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ORIGINAL RESEARCH ARTICLE

Diversity snapshot of green–gray space ants in two Mexican cities

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Abstract

This study evaluates changes in the diversity and composition of ants that inhabit contrasting environmental conditions (green and gray spaces) in two cities of different size and degree of urbanization: Xalapa and Coatepec (Veracruz, Mexico), both of which are surrounded by cloud forest remnants, croplands and pastures. In each city, a green space and a gray space of similar area were selected (~ 31 ha) and ten sampling sites were randomly placed within each environment. Tuna in oil and honey were used as baits to collect soil ants, entomological nets to capture vegetation ants and Winkler sacks for leaf-litter ants. Ant species richness (^{0}D) and diversity (^{1}D) was greater in Coatepec (the smaller and less urbanized city) than in Xalapa. However, the pattern observed when comparing green and gray spaces differed between the cities: the greatest diversity (^{0}D and ^{1}D) was observed in the gray space of Coatepec and the lowest diversity in the green space of Xalapa. In both cities, the similarity of species composition between habitat conditions was close to 50% and the comparison of green spaces between the cities showed that these are more different to each other than is the case with the gray spaces. These results suggest that the characteristics of each city influence the ant diversity contained in green and gray spaces differently and can promote differentiation in species composition within the same city.

Keywords Formicidae · Species diversity · Species composition · Neotropical cities · Cloud forest

Introduction

Accelerated human population growth in urban areas has transformed the landscape of the cities to include habitat patches with different degrees of disturbance (Faeth et al. 2005; Grimm et al. 2008; Beninde et al. 2015) and varying levels of environmental stress, such as increased temperatures, changes in availability of space and resources and different levels of pollution. These factors may act as ecological filters for many species (Ramalho and Hobbs 2012; Savage et al. 2014; Parris et al. 2018). One of the most studied habitat patches within cities are urban green spaces (forests, parks, private gardens), which present lower levels of stress and less disturbance than gray spaces (sidewalks, streets, buildings) (Savage et al. 2014; Parris et al. 2018). Green spaces generally consist of non-built and environmentally heterogeneous areas, characterized by high levels of diversity of flora and fauna that constitute critical biodiversity hotspots within cities (Nielsen et al. 2014). The opposite diversity patterns occur in gray spaces, since the removal of vegetation cover usually causes changes in the microclimate and availability of resources (Pećarević et al. 2010; Savage et al. 2014). Gray spaces are typical of high-density built up areas and present a high proportion of impervious surfaces. This urban environment generally supports only a few abundant species (Møller et al. 2012), which are often the same throughout the urban space (i.e., similarity in species composition across large spatial scales) (McKinney 2006; Ferenc et al. 2014).

Diversity studies in cities generally focus on comparisons among green spaces such as parks (Nielsen et al. 2014), natural and cultivated greenery (Chong et al. 2014), street median strips and parks or urban forests (Youngsteadt et al. 2014; Savage et al. 2014), urban parks of different areas and ages (Vignoli et al. 2009; Nielsen et al. 2014), forest remnants, community gardens and vacant lots (Uno et al. 2010; Philpott et al. 2014). One general assumption of such studies is that diversity increases with the size of green spaces (Clark

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et al. 2007; Carbó-Ramírez and Zuria 2011) or with increasing vegetation cover (Daniels and Kirkpatrick 2006; Fontana et al. 2011; MacGregor-Fors and Schondube 2011); however, while there are species with the capacity to adapt to different urban stress conditions (McKinney and Lockwood 1999), e.g., ants (Vergnes et al. 2017; Santos et al. 2019), there have been no studies of differences in the species diversity of habitats with contrasting environmental conditions (i.e., green and gray spaces) between cities of different sizes and levels of urbanization.

Ants are particularly suited to applied biodiversity studies given their high abundance and species richness, their regular occurrence throughout the year and nest stability (Alonso and Agosti 2000; Kaspari 2000), as well as the ease of collection and application of standardized sampling designs (Bestelmeyer et al. 2000). The study of the diversity and structure of ant communities may be useful for evaluating the quality of urban environments related to increased urbanization (Santos et al. 2019). It has recently been found that ants are one of the most conspicuous and successful groups of animals in different environments within cities (Santos 2016). They can persist in disturbed environments such as man-made soils (Technosols) used in urban parks (Vergnes et al. 2017) and impervious surfaces (Pećarević et al. 2010). Ecological studies of urban ants have documented changes in diversity and species composition in urban habitat green patches of different sizes (Gibb and Hochuli 2002; Uno et al. 2010; Savage et al. 2014) and degrees of urbanization (Majer and Brown 1986; Brown et al. 2013).

Many urban ant diversity studies have focused on green spaces, but little is known about ant diversity and composition in gray spaces (MacGregor-Fors et al. 2015; Vergnes et al. 2017). More studies of urban ant ecology are therefore required (Vergnes et al. 2017), particularly in contrasting habitats (i.e., green and gray spaces) in small to medium-sized cities characterized by high vegetation coverage but with different urbanization processes. There have been few studies to date on ant diversity within urban areas in Mexico (López-Moreno et al. 2003; Cupul-Magaña 2009), and two of those that do exist are part of multi-taxonomic studies in Xalapa city only. These studies show that ant species richness is lower in highly–urbanized areas compared with lowly–urbanized areas (13% less rich), although no statistically significant differences were detected (MacGregor-Fors et al. 2015). The highest ant species richness is found in the smallest, heavily managed and visited green spaces rather than in larger and less managed green spaces (MacGregor-Fors et al. 2016).

The aim of this study was to compare the diversity and species composition of ant assemblages that inhabit green and gray spaces in two Mexican cities: Xalapa de Enríquez and Coatepec. Both cities are Neotropical urban settlements located in a region of tropical montane cloud forest, one of the ecosystems of greatest diversity and highest endemism levels in Mexico (Rzedowski 1996), but one that is under a high degree of threat due to the increase in cultivated areas and unplanned urban expansion over recent decades (Williams-Linera et al. 2002; Cruz et al. 2010). Xalapa has a higher degree of urbanization, a higher population and is ten times larger in area than Coatepec (Lemoine-Rodríguez 2012; Falfán and MacGregor-Fors 2016). Given that many studies have shown than canopy cover in green spaces can predict high species diversity because it offers the ants shelter and food (Reviewed by Santos 2016), in addition to suitable microclimatic conditions, ant diversity is expected to be greater in the green spaces regardless of the characteristics of the city. Green spaces are also expected to present a species composition that differs from that of the gray spaces and that these differences will be greater in the larger of the two cities.

Materials and methods

Cities

Xalapa, capital of the state of Veracruz (19°32′37” N, 96°54′ 37” W; precipitation: 1100–1600 mm/year; elevation: 1100–1560 m a.s.l), is considered a medium-sized city (~64 km^2; INEGI 2009, 2010) and has ~600,000 inhabitants (INEGI 2010). In three decades (1980 to 2010) the population increased by approximately 50% (Lemoine-Rodríguez et al. 2019) and the urban area increased 8.6 times (SEDESOL 2011; Chávez-Alaffita 2014). In 2010, Xalapa was declared a metropolitan area to include five small neighboring cities (CONAPO 2010). Xalapa is considered one of the state capital cities of Mexico with the highest vegetation coverage (Williams-Linera et al. 2002), since around 20% of its area comprises trees and shrubs (Lemoine-Rodríguez 2012; Lemoine-Rodríguez et al. 2019). The urban area of Xalapa corresponds to 51% of the municipality and it is immersed within areas of cultivation (35%, mainly of sugar cane and shade coffee), grasslands (9%) and remnants of cloud forest (5%). Due to its status as the state capital, the predominant urban land uses are public buildings (schools, universities and government), thoroughfares and commercial activities (Benítez et al. 2012).

Coatepec, the administrative center of the Municipality of Coatepec (19°27′19” N, 96°57′31” W; precipitation: 1100–2100 mm/year; elevation: 1200 m a.s.l) is a small city (~6.4 km^2 and ~ 53,000 inhabitants, INEGI 2009, 2010) located 8 km southwest of Xalapa. The population of this city has grown by 8% over the last 20 years (INEGI 2010). Coatepec presents lower quantities of infrastructure (avenues, public buildings and vehicles) than Xalapa. The land use of its surrounding landscape is mainly agricultural (61%, mainly shade coffee), grassland (18%) and forest (13%) (INEGI 2009). The economic activity of this urban settlement is also focused on services such as public administration, local tourism, commerce and coffee production (Gobierno del Estado de Veracruz 2016).

Urban green spaces

Two of the largest urban green spaces in each city were selected: Parque Ecológico Macuiltépetl in Xalapa and Cerro de las Culebras in Coatepec (López-Falfán 2017). The Parque Ecológico Macuiltépetl (referred to hereafter as Macuiltépetl; 31 ha, ~1600 m a.s.l.) has been a Protected Natural Area since 1978 and is located in the central part of Xalapa, comprising approximately 0.5% of the total city area (Fig. 1). It presents moderately high management and continuous human use for recreational purposes. The vegetation on this inactive volcano includes secondary cloud forest, although exotic ornamental species are also present in the park (Williams-Linera et al. 2002). Management activities include gardening along the main trails and specific areas, tree removal and pruning, as well as maintenance of a paved road. Human activities are considerable and include jogging, picnicking, group activities (e.g., dancing, martial arts), among others, that peak during weekends (Ortiz-Rodríguez 2015).

The Cerro de las Culebras has been a municipal ecological Reserve since 1992 (37 ha; ~ 1300 m a.s.l.). It is located in the northern part of Coatepec city and considered the largest green space within the city, encompassing 6% of the total urban area (Fig. 1). In addition to helping to regulate the local climate, capture water and control erosion, this reserve maintains representative species of the tropical montane cloud forest and shaded coffee plantations (the most important commercial crop in the region). In spite of its conservation status, the Cerro de las Culebras is subject to various pressures, including urban development on its hillsides and uncontrolled recreational use. This green space presents low management and high visitor rates (López-Falfán 2017).

Design and sampling methods

Since the urban landscape of both cities is heterogeneous (López-Falfán 2017), and Cerro de las Culebras is the only public green space in Coatepec city, a sampling area of similar size was considered in both types of urban habitat conditions (~31 ha, corresponding to the area of Macuiltépetl, since this is the smallest of the two areas). The distance between the green and gray spaces in each city was greater than 1 km (Fig. 1). Within each green and gray space, ten sampling sites were located randomly (20 sites per city) covering as much as possible the complete extension of the selected sampling area (Fig. 1). A total of 62 ha within each city were sampled.

Ants were collected between April and July 2016 (which corresponds to the transition between the dry and rainy season in the region). In order to obtain the most complete inventory of ants in all habitat conditions, three sampling techniques were used: 1) Using two bait types (tuna in oil and honey); at each site, two sampling stations were placed at 50 m apart. Four 10 cm^2 white paper squares were placed at each station, two with tuna and two with honey, interspersed at a distance of 2 m apart. Each bait was left out for ~1 h to avoid competitive exclusion of the ants (Uno et al. 2010). Subsequently, 70% ethyl alcohol was poured onto each baited paper square with attracted specimens, which were then placed individually in tightly sealed and labeled plastic bags. 2) Manual capture (for ants foraging on vegetation and soil); the vegetation available at each station was sampled for 15 min with an entomological net (Bestelmeyer et al. 2000). 3) Winkler samples were used to collect leaf litter ants in five of ten selected points within each space (for a total of 10 samples/city). Since not all sites within

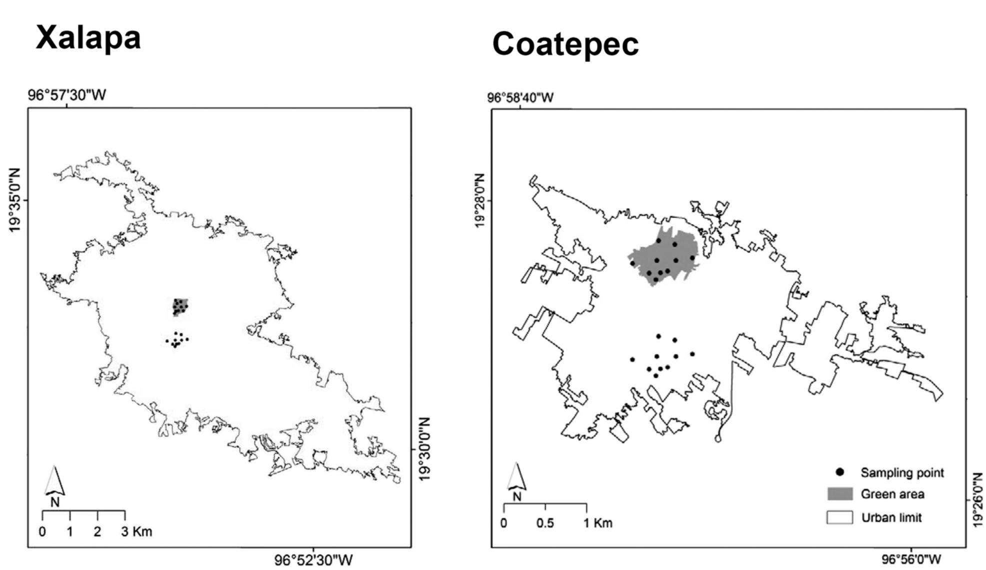

Fig. 1 Location of the green and gray spaces in two cities of Veracruz state, Mexico and distribution of the sampling points from which ants were collected

the gray space of the city presented leaf litter, both leaf litter and accumulated detritus from the flower beds and gardens of houses near the sampling sites were sampled. Following capture, all individuals were identified with the aid of specialized taxonomic keys (MacKay and MacKay 1989; Bolton 1994). Reference specimens of all species collected were deposited in the entomological collection of the Instituto de Investigaciones Biológicas, Xalapa (IIB-UV).

Data analysis

Diversity was estimated as the effective number of species or diversity of order-q (${}^qD$; Jost 2006):

$$ {}^qD = \left(\sum_{i=1}^{S} p_i^q \right)^{1/(1-q)} $$

Where Pi is the proportional abundance of species, S is the number of species and q is the order of diversity. The exponent q determines the influence of species abundance on the diversity values. For the comparisons, diversities of orders 0 and 1 were calculated: When $q = 0$, species richness is obtained, which is a measure of diversity that gives a disproportionate weight to rare species (Jost 2006). When $q \approx 1$, the Shannon diversity is obtained, which weighs each species according to its abundance (in our case, the frequency) in the community, and can therefore be interpreted as the number of "common" or "typical" species in the community (Jost 2006).

Comparisons of diversity values (${}^qD$) between cities, and between green and gray spaces within each city, were made under the same sampling coverage ($\hat{C}n$), which evaluated completeness of the inventory as the proportion of the community that is represented by the number of species captured in the sample. The value of $\hat{C}n$ varies between 0 (low completeness) and 100% (high completeness) (Chao and Jost 2012). As a statistical criterion for comparison between cities and between spaces (green – gray), the 95% CI was used. Non–overlap of the confidence intervals indicates that there is sufficient evidence to show significant differences between the estimated values of diversity (Cumming et al. 2007). The estimate of ${}^qD \pm 95\%$ CI, and its respective sampling coverage for each habitat condition, was conducted using the iNEXT package of R (Hsieh et al. 2016).

Following the recommendation by Magurran (2004), range–abundance curves (considering the frequency of occupation of the sites) were used to examine changes in the structure of ant assemblages between the green and gray spaces of each city. Range–abundance curves were also used to determine changes in the identity of the most frequent or dominant species. In these curves, information relating to changes in the distribution of abundance indicated differences in species evenness between assemblages (Magurran 2004).

In order to evaluate differences in the composition of species between cities and between habitat conditions (green–gray spaces) within each city, the Sørensen index was used as a measure of overlap of the assemblages. This index indicates the proportion of species shared in each assemblage (Wolda 1981; Jost et al. 2011). Values vary from 0 (minimum similarity or zero overlap) to 1 (maximum similarity or maximum overlap). In addition, Venn Euler diagrams were generated in R-Project (using the *VennDiagram* package) (Chen and Boutros 2011) in order to represent the number of shared and exclusive species in each comparison: 1) between cities, 2) between spaces (green–gray) in each city and 3) among spaces of similar condition (green–green and gray–gray) within each city.

Results

A total of 22,191 individuals belonging to 60 ant species (30 genera) were collected. The richest genera was *Pheidole* (16% of the total species), followed by *Camponotus* (12%), *Solenopsis* and *Pseudomyrmex* (7%) (Table 1). The species *Solenopsis geminata* represented 64% of the total captured individuals (occupying 38 of the 40 sampling sites) and almost twice as many individuals were collected in the green space of both cities (Table 1). In Xalapa, *Nylanderia fulva* (an introduced species known as the "crazy ant") was also found in most sites, but in low abundance (Table 1). Despite the dominance of these two species in both cities, species evenness tended to be higher in the gray spaces compared to green spaces, particularly in Coatepec city (Fig. 2).

Species diversity

About 60% of the total individuals were collected in Coatepec, with the green space of this city providing the largest number of individuals (~34%). Sample coverage ranged from 82 to 92% (Table 1). Comparison of diversity values of the same sample coverage (90%), considering both species richness (${}^0D$) and Shannon diversity (${}^1D$), showed that Xalapa was significantly less rich and diverse than Coatepec (Fig. 3a, b). The gray space was significantly more diverse than the green space, in both cities (Fig. 4a, b). The greatest difference was found when comparing the diversity of ant assemblages among the green spaces of each city: in general terms, diversity in the green space of Xalapa was significantly lower compared that of Coatepec (Fig. 4a, b). While no significant differences were detected between the gray spaces of both cities, the gray space of Xalapa tended to be less diverse than its equivalent in Coatepec (Fig. 4a, b).

Table 1 Ant species and number of individuals collected (total frequency in brackets) in the green – gray spaces in two cities of Veracruz State, Mexico

Species	Xalapa		Coatepec		Total
	Green (*n* = 10)	Gray (10)	Green (10)	Gray (10)	(40)
Dolichoderinae					
Dorymyrmex bicolor	_	3 (1)	_	39 (5)	42 (6)
Forelius damiani	_	_	8 (2)	_	8 (2)
Linepithema dispertitum	2 (1)	30 (6)	_	27 (5)	59 (12)
Tapinoma ramulorum	_	15 (1)	_	5 (2)	20 (3)
Dorylinae					
Neivamyrmex swainsonii	_	1 (1)	_	_	1 (1)
Formicinae					
Brachymyrmex sp. 1	_	1 (1)	1 (1)	6 (3)	8 (5)
Brachymyrmex sp. 2	_	14 (3)	_	275 (8)	289 (11)
Camponotus albicoxis	_	1 (1)	1 (1)	_	2 (2)
Camponotus atriceps	18 (3)	3 (2)	_	1 (1)	22 (6)
Camponotus brettesi	_	_	_	6 (1)	6 (1)
Camponotus novogranadensis	_	_	_	13 (3)	13 (3)
Camponotus planatus	_	5 (2)	_	1 (1)	6 (3)
Camponotus sericeiventris	_	_	1 (1)	_	1 (1)
Camponotus striatus	_	_	7 (4)	2 (1)	9 (5)
Nylanderia austroccidua	22 (4)	10 (2)	_	_	32 (6)
Nylanderia fulva	23 (9)	40 (8)	30 (5)	131 (5)	224 (27)
Paratrechina longicornis	2 (2)	34 (4)	15 (7)	94 (7)	145 (20)
Myrmicinae					
Adelomyrmex silvestrii	2 (1)	_	1 (1)	3 (1)	6 (3)
Adelomyrmex tristani	34 (2)	_	_	_	34 (2)
Apterostigma mexicanum	_	_	1 (1)	_	1 (1)
Atta mexicana	_	_	10 (3)	5 (1)	15 (4)
Cardiocondyla minutior	_	3 (2)	_	1 (1)	4 (3)
Carebara sp. 1	77 (5)	44 (4)	34 (4)	_	155 (13)
Carebara urichi	_	_	8 (1)	94 (2)	102 (3)
Crematogaster nigropilosa	_	_	15 (1)	4 (1)	19 (2)
Crematogaster sp. 1	1 (1)	4 (1)	41 (1)	_	46 (3)
Cyphomyrmex rimosus	_	_	1 (1)	8 (2)	9 (3)
Monomorium ebeninum	_	_	_	732 (4)	732 (4)
Octostruma balzani	_	_	8 (2)	_	8 (2)
Pheidole bilimeki	10 (4)	666 (6)	8 (2)	552 (8)	1236 (20)
Pheidole gula	297 (4)	_	_	4 (2)	301 (6)
Pheidole hyatti	_	_	42 (3)	_	42 (3)
Pheidole megacephala	_	924 (7)	4 (1)	_	928 (8)
Pheidole nubicola	511 (8)	1 (1)	14 (2)	18 (3)	544 (14)
Pheidole punctatissima	_	13 (3)	12 (4)	75 (4)	100 (11)
Pheidole soritis	1 (1)	29 (1)	_	10 (2)	40 (4)
Pheidole synanthropica	443 (2)	1 (1)	_	2 (1)	446 (4)
Pheidole tschinkeli	25 (5)	48 (3)	40 (2)	159 (5)	272 (15)
Pheidole xyston	_	22 (2)	2 (2)	_	24 (4)
Solenopsis geminata	3208 (8)	1740 (10)	6435 (10)	2825 (10)	14,208 (38)
Solenopsis picea	_	261 (2)	793 (5)	306 (6)	1360 (13)
Solenopsis sp. 1	2 (2)	123 (7)	21 (4)	12 (3)	158 (16)

Table 1 (continued)

Species	Xalapa		Coatepec		Total
	Green (*n* = 10)	Gray (10)	Green (10)	Gray (10)	(40)
Solenopsis sp. 2	78 (4)	1 (1)	5 (1)	7 (2)	91 (8)
Strumigenys brevicornis	25 (3)	_	15 (1)	_	40 (4)
Strumigenys louisianae	_	2 (1)	_	8 (5)	10 (6)
Strumigenys margaritae	_	_	1 (1)	_	1 (1)
Temnothorax sp.1	_	77 (3)	_	18 (5)	95 (8)
Wasmannia auropunctata	_	_	_	92 (2)	92 (2)
Ponerinae					
Gnamptogenys strigata	5 (2)	_	1 (1)	12 (3)	18 (6)
Hypoponera opacior	_	101 (7)	_	12 (3)	113 (10)
Hypoponera punctatissima	_	3 (2)	_	_	3 (2)
Hypoponera sp. 1	_	2 (1)	2 (1)	_	4 (2)
Rasopone ferruginea	_	2 (1)	_	_	2 (1)
Odontomachus laticeps	1 (1)	4 (3)	_	14 (3)	19 (7)
Pachycondyla harpax	_	_	_	1 (1)	1 (1)
Ponera exótica	1 (1)	_	_	5 (3)	6 (4)
Pseudomyrmicinae					
Pseudomyrmex ejectus	_	_	_	1 (1)	1 (1)
Pseudomyrmex euryblemma	_	_	_	2 (1)	2 (1)
Pseudomyrmex gracilis	_	_	1 (1)	12 (5)	13 (6)
Pseudomyrmex pallidus	_	_	3 (1)	_	3 (1)
Number of individuals	4788	4228	7581	5594	22,191
Sample coverage ($\hat{C}n$) in %	92	89	82	91	

The script - indicates that the species was not captured

Species composition

Despite the high similarity observed between cities (~75%), the number of species exclusive to each differed markedly: Coatepec had a number of exclusive species four times higher than that found in Xalapa (Fig. 5a). Comparison of the species composition in the green and gray space ant assemblages of each city ranged from 57% in Xalapa to 51% in Coatepec (Fig. 5b, c). In general, the gray spaces of both cities presented greater similarity to each other (64%) and contributed a

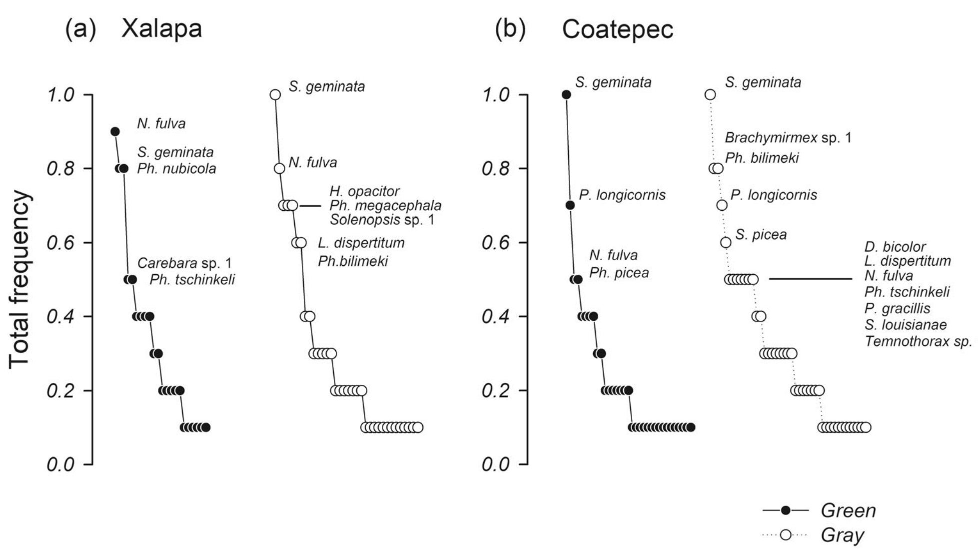

Fig. 2 Range–abundance curves (using capture frequency) for assemblages of ants collected in each environmental condition in two cities of Veracruz State, Mexico

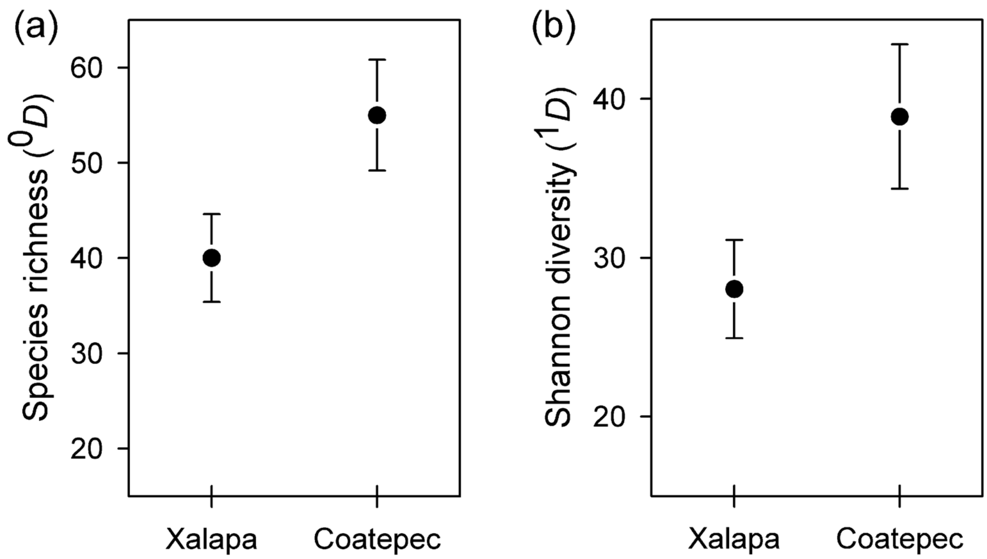

Fig. 3 Comparison of values of species richness (**a**) and Shannon (**b**) diversity of ants in each of two cities in Veracruz State, Mexico. Error bars represent the 95% confidence interval

greater number of exclusive species compared to the green spaces, which tended to differ taxonomically (47% similarity, Fig. 5b, c). The number of exclusive species in the green and gray spaces of Coatepec was almost double that found in Xalapa (Fig. 5d, e).

Discussion

Contrary to our expectations, the species richness and diversity of ants of the green spaces in both cities was lower than that of the gray spaces, and both habitat conditions shared approximately half of the ant species. These results suggest that differences in urbanization level and city size may affect ant diversity and change the composition of species that inhabit the green–gray spaces within urban areas. In general, both cities contain a high diversity of ant species. This is related to the presence of a very diverse regional pool of species that inhabit coffee plantations (106 species; Valenzuela-González et al. 2008), riparian vegetation (53 species; García-Martínez et al. 2015) and cloud forest remnants (75 species; García-Martínez et al. 2016). The presence of remnants of forests and agroforestry systems around urban centers are of great importance in terms of ensuring the viability of the populations and maintaining biodiversity within the cities (see source-sink dynamics hypothesis, Pulliam 1988). Different land uses should therefore be integrated into urban growth planning.

The results show that the smallest and least urbanized of the two cities (Coatepec) is ~25% more diverse and contributed four times more exclusive species than Xalapa. This result is based on a complete inventory of the ant fauna taken in similar sampling areas (~ 31 ha) for each habitat condition within each city, using several standardized ant sampling methods

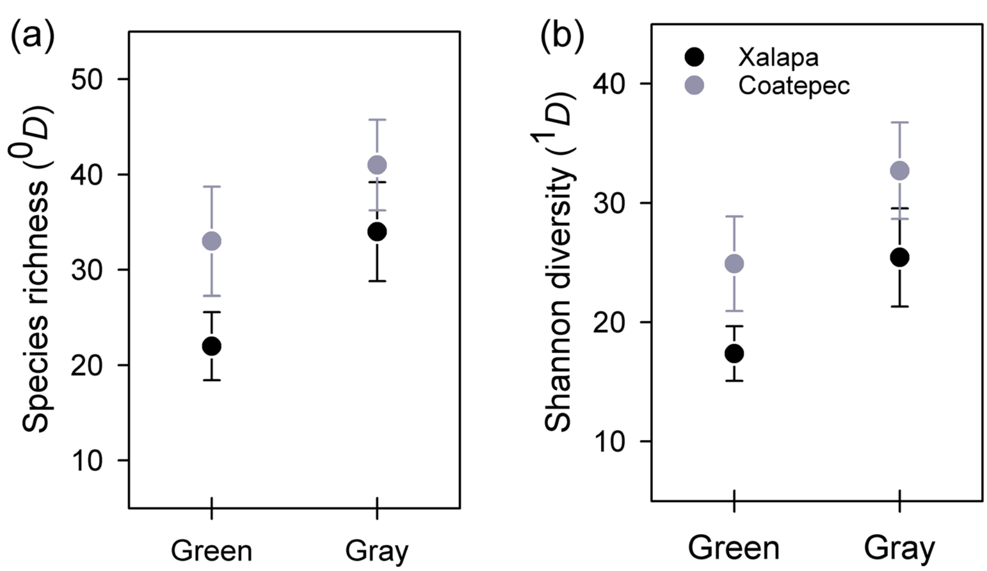

Fig. 4 Comparison of values of species richness (**a**) and Shannon (**b**) diversity of ants in each environmental condition (green and gray spaces) within two cities of Veracruz State, Mexico. Error bars represent the 95% confidence interval

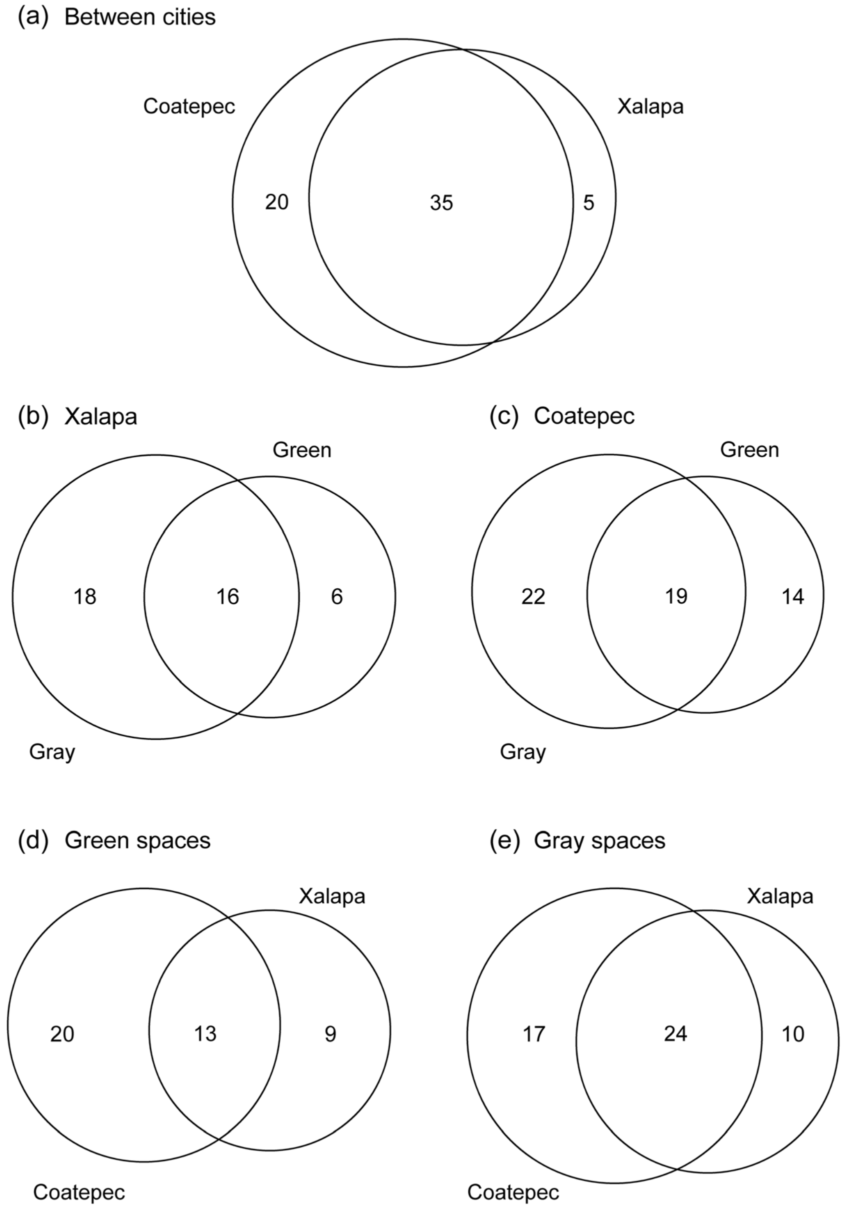

Fig. 5 Venn diagrams representing the overlap in ant species composition (calculated with the Sørensen index) between two cities of Veracruz state, Mexico (**a**), between green and gray spaces within each city (**b**, **c**) and between the spaces of each city (**d**, **e**). Circle size denotes the differences in species richness. Each panel includes the number of shared and exclusive species in each comparison

in order to include species with different foraging habits and nesting behavior. Xalapa is ten times larger than Coatepec city, relatively more urbanized and is located in the central part of the metropolitan area, such that the matrix that surrounds it comprises six expanding urban centers (CONAPO 2010; Benítez et al. 2012), immersed in sugarcane crops and road infrastructure. This has contributed to reducing the area of vegetation coverage in the city to 8% over the last 30 years (Benítez et al. 2012), which can negatively affect species diversity. This inverse relationship between ant diversity and city size is similar to that found for carabid beetles (Magura et al. 2004) and other groups, such as birds (Sorace and Gustin 2010; Ferenc et al. 2014), plants (Wang et al. 2014) and certain mammals (Łopucki and Kitowski 2017). However, more studies are necessary to fully assess the impact of small to medium-sized cities on biodiversity (Wang et al. 2014; Łopucki and Kitowski 2017) since global urban growth is expected to take place in such cities, which are generally considered to be reservoirs of biodiversity.

This study highlights the importance of different habitats in terms of the conservation of greater ant diversity within urban areas, especially when it has been found that city size and degree of urbanization could affect not only the total number of species within a city but also the species composition of individual habitats (Čeplová et al. 2017). The lower diversity and evenness of ant assemblages inhabiting green spaces not only reflects the influence of the size of these cities but also the individual characteristics of the green spaces (e.g., use and management type, geographical position within the city and isolation).

Characteristics such as vegetation type, intensity of use and management of green spaces can also explain the lower diversity found in this environment within the larger of the two cities. While the green spaces of both cities present a high rate of visitors for recreational purposes (Vázquez-Torres et al. 2010), they do differ in certain aspects. Macuiltépetl Park in Xalapa presents a high proportion of exotic ornamental species (Vázquez-Torres et al. 2010) that generally provide fewer resources than the natural vegetation (Siemann et al. 1998; Wilde et al. 2015), and the park management is directed mainly towards keeping the areas of frequent recreational use and roads clean and cleared of vegetation (Ortiz-Rodríguez 2015). This implies a chronic disturbance that can modify micro-environmental conditions and the supply of resources for feeding and nesting ants, favoring opportunistic species. In contrast, the Cerro de las Culebras in Coatepec is a protected area with little management and, while the native vegetation present has been modified, it still preserves elements of the original vegetation (López-Falfán 2017). Unlike the green space in Xalapa, these characteristics would favor higher ant species diversity, as has also been found for woody plants (López-Falfán 2017).

The degree of isolation of the urban habitats and their surrounding matrix type are other characteristics that may determine ant diversity (Uno et al. 2010; Perfecto and Vandermeer 2002; Philpott et al. 2014; Santos et al. 2019). Although Macuiltépetl Park is one of the largest green spaces in Xalapa, it can be considered an "island of vegetation", located towards the *central* part of the city (Fig. 1) and disconnected from its other green spaces (MacGregor-Fors et al. 2016). This geographical situation may act to limit the colonization/recolonization dynamics of ants in different environments within the city. A recent study of 11 taxonomic groups in green spaces of different sizes in Xalapa revealed lower species richness in Macuiltépetl Park compared to the smaller green spaces (MacGregor-Fors et al. 2016). Although Coatepec does not have a system of public green areas such as that of Xalapa (Falfán and MacGregor-Fors 2016; López-Falfán 2017), much of its green areas are located in the gardens of houses, which together with the type of matrix (dominated by shade coffee crops) that surrounds the city seem to favor the high diversity of ants observed in this green space. Shade coffee crops are recognized for maintaining a high diversity of insects, particularly ants (Perfecto and Vandermeer 2002; Armbrecht and Perfecto 2003; Philpott et al. 2014). Differences in isolation and matrix characteristics between the two cities may therefore influence ant diversity in different ways.

The results of this study indicate that the gray spaces of both cities contributed to a set of different species, many of them typical of modified environments. It is therefore possible to conclude that the ant species used green and gray spaces differentially in both cities as a result of differences in the micro-climatic conditions and supply of resources for nesting and feeding. Ants in urban areas seem to benefit from open and disturbed habitats due to a greater availability of food (highly energetic waste) abandoned by pedestrians (Savage et al. 2014). This could explain the greater diversity observed in the gray spaces of both cities. Future studies should evaluate the role of microclimatic differences and supply of food and nesting resources on the ant diversity and community structure in different urban habitats.

Recent studies have shown that urban ants are important for removing food waste in a highly urbanized environment (Youngsteadt et al. 2014; Penick et al. 2015) where generalist ants tend to increase in abundance, as is the case of the fire ant *Solenopsis geminata,* which is widespread in tropical and subtropical regions (Gotzek et al. 2015). This species is considered a pioneer species (Perfecto 1991) and a generalist keystone predator (Risch and Carroll 1982), in terms of its food and shelter needs, that readily occupies urban and agro-ecosystems (Perfecto 1991; Holway et al. 2002; Perfecto and Vandermeer 2002). For this reason, it is unsurprising to find this species in all of the sites sampled, but it is striking that its greatest abundance was found in green spaces of both cities, since it is generally associated more with disturbed areas. *Solenopsis geminata* is notorious for its aggressive behavior (Perfecto 1991, 1994) and it may therefore have a competitive advantage with which to displace other species. This could negatively impact the species diversity of these green spaces as it has done with vertebrates (Travis 1941; Plentovich et al. 2009) and invertebrates (Travis 1941; Risch and Carroll 1982).

In general, gray spaces in cities are considered novel habitats that favor generalist ant species (Pećarević et al. 2010) characterized by unicolonial population structure (colonies that are not independent of each other), and high-density populations of high competitive capacity that are often ecologically dominant (Helanterä et al. 2009), as in the case of species of the genera Solenopsis, *Pheidole* and Nylanderia (Perfecto 1991, 1994; Kumar et al. 2015). Given the high similarity of species of generalist ants in the gray spaces of both cities in this study, an aspect of interest for future studies would be to determine how the structure of the colonies and the competition of the generalist ants vary between the green and gray spaces of both cities.

Conclusions

To explain the differences in diversity and species composition between cities, it is not only important to consider their size, but also other characteristics of the green and gray spaces within cities, such as geographical position, degree of isolation, management intensity and matrix type surrounding the cities. Ant diversity comparisons between contrasting habitats showed that, in two medium and small cities, gray spaces do not negatively affect the diversity of ants. This highlights the value of this habitat type for ants, given the characteristics of the physical space in terms of offering a high availability of resources that can favor the high abundance of some generalist species. Understanding the role that small and medium-sized cities play in terms of species diversity is therefore an important element for the design and planning of city growth, particularly when studies show that global human population growth in the future will be concentrated in such urban areas.

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References

Alonso LE, Agosti D (2000) Biodiversity studies, monitoring, and ants: an overview. In: Agosti D, Majer JD, Alonso L.E, Schultz TR (eds) Ants: standard methods for measuring and monitoring biodiversity. Smithsonian Institution Press, Washington, DC pp 1–8

Armbrecht I, Perfecto I (2003) Litter-twig dwelling ant species richness and predation potential within a forest fragment and neighboring coffee plantations of contrasting habitat quality in Mexico. Agric Ecosyst Environ 97(1–3):107–115

Beninde J, Veith M, Hochkirch A (2015) Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. Ecol Lett 18(6):581–592

Benítez G, Pérez-Vázquez A, Nava-Tablada M, Equihua M, Álvarez-Palacios JL (2012) Urban expansion and the environmental effects of informal settlements on the outskirts of Xalapa city, Veracruz, Mexico. Environ Urban 24(1):149–166

Bestelmeyer BT, Agosti D, Alonso LE, Brandao CRF, Brown WL Jr, JHC D, Silvestre R (2000) Field techniques for the study of ground-dwelling ants. In: Agosti D, Majer JD, Alonso LE, Schultz TR (eds) Ants: standard methods for measuring and monitoring biodiversity. Smithsonian Institution Press, Washington, DC, pp 122–144

Bolton B (1994) Identification guide to the ant genera of the world. Harvard University Press, Massachusetts

Brown PH, Miller DM, Brewster CC, Fell RD (2013) Biodiversity of ant species along a disturbance gradient in residential environments of Puerto Rico. Urban Ecosyst 16(2):175–192

Carbó-Ramírez P, Zuria I (2011) The value of small urban green spaces for birds in a Mexican city. Landsc Urban Plan 100:213–222

Čeplová N, Kalusová V, Lososová Z (2017) Effects of settlement size, urban heat island and habitat type on urban plant biodiversity. Landsc Urban Plan 159:15–22

Chao A, Jost L (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93:2533–2547

Chávez-Alaffita L (2014) Áreas naturales urbanas intervenidas como espacios públicos abiertos. Caso de estudio: la Ciudad de Xalapa, Ver. (2003–2013). Dissertation. Universidad Veracruzana, Xalapa, Mexico

Chen H, Boutros PC (2011) VennDiagram: a package for the generation of highly-customizable Venn and Euler diagrams in R. BMC Bioinform 12(1):35

Chong KY, Teo S, Kurukulasuriya B, Chung YF, Rajathurai S, Tan HTW (2014) Not all green is as good: different effects of the natural and cultivated components of urban vegetation on bird and butterfly diversity. Biol Conserv 171:299–309

Clark PJ, Reed JM, Chew FS (2007) Effects of urbanization on butterfly species richness, guild structure, and rarity. Urban Ecosyst 10(3): 321–337

Consejo Nacional de Población (CONAPO) (2010) Proyecciones de la población de los municipios 2010–2050. http://www.conapo.gob.mx/es/CONAPO/Proyecciones_Datos. Accessed 26 July 2018

Cruz A, Escobar F, Gerez P, Muñiz-Castro MA, Ramírez F, Williams G (2010) Centro de Veracruz. In: Toledo Aceves T (ed) El Bosque Mesófilo de Montaña en México: Amenazas y oportunidades para su conservación y manejo sostenible. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México, pp 80–87

Cumming G, Fidler F, Vaux DL (2007) Error bars in experimental biology. J Cell Biol 177:7–11

Cupul-Magaña FG (2009) Diversidad y abundancia de hormigas (Formicidae) en las viviendas de Puerto Vallarta, Jalisco, México. Ecol Aplicada 8(1–2):115–117

Daniels G, Kirkpatrick J (2006) Does variation in garden characteristics influence the conservation of birds in suburbia? Biol Conserv 133: 326–335

Faeth SH, Warren PS, Shochat E, Marussich WA (2005) Trophic dynamics in urban communities. AIBS Bull 55(5):399–407

Falfán I, MacGregor-Fors I (2016) Woody neotropical streetscapes: a case study of tree and shrub species richness and composition in Xalapa. Madera Bosques 22(1):95–110

Ferenc M, Sedláček O, Fuchs R, Dinetti M, Fraissinet M, Storch D (2014) Are cities different? Patterns of species richness and beta diversity of urban bird communities and regional species assemblages in Europe. Glob Ecol Biogeogr 23(4):479–489

Fontana S, Sattler T, Bontadina F, Moretti M (2011) How to manage the urban green to improve bird diversity and community structure. Landsc Urban Plan 101(3):278–285

García-Martínez MA, Martínez-Tlapa DL, Pérez-Toledo GR, Quiroz-Robledo LN, Valenzuela-González JE (2015) Myrmecofauna (Hymenoptera: Formicidae) response to habitat characteristics of tropical montane cloud forests in Central Veracruz, Mexico. Fla Entomol 99(2):1–9

García-Martínez MA, Escobar-Sarria F, López-Barrera F, Castaño-Meneses G, Valenzuela-González JE (2016) Value of riparian vegetation remnants for leaf-litter ants in a human-dominated landscape. Environ Entomol 44(6):1488–1497

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

Gobierno del Estado de Veracruz, SEFIPLAN, Sistema de Información Municipal. 2016. Cuadernillos municipales. Coatepec. http://ceieg.veracruz.gob.mx/wp-content/uploads/sites/21/2016/05/Xalapa.pdf. Accessed 5 January 2017

Gotzek D, Axen HJ, Suarez AV, Helms Cahan S, Shoemaker D (2015) Global invasion history of the tropical fire ant: a stowaway on the first global trade routes. Mol Ecol 24(2):374–388

Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X, Briggs JM (2008) Global change and the ecology of cities. Science 319(5864):756–760

Helanterä H, Strassmann JE, Carrillo J, Queller DC (2009) Unicolonial ants: where do they come from, what are they and where are they going? Trends Ecol Evol 24(6):341–349

Holway DA, Lach L, Suarez AV, Tsutsui ND, Case TJ (2002) The causes and consequences of ant invasions. Annu Rev Ecol Syst 33:181–233

Hsieh T, Ma K, Chao A (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (hill numbers). Methods Ecol Evol 7:1451–1456

Instituto Nacional de Estadística, Geografía e Informática (INEGI) (2009) Prontuario de información geográfica municipal de los Estados Unidos Mexicanos-Xalapa, Veracruzhttp://www3.inegi.org.mx/contenidos/app/mexicocifras/datos_geograficos/30/30087.pdf. Accessed 3 April 2018

Instituto Nacional de Estadística y Geografía (INEGI) (2010) Censo de población y vivienda 2010. micro datos para Veracruz de Ignacio de la Llave. INEGI. https://www.inegi.org.mx/programas/ccpv/2010/default.html#Microdatos. Accessed 3 April 2018

Jost L (2006) Entropy and diversity. Oikos 113:363–375

Jost L, Chao A, Chazdon RL (2011) Compositional similarity and β (beta) diversity. In: Magurran AE, McGill BJ (eds) Biological diversity: frontiers in measurement and assessment. Oxford University Press, New York, pp 66–84

Kaspari M (2000) A primer on ant ecology. In: Agosti D, Majer JD, Alonso LE, Schultz TR (eds) Ants: standard methods for measuring and monitoring biodiversity. Smithsonian Institution Press, Washington, DC, pp 9–24

Kumar S, LeBrun EG, Stohlgren TJ, Stabach JA, McDonald DL, Oi DH, LaPolla JS (2015) Evidence of niche shift and global invasion potential of the tawny crazy ant, *Nylanderia fulva*. Ecol Evol 5(20): 4628–4641

Lemoine-Rodríguez R (2012) Cambios en la cobertura vegetal de la ciudad de Xalapa-Enríquez, Veracruz y zonas circundantes entre 1950 y 2010. Dissertation, Universidad Veracruzana, Xalapa, México

Lemoine-Rodríguez R, MacGregor-Fors I, Muñoz-Robles C (2019) Six decades of urban green change in a neotropical city: a case study of Xalapa, Veracruz. Mexico Urban Ecosyst:1–10

López-Falfán IS (2017) Cobertura, riqueza, composición de especies y percepción social de la vegetación urbana de Xalapa y Coatepec, Veracruz. Dissertation, Instituto de Ecología. A.C. México

López-Moreno IR, Diaz-Betancourt ME, Suarez-Landa T (2003) Insectos sociales en ambientes antropizados: Las hormigas de la ciudad de Coatepec, Veracruz, México. Sociobiology 42(3):604–622

Łopucki R, Kitowski I (2017) How small cities affect the biodiversity of ground-dwelling mammals and the relevance of this knowledge in planning urban land expansion in terms of urban wildlife. Urban Ecosyst 20(4):933–943

MacGregor-Fors I, Schondube JE (2011) Gray vs. green urbanization: relative importance of urban features for urban bird communities. Basic Appl Ecol 12(4):372–381

MacGregor-Fors I, Avendaño-Reyes S, Bandala VM, Chacón-Zapata S, Díaz-Toribio MH et al (2015) Multi-taxonomic diversity patterns in a neotropical green city: a rapid biological assessment. Urban Ecosyst 18(2):633–647

MacGregor-Fors I, Escobar F, Rueda-Hernández R, Avendaño-Reyes S, Baena ML et al (2016) City "green" contributions: the role of urban greenspaces as reservoirs for biodiversity. Forests 7(7):1–14

Mackay WP, Mackay EE (1989) The ants of New Mexico (Hymenoptera: Formicidae). Lewiston, Edwin Mellen Press, New York

Magura T, Tóthmérész B, Molnár T (2004) Changes in carabid beetle assemblages along an urbanization gradient in the city of Debrecen, Hungary. Landsc Ecol 19:747–759

Magurran AE (2004) Measuring biological diversity. Blackwell Publishing, Oxford

Majer JD, Brown KR (1986) The effects of urbanization on the ant fauna of the swan coastal plain near Perth, Western Australia. J Roy Soc West Aust 69:13–18

McKinney ML (2006) Urbanization as a major cause of biotic homogenization. Biol Conserv 127(3):247–260

McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol Evol 14(11):450–453

Møller A, Diaz M, Flensted-Jensen E, Grim T, Ibáñez-Álamo et al (2012) High urban population density of birds reflects their timing of urbanization. Oecologia 170(3):867–875

Nielsen AB, Van Den Bosch M, Maruthaveeran S, Van den Bosch CK (2014) Species richness in urban parks and its drivers: a review of empirical evidence. Urban Ecosyst 17(1):305–327

Ortiz-Rodríguez AM (2015) Propuesta de un programa de manejo para el área natural protegida Cerro de Macuiltépetl ubicada en la ciudad de Xalapa, Veracruz. Dissertation, Universidad Veracruzana. México

Parris KM, Amati M, Bekessy SA, Dagenais D, Fryd O et al (2018) The seven lamps of planning for biodiversity in the city. Cities 83:44–53

Pećarević M, Danoff-Burg J, Dunn RR (2010) Biodiversity on Broadway-enigmatic diversity of the societies of ants (Formicidae) on the streets of New York City. PLoS One 5(10):e13222

Penick CA, Savage AM, Dunn RR (2015) Stable isotopes reveal links between human food inputs and urban ant diets. Proc R Soc B 282(1806):20142608

Perfecto I (1991) dynamics of *Solenopsis geminata* in a tropical fallow field after ploughind. Oikos 62:139–144

Perfecto I (1994) Foraging behavior as a determinant of asymmetric competitive interactions between two ant species in a tropical agroecosystem. Oecologia 98:184–192

Perfecto I, Vandermeer J (2002) Quality of agroecological matrix in a tropical montane landscape: ants in coffee plantations in southern Mexico. Conserv Biol 16(1):174–182

Philpott SM, Cotton J, Bichier P, Friedrich RL, Moorhead LC, Uno S, Valdez M (2014) Local and landscape drivers of arthropod abundance, richness, and trophic composition in urban habitats. Urban Ecosyst 17(2):513–532

Plentovich S, Hebshi A, Conant S (2009) Detrimental effects of two widespread invasive ant species on weight and survival of colonial nesting seabirds in the Hawaiin Islands. Biol Invasions 11:289–298

Pulliam HR (1988) Sources, sinks, and population regulation. Am Nat 132:652–661

Ramalho CE, Hobbs RJ (2012) Time for a change: dynamic urban ecology. Trends Ecol Evol 27:179–189

Risch SJ, Carroll CR (1982) Effect of a keystone predaceous ant, *Solenopsis geminata*, on arthropods in a tropical agroecosystem. Ecology 63:1979–1983

Rzedowski J (1996) Análisis preliminar de la flora vascular de los bosques mesófilos de montaña de México. Acta Bot Mex 35:25–44

Santos NM (2016) Research on urban ants: approaches and gaps. Insect Soc 63(3):359–371

Santos NM, Delabie JHC, 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

Savage AM, Hackett B, Guénard B, Youngsteadt EK, Dunn RR (2014) Fine-scale heterogeneity across Manhattan's urban habitat mosaic is associated with variation in ant composition and richness. Insect Conserv Divers 8(3):216–228

Secretaría de Desarrollo Social (SEDESOL) (2011) La expansión de las ciudades 1980–2010. Secretaría de Desarrollo Social, México, pp 1–62

Siemann E, Tilman D, Haarstad J (1998) Experimental tests of the dependence of arthropod diversity on plant diversity. Am Nat 152:738–750

Sorace A, Gustin M (2010) Bird species of conservation concern along urban gradients in Italy. Biodivers Conserv 19:205–221

Travis BV (1941) Notes on the biology of the fire ant *Solenopsis geminata* (F.) in Florida and Georgia. Fla Entomol 24(1):15–22

Uno S, Cotton J, Philpott SM (2010) Diversity, abundance, and species composition of ants in urban green spaces. Urban Ecosyst 13(4): 425–441

Valenzuela-González J, Quiroz-Robledo L, Martínez-Tlapa D (2008) Hormigas (Insecta: Hymenoptera: Formicidae). In: Manson RH, Hernández-Ortíz V, Gallina S, Mehltreter K (eds) Agroecosistemas cafetaleros de Veracruz: biodiversidad, manejo y conservación. Instituto de Ecología de Instituto A.C, Xalapa, pp 107–122

Vázquez-Torres SM, Carvajal-Hernandez CI, Aquino-Zapata AM (2010) Áreas Naturales Protegidas. In: Bedtez-Badillo G, Welsh-Rodnguez C (eds) Atlas del patrimonio natural, histórico y cultural de Veracruz, vol 1. Xalapa, Veracruz, pp 249–274

Vergnes A, Blouin M, Muratet A, Lerch TZ, Mendez-Millan M et al (2017) Initial conditions during Technosol implementation shape earthworms and ants diversity. Landsc Urban Plan 159:32–41

Vignoli L, Mocaer I, Luiselli L, Bologna MA (2009) Can a large metropolis sustain complex herpetofauna communities? An analysis of the suitability of green space fragments in Rome. Anim Conserv 12: 456–466

Wang G, Zuo J, Li XR, Liu Y, Yu J et al (2014) Low plant diversity and floristic homogenization in fast-urbanizing towns in Shandong peninsular, China: effects of urban greening at regional scale for ecological engineering. Ecol Eng 64:179–185

Wilde HD, Gandhi KJ, Colson G (2015) State of the science and challenges of breeding landscape plants with ecological function. Horticul Res 2:1–8

Williams-Linera G, Manson RH, Vera EI (2002) La fragmentación del bosque mesófilo de montaña y patrones de uso del suelo en la región oeste de Xalapa, Veracruz, México. Madera Bosques 8(1):73–89

Wolda H (1981) Similarity indices, sample size and diversity. Oecologia 50:296–302

Youngsteadt E, Henderson RC, Savage AM, Ernst AF, Dunn RR, Frank SD (2014) Habitat and species identity, not diversity, predict the extent of refuse consumption by urban arthropods. Glob Chang Biol 21(3):1103–1115