoekstra JM, Boucher TM, Ricketts TH, Roberts C (2005) Confronting a biome crisis: global disparities of habitat loss and protection. *Ecol Lett* 8(1):23–29. <https://doi.org/10.1111/j.1461-0248.2004.00686.x>
- Hölldobler B, Wilson EO (2009) *The superorganism: the beauty, elegance, and strangeness of insect societies*. Norton, New York
- Holway DA, Suarez AV (2006) Homogenization of ant communities in Mediterranean California: the effects of urbanization and invasion. *Biol Conserv* 127(3):319–326. <https://doi.org/10.1016/j.biocon.2005.05.016>
- Holway DA, Lach L, Suarez AV, Tsutsui ND, Case TJ (2002) The causes and consequences of ant invasions. *Ann Rev Ecol Sys* 33(1):181–233. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150444>
- Hsieh TC, Ma KH, Chao A (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods Ecol Evol* 7(12):1451–1456. <https://doi.org/10.1111/2041-210X.12613>
- Ishitani M, Kotze DJ, Niemelä J (2003) Changes in carabid beetle assemblages across an urban-rural gradient in Japan. *Ecography* 26:481–489. <https://doi.org/10.1034/j.1600-0587.2003.03436.x>
- Ives CD, Lentini PE, Threlfall C, Ikin K, Shanahan DF, Garrard GE, Bekessy SA, Fuller RA, Mumaw L, Rayner L, Rowe R, Valentine L, Kendal D (2016) Cities are hotspots for threatened species. *Glob Ecol Biogeogr* 25(1):117–126. <https://doi.org/10.1111/geb.12404>
- Jacobsen SK, Sigsgaard L, Johansen AB, Thorup-Kristensen K, Jensen PM (2022) The impact of reduced tillage and distance to field margin on predator functional diversity. *J of Ins Conserv* 26(3):491–501. <https://doi.org/10.1007/s10841-022-00370-x>
- Jaramillo G, Chacón de Ulloa P (2003) La hormiga fantasma *Tapi-noma melanocephalum* (Hymenoptera: Formicidae): fecundidad de reinas y desarrollo de colonias experimentales. *Rev Col Entomol* 29(2):227–230. <https://doi.org/10.25100/socolen.v29i2.9609>
- Ješovnik A, Bujan J (2021) Wooded areas promote species richness in urban parks. *Urban Ecosyst* 24(6):1305–1315. <https://doi.org/10.1007/s11252-021-01112-8>

- Koivula MJ, Vermeulen HJ (2005) Highways and forest fragmentation—effects on carabid beetles (Coleoptera, Carabidae). *Landsc Ecol* 20:911–926. <https://doi.org/10.1007/s10980-005-7301-x>
- Kotze DJ, O'hara RB (2003) Species decline—but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. *Oecol* 135:138–148. <https://doi.org/10.1007/s00442-002-1174-3>
- Kotze DJ, Lehvavirta S, Koivula M, O'Hara RB, Spence JR (2012) Effects of habitat edges and trampling on the distribution of ground beetles (Coleoptera, Carabidae) in urban forests. *J Ins Conserv* 16(6):883–897. <https://doi.org/10.1007/s10841-012-9475-2>
- Leal IR, Filgueiras BK, Gomes JP, Iannuzzi L, Andersen AN (2012) Effects of habitat fragmentation on ant richness and functional composition in Brazilian Atlantic Forest. *Biodivers Conserv* 21:1687–1701. <https://doi.org/10.1007/s10531-012-0271-9>
- Lemmon PE (1956) A spherical densiometer for estimating forest overstory density. *For Sci* 2(4):314–320. <https://doi.org/10.1093/forestscience/2.4.314>
- Liu K, Peng M, Hung, Neoh K (2019) Effects of park size, peri-urban forest spillover, and environmental filtering on diversity, structure, and morphology of ant assemblages in urban park. *Urban Ecosyst* 22:643–656. <https://doi.org/10.1007/s11252-019-00851-z>
- Lövei GL (2008) Ecology and conservation biology of ground beetles (Coleoptera: Carabidae) in an age of increasing human dominance. Conference Proceedings
- Lövei GL, Sunderland KD (1996) Ecology and behavior of ground beetles. *Ann Rev Entomol* 41:231–256. <https://doi.org/10.1146/annurev.en.41.010196.001311>
- Luna Á, Romero-Vidal P, Hiraldo F, Tella JL (2018) Cities may save some threatened species but not they ecological functions. *PeerJ* 6:e4908. <https://doi.org/10.7717/peerj.4908>
- MacArthur RH, Wilson EO (1967) The theory of island biogeography. MacArthur RH, editor. MPB 10: 1796430
- Mack RN, Simberloff D, Mark Lonsdale W, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol Appl* 10(3):689–710. [https://doi.org/10.1890/1051-0761\(2000\)010%5b0689:BICEGC%5d2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010%5b0689:BICEGC%5d2.0.CO;2)
- Magura T, Lövei GL (2021) Consequences of urban living: urbanization and ground beetles. *Curr Landsc Ecol Rep* 6:9–21. <https://doi.org/10.1007/s40823-020-00060-x>
- Magura T, Lövei GL, Tóthmérész B (2010) Does urbanization decrease diversity in ground beetle (Carabidae) assemblages? *Glob Ecol Biogeogr* 19(1):16–26. <https://doi.org/10.1111/j.1466-8238.2009.00499.x>
- Makwela MM, Slotow R, Munyai TC (2023) Carabid beetles (Coleoptera) as indicators of sustainability in agroecosystems: a systematic review. *Sustainability* 15(5):3936. <https://doi.org/10.3390/su15053936>
- Martínez C (2005) Introducción a los escarabajos Carabidae (Coleoptera) de Colombia. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá
- McDonald RI, Kareiva P, Forman RTT (2008) The implications of current and future urbanization for global protected areas and biodiversity conservation. *Biol Conserv* 141:1695–1703. <https://doi.org/10.1016/j.biocon.2008.04.025>
- McGlynn TP, Fawcett RM, Clark DA (2009) Litter biomass and nutrient determinants of ant density, nest size, and growth in a Costa Rican tropical wet forest. *Biotrop* 41(2):234–240. <https://doi.org/10.1111/j.1744-7429.2008.00465.x>
- McKinney ML (2002) Urbanization, biodiversity, and conservation. The impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. *Bioscience* 52(10):883–890. [https://doi.org/10.1641/0006-3568\(2002\)052\[0883:UBAC\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2)
- McKinney M (2006) Urbanization as a major cause of biotic homogenization. *Biol Conserv* 127(3):247–260. <https://doi.org/10.1016/j.biocon.2005.09.005>
- Miller JR, Hobbs RJ (2002) Conservation where people live and work. *Conserv Biol* 16:330–337. <https://doi.org/10.1046/j.1523-1739.2002.00420.x>
- Mitchell JC, D'Amico III, Trammell TL, Frank SD (2023) Carabid specialists respond differently to nonnative plant invasion in urban forests. *Urban Ecosyst* 26:377–393. <https://doi.org/10.1007/s11252-022-01323-7>
- Montoya-Lerma J, Castaño-Quintana K, Rodríguez J (2023) *Atta cephalotes* (Hymenoptera: Myrmicinae) is colonizing urban areas in Cali, Colombia? *Urban Ecosyst*. <https://doi.org/10.1007/s11252-023-01469-y>
- Müller N, Ignatieva M, Nilon CH, Werner P, Zipperer WC (2013) Patterns and trends in urban biodiversity and landscape design (pp. 123–174). In: Elmqvist T, Fragkias M, Goodness J, Güneralp B, Marcotullio PJ, McDonald RI, Parnell S, Schewenius M, Sendstad M, Seto KC, Wilkinson C (Eds) *Urbanization, biodiversity and ecosystem services: challenges and opportunities: a global assessment*. Springer Nature. <https://link.springer.com/book/https://doi.org/10.1007/978-94-007-7088-1>
- Niemelä J, Kotze J, Ashworth A, Brandmayr P, Desender K, New T, Penev L, Samways MJ, Spence J (2000) The search for common anthropogenic impacts on biodiversity: a global network. *J Ins Conserv* 4:3–9. <https://doi.org/10.1023/A:1009655127440>
- Niemelä J, Kotze DJ, Venn S, Penev L, Stoyanov I, Spence J, Hartley D, de Oca EM (2002) Carabid beetle assemblages (Coleoptera, Carabidae) across urban-rural gradients: an international comparison. *Landsc Ecol* 17:387–401. <https://doi.org/10.1023/A:1021270121630>
- Oksanen J, Guillaume F, Michael F, Roeland K, Pierre L, Dan Mc, Peter M, O'Hara RB, Gavin LS, Peter S, Henry H, Eduard S, Helene W (2019) *Community Ecology Package*. URL <https://cran.r-project.org>, <https://github.com/vegandevs/vegan>
- Olaya-Masmela LA, Chacón de Ulloa P, Payán A (2005) Hormigas (Hymenoptera: Formicidae) en centros hospitalarios del Valle del Cauca como vectores de patógenos nosocomiales. *Rev Col Entomol* 31(2):183–187
- Paarmann W, Adis J, Stork N et al (2001) The structure of ground beetle assemblages (Coleoptera: Carabidae) at fig fruit falls (Moraceae) in a terra firme rain forest near Manaus (Brazil). *J of Trop Ecol* 17:549–561. <https://doi.org/10.1017/S0266467401001419>
- Pacheco R, Silva RR, Morini M, Brandão C (2009) A comparison of the leaf-litter ant fauna in a secondary atlantic forest with an adjacent pine plantation in southeastern Brazil. *Neotropical Entomol* 38:55–65. <https://doi.org/10.1590/S1519-566X2009000100005>
- Parr C, Bishop T (2022) The response of ants to climate change. *Glob Change Biol* 28(10):3188–3205. <https://doi.org/10.1111/gcb.16140>
- Passera L (1994) Characteristics of tramp species, pp. 23–43. In D. F. Williams [ed.], *exotic ants*. Westview Press, Boulder, CO
- Pizano C, González R, Hernández-Jaramillo A, García H (2017) Agenda de investigación y monitoreo en bosques secos de Colombia (2013–2015): fortaleciendo redes de colaboración para su gestión integral en el territorio. *Biodiversidad en la Práctica* 2(1):87–121
- Portillo-Quintero CA, Sánchez-Azofeifa GA (2010) Extent and conservation of tropical dry forests in the Americas. *Biol Conserv* 143(1):144–155. <https://doi.org/10.1016/j.biocon.2009.09.020>
- Poveda G, Mesa ÓJ (1996) Las fases extremas del fenómeno ENSO (El Niño y La Niña) y su influencia sobre la hidrología de Colombia. *Tecnología Y Ciencias Del Agua* 11(1):21–37
- Ramos-Ortega LM, Sierra H, Roncallo JD, Guerrero RJ (2022) Hormigas asociadas a fragmentos de bosque seco y ambientes urbanos

- de Santa Marta, Colombia. *Biota Col* 23(1). <https://doi.org/10.21068/2539200x.978>
- Reichardt H (1977) A synopsis of the genera of Neotropical Carabidae (Insecta: Coleoptera). *Quaest Entomol* 13(4):346–493
- Ribas CR, Schoereder JH, Pic M, Soares SM (2003) Tree heterogeneity, resource availability, and larger scale processes regulating arboreal ant species richness. *Austral Ecol* 28(3):305–314. <https://doi.org/10.1046/j.1442-9993.2003.01290.x>
- Ribas CR, Solar RR, Campos RB, Schmidt FA, Valentim CL, Schoereder JH (2012) Can ants be used as indicators of environmental impacts caused by arsenic? *J Ins Conserv* 16:413–421. <https://doi.org/10.1007/s10841-011-9427-2>
- Rivera-Pedroza LF, Escobar F, Philpott SM, Armbrecht I (2019) The role of natural vegetation strips in sugarcane monocultures: ant and bird functional diversity responses. *Agric Ecosyst Environ* 284. <https://doi.org/10.1016/j.agee.2019.106603>
- Roncillo J, Ortega LMR, Guerrero RJ, Sierra H (2022) Las hormigas exóticas en ambientes urbanos de Santa Marta, Colombia *Intropica* 17:2. <https://doi.org/10.21676/23897864.4758>
- RStudio T, RStudio (2022) PBC, Boston, MA URL <http://www.rstudio.com/>
- Sánchez-Cuervo AM, Aide TM (2013) Consequences of the armed conflict forced human displacement, and land Abandonment on forest cover change in Colombia: a multi-scaled analysis. *Ecosyst* 16(6):1052–1070. <https://doi.org/10.1007/s10021-013-9667-y>
- Sanders NJ, Gotelli NJ, Wittman SE, Ratchford JS, Ellison AM, Jules ES (2007) Assembly rules of ground-foraging ant assemblages are contingent on disturbance, habitat and spatial scale. *J Biogeogr* 34(9):1632–1641. <https://doi.org/10.1111/j.1365-2699.2007.01714.x>
- Santos MN, Delabie JH, Queiroz JM (2019) Biodiversity conservation in urban parks: a study of ground-dwelling ants (Hymenoptera: Formicidae) in Rio De Janeiro City. *Urban Ecosyst* 22:927–942. <https://doi.org/10.1007/s11252-019-00872-8>
- Seto KC, Güneralp B, Hutyra LR (2012) Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proc Nat Acad Sci* 109:16083–16088. <https://doi.org/10.1073/pnas.1211658109>
- Silva R, Feitosa R, Eberhardt F (2007) Reduced ant diversity along a habitat regeneration gradient in the southern Brazilian Atlantic Forest. *For Ecol Manag* 240(1–3):61–69. <https://doi.org/10.1016/j.foreco.2006.12.002>
- Silva PS, Bieber A, Corrêa M, Leal I (2011) Do leaf-litter attributes affect the richness of leaf-litter ants? *Neotrop Entomol* 40:542–547. <https://doi.org/10.1590/S1519-566X2011000500004>
- Soanes K, Lentini PE (2019) When cities are the last chance for saving species. *Front Ecol Environ* <https://doi.org/10.1002/fee.2032>
- Tabarelli M, Aguiar A, Ribeiro M, Metzger J, Peres C (2010) Prospects for biodiversity conservation in the Atlantic Forest: lessons from aging human-modified landscapes. *Biol Conserv* 143(10):2328–2340. <https://doi.org/10.1016/j.biocon.2010.02.005>
- Torres-Domínguez DM, Arenas-Clavijo A, Londoño-Sánchez C, Armbrecht I, Montoya-Lerma J (2020) First report in South America of the ground beetle *Mochtherus tetraspilotus* (Macleay, 1825) (Carabidae, Lebiini, Pericalina). *BioInvasions Rec* 9 (1): 44–49. <https://doi.org/10.3391/bir.2020.9.1.06>
- United Nations, Secretariat of the Convention on Biological Diversity (2012) <https://sdgs.un.org/publications/cities-and-biodiversity-outlook-action-and-policy-17743>. Accessed 21 March 2023
- Uribe M, Vallejo LF (2013) Diversidad De Escarabajos Carabidae Y Scarabaeidae De Un bosque tropical en El Magdalena medio colombiano. *Bol Cient Cent Mus* 17(2):174–196
- Vasconcelos HL, Vilhena JM, Magnusson WE, Albernaz ALM (2006) Long-term effects of forest fragmentation on amazonian ant communities. *J Biogeogr* 33(8):1348–1356. <https://doi.org/10.1111/j.1365-2699.2006.01516.x>
- Vasconcelos HL, Maravalhas JB, Feitosa RM, Pacheco R, Neves KC, Andersen AN (2018) Neotropical savanna ants show a reversed latitudinal gradient of species richness, with climatic drivers reflecting the forest origin of the fauna. *J Biogeogr* 45(1):248–258. <https://doi.org/10.1111/jbi.13113>
- Venn SJ, Kotze DJ, Niemela JARI (2003) Urbanization effects on carabid diversity in boreal forests. *Eur J Entomol* 100(1):73–80
- Venn SJ, Kotze DJ, Lassila T, Niemelä JK (2013) Urban dry meadows provide valuable habitat for granivorous and xerophilic carabid beetles. *J Ins Conserv* 17:747–764. <https://doi.org/10.1007/s10841-013-9558-8>
- Vonshak M, Gordon DM (2015) Intermediate disturbance promotes invasive ant abundance. *Biol Conserv* 186:359–367
- Weller B, Ganzhorn JU (2004) Carabid beetle community composition, body size, and fluctuating asymmetry along an urban-rural gradient. *Bas Appl Ecol* 5(2):193–201. <https://doi.org/10.1078/1439-1791-00220>
- Wrenkraud V, Fergnani PN, Ruggiero A (2015) Ants at the edge: a sharp forest-steppe boundary influences the taxonomic and functional organization of ant species assemblages along elevational gradients in northwestern Patagonia (Argentina). *Biodivers Conserv* 24(2):287–308. <https://doi.org/10.1007/s10531-014-0808-1>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.