

Effects of Urbanization on the Diversity, Abundance, and Composition of Ant Assemblages in an Arid City

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Abstract

Cities within arid regions make up a significant but understudied subset of the urban ecosystems of the world. To assess the effects of urbanization, fragmentation, and land-use change in an arid city, we sampled the ant assemblages in three habitat types in Tucson, Arizona: irrigated neighborhood parks, urban desert remnants, and preserved desert. We analyzed the abundance, species richness, evenness, as well as the species and functional group composition of ant assemblages. We found no significant differences in species richness or evenness. However, irrigated parks had significantly greater ant abundances. Although some exotic species were present in the urban habitats, they did not have significant effects on ant diversity. Ant assemblages from all three habitat types were distinct from each other in their composition. Irrigated parks included a significantly higher proportion of species typically found in cooler and wetter climates. The differences in abundance and species composition between irrigated parks and the other habitats are likely the effect of irrigation removing water as a limiting factor for colony growth and increasing resource availability, as well as producing a localized cooling effect. Our results show that arid urban ecosystems may include considerable biodiversity, in part thanks to increased landscape heterogeneity resulting from the irrigation of green areas.

Resumen

Para evaluar los efectos de la urbanización, la fragmentación y los cambios de uso del suelo en una ciudad árida, muestreamos los ensamblajes de hormigas en tres tipos de hábitats en Tucson, Arizona: parques irrigados, remanentes urbanos del desierto y desierto preservado. Analizamos la abundancia, riqueza de especies, equidad, así como la composición de especies y de grupos funcionales. No encontramos diferencias significativas en la riqueza de especies o la equidad. Sin embargo, los parques irrigados tuvieron abundancias de hormigas significativamente mayores. Aunque algunas especies exóticas estuvieron presentes en los hábitats urbanos, estas no tuvieron efectos significativos en la diversidad de hormigas. Los ensamblajes de hormigas en los tres tipos de hábitats fueron distintos entre sí en su composición. Los parques irrigados incluyeron una proporción significativamente mayor de especies que típicamente se encuentran en climas menos cálidos y con mayor precipitación. Las diferencias en la abundancia y la composición de especies entre los parques irrigados y los otros hábitats son probablemente resultado de la irrigación que elimina la disponibilidad de agua como un factor limitante y produce un efecto de enfriamiento localizado. Nuestros resultados muestran que los ecosistemas urbanos áridos pueden incluir una biodiversidad considerable, en parte gracias a la mayor heterogeneidad del paisaje resultante del riego de áreas verdes.

Key words: urbanization, ant diversity, urban heat island, park cool island

The growth and development of cities have profound effects on the diversity and composition of biotas at multiple scales. Globally, urban areas are predicted to negatively affect biodiversity by expanding into land currently occupied by biodiversity hotspots and the habitat of rare and threatened species (McDonald et al.

2008, Seto et al. 2012). At regional scales, urbanization often results in biotic homogenization, the loss of biological distinctiveness among biotas (McKinney 2006, Knop 2016). This process is often described as a result of the replacement of unique endemic organisms by already widespread invasive and synanthropic species

(McKinney and Lockwood 1999, Shochat et al. 2010). At the local scale, urbanization often reduces biodiversity and results in cities that are less diverse than the surrounding rural areas (McKinney 2008, Faeth et al. 2011). Furthermore, the composition of ecological communities tends to change with urbanization in ways that affect ecosystem function and services (Eigenbrod et al. 2011).

Furthermore, cities are different from rural environments due to variations in their climate caused by land-use change. The urban heat island (UHI) effect is the occurrence of higher temperatures within cities as a result of a variety of factors including a higher cover of heat-retaining surfaces, reduced evapotranspiration from plants, and anthropogenic heat sources such as cars (Hart and Sailor 2009, Imhoff et al. 2010). The UHI has ecological effects such as a higher prevalence of heat-tolerant species (Menke et al. 2010b, Piano et al. 2017), and increased heat tolerance by species adapted to urban environments (Diamond et al. 2015, Brans et al. 2017). One of the strategies for the mitigation of the UHI effect is the creation and expansion of green irrigated areas (Norton et al. 2015), which have a localized cooling influence often called the park cool island (PCI) effect (Chow et al. 2011). The PCI effect is likely to affect the composition of ecological communities within green urban areas; although, to our knowledge, no previous studies have considered that possibility.

Urban environments within arid and semiarid regions are an important subset of the growing urban areas of the world. Over 40% of the world's land surface is covered by drylands, defined as areas where primary productivity and nutrient cycling are limited by water availability (Safriel et al. 2005). Over 20% of the world's urban population lives in such areas (McDonald et al. 2011). Although urbanization might have similar effects in dry regions to those observed in mesic cities, there are at least a few marked differences. In particular, the introduction of irrigation in water-limited environments is likely to have significant effects on plant productivity, trophic dynamics, and local biodiversity (Cook and Faeth 2006, Bang et al. 2012). These effects might contribute to the observed pattern in which cities within arid regions are more likely to experience increases in organism abundance and less likely to experience decreases in species richness than cities in temperate and tropical areas (Faeth et al. 2011). The increased diversity and abundance associated with resource-rich patches within cities, such as irrigated areas in arid regions, is sometimes called an 'oasis effect' (Bock et al. 2008). Despite recent efforts (Cook and Faeth 2006, Bang et al. 2012, Davis et al. 2015), the ecological dynamics of arid and semiarid cities are only beginning to be understood.

Arthropods are ideal organisms for the study of urban biodiversity. Their small size and variety of life histories and environmental needs make them predominant components of urban faunas. Multiple studies have shown that complex arthropod communities can be found in urban environments (Cook and Faeth 2006, Sattler et al. 2011) and that their overall response to urbanization is similar to that of other urban taxa such as plants and birds (McKinney 2008, Knop 2016). In recent years, ants have been used prominently to investigate the effects of urban development on biological diversity (Santos 2016). Ants are well suited for this kind of research because they are nearly ubiquitous, highly diverse, and responsive to environmental change (Alonso and Agosti 2000). Ants are also remarkable for their diverse interactions with other organisms and their capacity to provide ecosystem services such as soil aeration and seed dispersal (Del Toro et al. 2012). Some ant species are also important due to their role as invasive organisms. As defined by Holway et al. (2002), invasive ants are distinguished by having detrimental effects on local biodiversity and ecosystem

functioning. Most studies of urban ant assemblages have recorded such invasive species, and many have associated their presence to a decrease in local ant biodiversity (Stringer et al. 2009, Uno et al. 2010). Despite their suitability as research subjects in urban habitats, few studies have considered urban ant assemblages within arid regions, and almost none have examined their diversity at the species level.

This study focuses on the ecology of ant assemblages in urban habitats subjected to fragmentation and human manipulation in an arid city. It was carried out in Tucson, AZ and involved the ant assemblages found in irrigated urban parks, urban remnants of the native desert and plots of preserved desert habitat. Our specific goals were to assess the effects of urbanization on ant abundance and diversity, to detect any differences in community composition, and to determine whether such differences are associated to the effects of changes in local climate caused by urbanization. We predicted that ant assemblages in irrigated parks would have greater diversity and abundance as a result of the localized abundance of water, a limited resource in arid regions. We also predicted that the UHI and PCI effects would result in ant assemblages including greater proportions of ant species typical of warmer climates in desert remnants and cooler climates in irrigated parks, respectively.

Materials and Methods

Study Area

Ants were sampled in Tucson, AZ, United States and the surrounding Sonoran Desert to the west of the city. Tucson is located within the Sonoran Desert biome and supports lower and upper Sonoran vegetation types and riparian corridors (Brown 1994). Slightly over a million people currently inhabit the Tucson metropolitan area, which covers approximately 600 square km (US Census Bureau 2011). Tucson has a desert climate (Köppen climate classification: *Bwh*) with summer temperatures over 38°C during the day. The weather has a monsoonal pattern with precipitation during the summer and winter (Douglas et al. 1993). The city displays a spatially variable UHI effect with urban early morning temperatures being approximately 3°C higher than those from nearby rural areas (Comrie 2000).

Sampling Methodology

We selected two land-use types to assess the effects of habitat modification and fragmentation on ant assemblages: desert remnants and irrigated parks (Fig. 1). Preserved desert plots were also sampled to allow comparison with ant assemblages under more natural conditions. We defined desert remnants as portions of urban land that had not been purposefully modified by human activity. To varying degrees, they included remnants of the original desert vegetation. Most were vacant lots, although they also included other undeveloped land patches. Irrigated parks were small neighborhood parks maintained by the city. They were characterized by irrigated lawns, a mixture of native and exotic arboreal vegetation and a lack of shrubs. Their landscaping regime involved daily irrigation through a sprinkler system and weekly lawn mowing. We established preserved desert study plots within four large areas of Sonoran Desert west of the city. One of those areas was entirely within a vast desert expanse inside a national park. The other three were officially considered city parks, but management practices had been aimed at maintaining the original structure of the ecosystem. Despite being partially surrounded by urban development, they each encompassed a surface equal or greater to 88 ha.



Fig. 1. Habitat types considered in this study: (a) Preserved desert, (b) Desert remnants, and (c) Irrigated parks.

To reduce variation due to unaccounted factors, we selected pairs of irrigated parks and desert remnants located within a 2 km radius or closer to each other. The location of preserved desert plots was selected to encompass the range of elevations of the study sites within the city. The size of each plot was equivalent to the average size of the desert remnant-irrigated park pair most similar to it in elevation. Twelve sites were selected for each habitat type. One of the desert remnant sites became unavailable and had to be excluded from the study after the first sampling season, bringing the number of sites to 35 (Fig. 2). All sites had an area between 0.67 and 1.19 ha (mean = 0.9 ha) to reduce variation due to size differences and ensure thorough sampling.

Ants were sampled in October and November of 2010, and April and May of 2011. Each site was sampled with 12 pitfall traps for each sampling season. Traps consisted of a straight-sided plastic jar, 6 cm in diameter and 8.5 cm deep (SKS Bottle and Packaging Inc., Watervliet, NY), to which two 12.7-cm-long machine bolts were attached with rubber bands. The bolts allowed for a 15 by 15 cm custom-cut square sheet of clear plexiglass acrylic to be attached suspended 5 cm above the jar with nuts. These plexiglass covers were spray-painted bright orange to prevent their destruction by lawnmowers in irrigated parks. We used propylene glycol-based antifreeze (Sierra Brand, Old World Industries Inc., Northbrook, IL) diluted 50% with water as a killing agent. Plastic jars were set flush inside the ground so that ants and other small arthropods walking near them would fall inside. Traps remained in the field for 72 h.

Traps were set at a minimum of 20 m apart and at least 10 m from the edge of each site. Areas of high traffic were avoided at the request of the local parks department and to prevent trap removal. For preserved desert sites, we set their limits as a rectangle drawn using Google Earth Pro (Google Inc. 2007) for which one of its dimensions was greater by one-third than the other one. This resembled the shape and proportions of most of our urban sites. For all sites, aerial images were used to distribute the location of traps uniformly. GPS coordinates were obtained for every trap from Google Earth and were used with a high-sensitivity GPS device (Garmin etrex Venture HC, Garmin Corp., Olathe, KS) and measurements in the field to determine their location within sites. Traps were sometimes removed or destroyed, leading to some small variation in sampling effort across sites. Nevertheless, we collected at least 10 traps from each site per sampling season.



Fig. 2. Location of sites sampled. Diamonds represent preserved desert sites, squares represent desert remnants, and triangles represent irrigated parks.

Ants were transferred to vials with 95% ethyl alcohol, then counted and identified to species using the guide to ant genera of North America (Fisher and Cover 2007) and genus-specific identification keys. Ants in the genus *Pheidole* were identified using an online lucid key (Longino 2009). Voucher specimens were deposited in the University of Arizona Insect Collection (UAIC, Tucson, AZ).

Data Analysis

Unless otherwise specified, parametric tests were carried out using JMP v.13.1 (SAS Institute 2016). Whenever we considered ant abundances, we used the geometric mean of individual counts to reduce the effects of extreme values resulting from ants' spatial clustering and social foraging activity. This is a common issue when assessing ants abundances and approaches that include logarithmic transformations, like those used for calculating geometric means, are an often used solution (Hoffmann and Andersen 2003, Longino and Colwell 2011).

To determine if any of the habitats studied harbored a greater abundance of ants and to assess if differences were constant across sampling seasons, we used a two-way repeated measures analysis of variance (ANOVA) to compare the geometric means of trap counts among habitats. As a follow-up analysis, we carried out two least square means contrasts comparing the abundance values between the fall and spring seasons: one for irrigated parks and another considering desert remnants and preserved desert.

We also considered differences in species diversity among habitats. In order to avoid redundancy in our dataset due to sampling the same trap locations twice, we pooled together the results from each trap location before analysis.

We used the iNext online (Chao et al. 2016) platform to obtain incidence-based species richness estimates for a sample coverage of 93%. We chose that value because it was approximately the average sampling completeness before interpolation or extrapolation, and using it allowed us to avoid overreliance on either procedure. As an estimator of evenness, we calculated 2D , the second order Hill number. 2D is a measurement of diversity that depends heavily on evenness and is robust to differences in sample size (Chase and Knight 2013). It is also a mathematical transformation of other frequently used indices of diversity and evenness such as Simpson's index and Hurlbert's probability of interspecific encounter (Jost 2006). Like other Hill numbers, its units are effective numbers of species. To estimate 2D , we used the geometric mean abundances of species per site to produce an evenness estimate derived from relative abundances. Diversity estimates were compared among habitat types with one-way ANOVAs. Whenever we detected significant differences in variance among groups, we used Welch's ANOVA procedure.

As part of our analysis, we considered the presence of exotic ant species as a factor affecting ant diversity in the habitats sampled. For this study, native species were those naturally occurring in the Nearctic region, while exotic species were those introduced from other biogeographical regions. We carried out analyses to assess the effects of the only widespread exotic species present, *Brachymyrmex patagonicus* Mayr (Hymenoptera: Formicidae), on ant diversity. For irrigated parks, we calculated simple linear regression tests considering either species richness or evenness as the response variable and the geometric mean of the abundance of *B. patagonicus* as the predictor. *Brachymyrmex patagonicus* was present in only a few desert remnants, so for them, we compared the same parameters between groups of sites with or without *B. patagonicus* with two-sample *t*-tests.

We used the vegan package (Oksanen et al. 2018) within the R environment (R Core Team 2018) to analyze the species composition of ant assemblages. Analyses were based on the Sørensen-Dice and Bray-Curtis similarity indices. The Sørensen-Dice index takes into account the presence or absence of species, whereas the Bray-Curtis index considers species' relative abundances. To determine if ant assemblages from different habitat types were compositionally distinct, we used a one-way permutational multivariate analysis of variance (MANOVA; adonis function in the vegan R package). As a follow-up, we used the RVAideMemoire R package (Hervé 2018) to calculate pairwise permutational MANOVAs with a Holm-Bonferroni correction. Both initial and post hoc analyses used 999 permutations.

The same procedure was used to test for differences in the functional composition of ant assemblages. Classifying ants in functional groups allows for the detection of general patterns of species composition that transcend biogeographical boundaries. This is accomplished by grouping together species that have similar responses to stress, disturbance, and competition (Andersen 2010). In this approach, stress is defined as the negative effect of abiotic factors, while disturbance is defined as any event that removes a portion of the biomass of the focal species. Ants that are heavily specialized for competition are classified within the 'Dominant Dolichoderinae' and 'subordinate Camponotini' functional groups. Ant species adapted to environmental stress are classified as 'Tropical', 'Cold Climate', or 'Hot Climate Specialists'. Disturbance-adapted species are included in the 'Opportunist' functional group. Ants that show a combination of adaptations for competition, stress, and disturbance are part of the 'Generalized Myrmicinae' group. Finally, some highly specialized ants such as 'Specialized Predators' and 'Cryptic species' are included in their own functional groups. This approach has been widely used to explain the effects of environmental change on ant assemblages (e.g., Hoffmann and Andersen 2003, Bestelmeyer 2005). We used the existing literature (Brown 2000, Bestelmeyer 2005, Andersen 2010) to classify the species we encountered into functional groups. The number of ants collected corresponding to each functional group in each trap was calculated. As with species composition, the geometric mean per site was calculated to reduce the effect of extreme values. We performed a permutational MANOVA based on the Bray-Curtis similarity to compare the functional group composition among habitats and followed it up with pairwise permutation tests.

To determine if the urban habitats considered had comparable levels of β diversity, we used a homogeneity of groups dispersions procedure (betadisper function in the vegan R package). We carried out a permutation test with 999 permutations to compare the mean distances to the centroid between irrigated parks and desert remnants for both similarity indices. Preserved desert sites were not considered for this analysis because their degree of spatial dispersion was different from that of urban sites due to limitations in the availability of comparable sampling sites near the city.

We predicted that greater water availability and the higher prevalence of shade-producing trees would favor the occurrence of ant species from wetter and cooler climates in irrigated parks. For desert remnants, we expected to find more heat-adapted species as a result of the UHI effect. To test these predictions, we gathered information about climate conditions typically experienced by the ant species we found. We obtained GPS coordinates for ant species records from antweb.com (Antweb.org 2018). When there were less than 15 reported locations for a species, we gathered additional records from the Integrated Digitized Biocollections (iDigBio) online platform (Integrated Digitized Biocollections 2018). To reduce the sampling bias resulting from the clustering of records near cities and research

institutions, we used the spThin R package (Aiello-Lammens et al. 2015) to exclude records so that for a given species records would be at least 5 km apart. Exotic species or those with less than five records after thinning were excluded. Using ArcMap 10.4 (ESRI 2016), we superimposed the location of ant species records to worldclim 2.0 layers (Fick and Hijmans 2017) at a resolution of one square km. We extracted the maximum temperature of the warmest month and minimum monthly precipitation values for those locations and calculated the average for each species. Then, we averaged the values corresponding to the species present in each site to obtain a Community Temperature Index (CTI) and a Community Precipitation Index (CPI) which summarize the climate of areas where the species from each assemblage are typically found. Finally, we compared the mean CTI and CPI values among habitat types with one-way ANOVAs. Tukey's HSD test was used for post hoc analysis. Comparison of CTI values has previously been used to assess the effect of urbanization (Menke et al. 2010b, Piano et al. 2017) and climate change (Bowler et al. 2015, Kwon 2017) on several insect groups.

Results

A total of 27,956 ants belonging to 53 species were collected from 799 pitfall traps during the two sampling seasons. There was substantial overlap in the ant species found in the habitat types considered (Fig. 3). Notably, a group of 15 species was found in all three of them. Nevertheless, each habitat type included some species that were exclusively found within it. Such species were most common in irrigated parks, which had nine of them. Our sampling efforts detected most of the species present in each site since the average sample coverage per site was 93% (range = 83.94–98.86%).

When considering the pattern of variation in ant abundance as measured by the geometric mean of the number of ants per trap, habitat type ($R^2 = 0.87$, $F = 25.01$, $df = 2, 32$; $P < 0.0001$), sampling season ($F = 29.43$; $df = 2, 32$; $P < 0.0001$), and their interaction ($F = 6.26$; $df = 2, 32$; $P = 0.0051$) were all significant explanatory factors. In general, irrigated parks had significantly higher numbers of ants per trap than the other land-use types except for desert

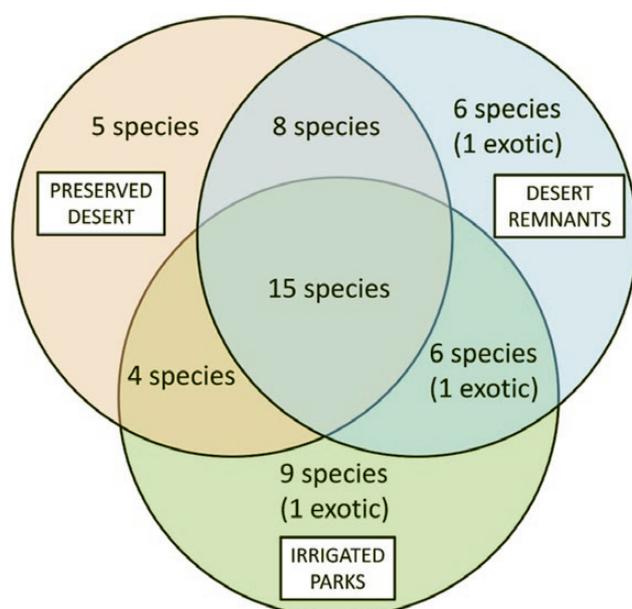


Fig. 3. Summarized Venn diagram of the number of species encountered in each habitat type.

remnants in the fall (Fig. 4). Both preserved desert and desert remnants had significantly greater ant abundances in the fall than in the spring ($F = 40.20$; $df = 1, 32$; $P < 0.001$), but this difference was not significant in irrigated parks ($F = 0.14$; $df = 1, 32$; $P = 0.7147$).

We found no significant differences among habitat types for the diversity parameters considered. There were no significant differences in local species richness ($F = 0.99$; $df = 2, 18.43$; $P < 0.392$). The average estimated species richness was 13.19 species ($s = 2.01$) for parks, while desert remnants and preserved desert had on average 15.31 ($s = 5.94$) and 12.48 ($s = 3.04$) species, respectively. There were also no significant differences in evenness ($F = 2.29$; $df = 2, 32$; $P < 0.4048$). The mean evenness value (2D) for parks was 4.68 ($s = 0.96$) effective species, while desert remnants and preserved desert sites had an average 3.82 ($s = 1.19$) and 4.27 ($s = 2.11$) effective species respectively.

Although most of the species we found were native to the United States, we also encountered three exotic ant species and one cosmopolitan species of uncertain origin (*Hypoponera opaciceps* (Mayr) (Hymenoptera: Formicidae)). Of these, only *B. patagonicus* was widespread, being found in all irrigated parks and four desert remnants. In parks, *B. patagonicus* was present in 84.25% of all traps and were relatively abundant (average geometric mean per site = 5.11 ants per trap; $s = 2.36$). There was no significant correlation between the geometric mean of *B. patagonicus* abundance per trap and the estimated species richness per site ($R^2 = 0.22$; $F = 2.75$; $df = 1, 10$; $P = 0.1281$). Evenness (2D) was not significantly correlated with *B. patagonicus* abundance either ($R^2 = 0.10$; $F = 1.10$; $df = 1, 10$; $P = 0.3187$). For desert remnants, there were no significant differences in estimated species richness ($t = 0.52$; $df = 9$; $P = 0.6141$) or evenness ($t = 0.46$; $df = 9$; $P = 0.6546$) between sites that included *B. patagonicus* and those that did not. Another exotic species, *Cardiocondyla mauritanica* Forel (Hymenoptera: Formicidae) and a possibly exotic cosmopolitan ant species (*H. opaciceps*) were also present in irrigated park sites, being found in small numbers in six and two of them, respectively. Neither *C. mauritanica* or *H. opaciceps* were particularly abundant (average geometric mean per site = 0.25 and 0.14 ants per trap, respectively). The crazy ant (*Paratrechina longicornis* (Latreille) (Hymenoptera: Formicidae)), an invasive species, was collected exclusively from three traps in one desert remnant site during the fall sampling season.

Each of the three land-use types studied harbored significantly distinct sets of ant species. This was the case whether only the presence or absence of species was considered (Sørensen-Dice index permutational MANOVA, $F = 13.30$, $df = 2, 32$; $P = 0.001$; all pairwise comparisons: $P = 0.003$) or when relative abundances were taken into account ($F = 11.09$; $df = 2, 32$; $P = 0.001$; all pairwise comparisons: $P = 0.003$). Differences in the functional composition of ant assemblages were also significant (per MANOVA, $F = 11.94$; $df = 2, 32$; $P = 0.001$). Preserved desert sites were significantly different from desert remnants (pairwise comparison; $P = 0.03$) and irrigated parks ($P = 0.003$). Desert remnants and irrigated parks were also significantly different from each other ($P = 0.003$). Differences between preserved desert sites and desert remnants were associated with an increase in the abundance of Dominant Dolichoderinae and Hot Climate Specialist functional groups (Fig. 5, Table 1). In contrast, irrigated parks were characterized by a considerable increase in the abundance of Generalized Myrmicinae and high abundances of two groups that were barely present in the other habitat types: Tropical Climate Specialists and Cryptic species (Fig. 5, Table 1).

Ant assemblages from irrigated parks were more similar to each other in their species composition than those from desert remnants when either the presence and absence ($F = 14.43$; $df = 1, 21$;

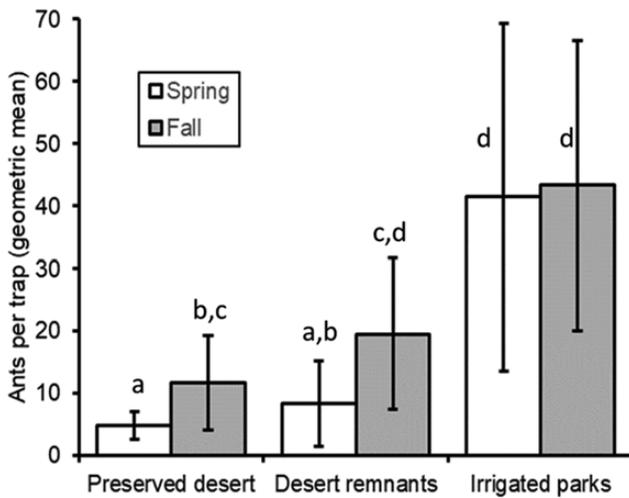


Fig. 4. Comparison of the ant abundance in the habitats studied summarized as the geometric mean of the number of ants found in pitfall traps in each site. The means of bars not labeled with the same letter are significantly different after a repeated measures ANOVA ($P < 0.05$). Error bars were constructed with the standard deviation.

$P = 0.0011$) or the relative abundances of species were considered ($F = 6.97$; $df = 1,21$; $P = 0.013$). Furthermore, a group of seven ant species (Table 1) were recorded in every irrigated park. When added together, these species represented most of the ants collected from parks, accounting for 87.3% of the individual ants found in that land-use type. In contrast, only three species (*D. insanus* (Buckley) (Hymenoptera: Formicidae), *F. mccooci* (McCook) (Hymenoptera: Formicidae), and *Solenopsis xyloni* McCook (Hymenoptera: Formicidae)) were present in all desert remnants, and only one (*Forelius pruinosus* (Roger) (Hymenoptera: Formicidae)) was found in all preserved desert sites.

We found significant differences for both the mean CTI and mean CPI of ant assemblages among the habitat types considered. Ant assemblages in irrigated parks were made up of species previously found in locations with significantly lower maximum temperature of the warmest month ($F = 15.27$; $df = 2,32$; $P = 0.0001$) and significantly higher minimum monthly precipitation ($F = 12.08$; $df = 2,32$; $P = 0.0001$) than those found in desert remnants or preserved desert (Fig. 6).

Discussion

According to our results, irrigated parks had greater ant abundances than either desert remnants or preserved desert sites. Similar results have been reported for arthropods (Cook and Faeth 2006) and for ants (Bang and Faeth 2011) by long-term urban studies in nearby Phoenix, AZ. A likely explanation for this pattern is that the presence of irrigation in green areas removes water as a limiting factor for population growth and increases resource availability through effects on plant productivity (Cook and Faeth 2006). In this study, the importance of water availability for ant abundance is further supported by the lack of significant differences between sampling seasons in irrigated parks contrasting with higher abundances in desert remnants and preserved desert after the monsoon season, when water is more abundant. In effect, irrigation seems to allow parks to maintain high ant abundances regardless of seasonal changes in water availability.

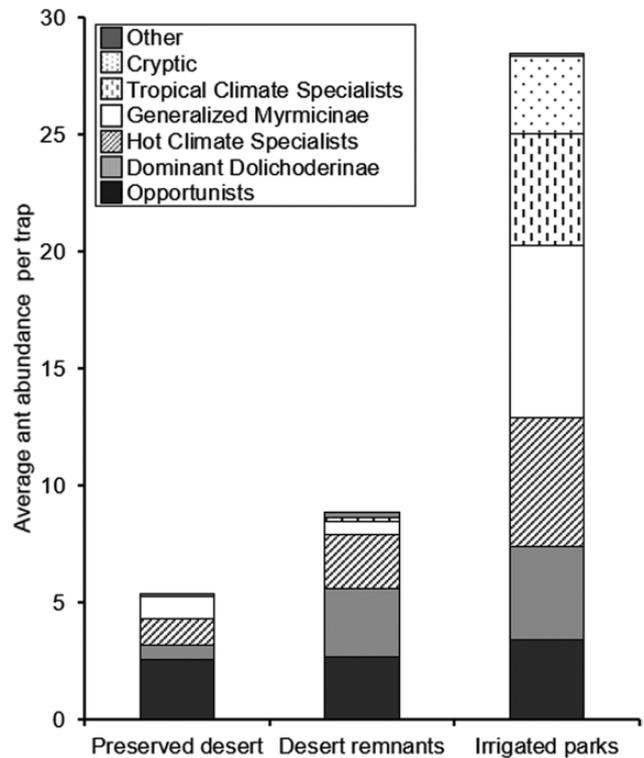


Fig. 5. Average functional group composition of the ant assemblages in the habitat types sampled. Values presented are based on the geometric mean-adjusted abundance of each functional group per trap.

Nevertheless, greater ant abundances might be the result of other differences between irrigated parks and xeric habitats. For example, nest site availability might be a limiting factor for nest density and ultimately ant abundance (Friedrich and Philpott 2009, Yasuda and Koike 2009). Whereas parks are covered with loosely packed, well-drained, moist soil that is likely convenient for nesting; the other habitat types we considered have soils that are hard to dig through and might be prone to flooding or excessive dryness. Another relevant factor might be the availability of human-made foods in irrigated parks. Recreation being their main purpose, irrigated parks are visited more frequently by humans, who might leave food behind. Studies by Penick et al. (2015) and Youngsteadt et al. (2015) have shown that human foods can make up a significant portion of urban ants' diets. This added resource might favor greater ant abundance in irrigated parks.

Contrary to our predictions, we found no significant differences in ant species richness or evenness across habitat types. Local animal biodiversity frequently decreases as a result of urbanization (McKinney 2008, Faeth et al. 2011). However, the diversity of small organisms might be less affected as they can survive in small habitat patches and might be favored by the heterogeneity of the urban landscape (McKinney 2008). In landscaped mesic parks, such as the irrigated parks studied here, some studies have found lower ant diversity than that found in rural habitats (Vepsäläinen et al. 2008, Savage et al. 2015), while others found no significant differences (Menke et al. 2010b) or even increased diversity (Bang and Faeth 2011). Although the higher ant abundance in our irrigated parks could be expected to be accompanied by greater diversity, this was not the case. One explanation for this could be that the increased abundance mainly involves urban exploiters, species that are well adapted to urban habitats and monopolize resources within them

Table 1. Proportional commonness, functional groups, and native or exotic status for ant species recorded

Species	% of traps	% of sites	Functional group	Native or exotic
Irrigated parks				
<i>Brachymyrmex patagonicus</i>	78.39	100	Tropical Climate Specialist	Exotic
<i>Pheidole tetra</i> Creighton (Hymenoptera: Formicidae)	71.06	100	Generalized Myrmicinae	Native
<i>Solenopsis xyloni</i>	68.13	100	Hot Climate Specialist	Native
<i>Forelius mccooki</i>	67.03	100	Dominant Dolichoderinae	Native
<i>Dorymyrmex insanus</i>	60.07	100	Opportunist	Native
<i>Pheidole hyatti</i> Emery (Hymenoptera: Formicidae)	42.86	100	Generalized Myrmicinae	Native
<i>Solenopsis molesta</i> (Say) (Hymenoptera: Formicidae)	31.5	100	Cryptic	Native
<i>Pheidole bicarinata</i> Mayr (Hymenoptera: Formicidae)	30.4	66.67	Generalized Myrmicinae	Native
<i>Formica perpilosa</i> Wheeler (Hymenoptera: Formicidae)	10.26	50	Opportunist	Native
Desert remnants				
<i>Forelius mccooki</i>	74.5	100	Dominant Dolichoderinae	Native
<i>Solenopsis xyloni</i>	42.23	100	Hot Climate Specialist	Native
<i>Dorymyrmex insanus</i>	40.64	100	Opportunist	Native
<i>Novomessor cockerelli</i> (André) (Hymenoptera: Formicidae)	25.9	45.45	Opportunist	Native
<i>Camponotus fragilis</i> Pergande (Hymenoptera: Formicidae)	17.53	81.82	Subordinate Camponotini	Native
<i>Tetramorium hispidum</i> (Wheeler) (Hymenoptera: Formicidae)	11.55	72.73	Opportunist	Native
<i>Monomorium cyaneum</i> Wheeler (Hymenoptera: Formicidae)	8.76	45.45	Generalized Myrmicinae	Native
<i>Pogonomyrmex imberbiculus</i> Wheeler (Hymenoptera: Formicidae)	7.17	63.64	Hot Climate Specialist	Native
<i>Monomorium minimum</i> (Buckley) (Hymenoptera: Formicidae)	6.77	45.45	Generalized Myrmicinae	Native
<i>Brachymyrmex patagonicus</i>	6.37	36.36	Tropical Climate Specialist	Native
<i>Pheidole sciophila</i> (Wheeler) (Hymenoptera: Formicidae)	6.37	45.45	Generalized Myrmicinae	Native
Preserved desert				
<i>Novomessor cockerelli</i>	36.36	66.67	Opportunist	Native
<i>Forelius pruinosus</i>	35.64	100	Dominant Dolichoderinae	Native
<i>Dorymyrmex insanus</i>	29.09	91.67	Opportunist	Native
<i>Solenopsis xyloni</i>	24	91.67	Tropical Climate Specialist	Native
<i>Tetramorium hispidum</i>	18.18	83.33	Opportunist	Native
<i>Pheidole micula</i> Wheeler (Hymenoptera: Formicidae)	11.27	91.67	Generalized Myrmicinae	Native
<i>Camponotus fragilis</i>	8.73	83.33	Subordinate Camponotini	Native
<i>Forelius mccooki</i>	7.27	58.33	Dominant Dolichoderinae	Native
<i>Solenopsis aurea</i> Wheeler (Hymenoptera: Formicidae)	7.27	50	Hot Climate Specialist	Native
<i>Pheidole tepicana</i> Pergande (Hymenoptera: Formicidae)	5.82	25	Generalized Myrmicinae	Native
<i>Myrmecocystus placodops</i> Forel (Hymenoptera: Formicidae)	4.73	58.33	Hot Climate Specialist	Native
<i>Pogonomyrmex imberbiculus</i>	4.73	50	Hot Climate Specialist	Native

Proportional commonness is estimated as the percentage of traps or percentage of sites within each habitat type that included each ant species. The most common species cumulatively corresponding to approximately 85% of the species occurrences in traps within each habitat type are included in the table.

(Shochat et al. 2006). Seven ant species that were present at high abundances in every park were likely behaving in that way. We also found no significant differences between the species richness or evenness of urban desert remnants and preserved desert. Although habitat fragmentation sometimes results in local reductions in ant diversity (Philpott et al. 2010), that pattern is not universal (Crist 2009). The high dispersal capabilities of most ant species might allow them to persist in small habitat patches as long as fragmentation is not associated with habitat degradation.

Another factor explaining the lack of significant differences in diversity among the habitats sampled might be the rarity of invasive species in our study sites. Invasive ants tend to be competitive and are usually associated with reductions in the species richness and evenness of local ant communities, including those in urban environments (Holway et al. 2002, Lach and Hooper-Bui 2010). Of the exotic ants we found, only the crazy ant (*P. longicornis*) can truly be considered invasive since it is known to cause ecological damage by aggressively outcompeting other ants (Wetterer 2008). However, *P. longicornis* was only found in one desert remnant during the first sampling season. The most prominent exotic species we collected, *B. patagonicus*, was found in all the irrigated parks sampled as well as four desert remnants. That species was remarkably common in irrigated parks, being found in over 80% of the traps in that habitat.

Its higher prevalence in an irrigated environment is not surprising as *B. patagonicus* is tropical in origin and is usually associated with high levels of moisture (MacGown et al. 2007). Nevertheless, the abundance of *B. patagonicus* in irrigated parks was not related to any noticeable reduction in species richness or evenness. Although little is known about the biology and behavior of dark rover ants, their small worker size (4–5 mm) and ease of coexistence with larger, more aggressive ant species (MacGown et al. 2007) suggest that they might avoid direct competition with other ants. Other confirmed (*C. mauritanica*) or suspected (*H. opaciceps*) exotic ant species recorded in our study sites were not known to behave as invasives (Wetterer 2012, 2015) and were only found in small numbers.

Our analysis revealed that preserved desert plots, urban desert remnants and irrigated urban parks each included a significantly distinct ant fauna. This outcome is consistent with a previous study in arid Phoenix, AZ which found significantly different ant assemblages at the genus level in contrasting mesic and xeric habitats (Bang and Faeth 2011). Such differences are to be expected because ants are highly responsive to environmental variation (Underwood and Fisher 2006), and ant assemblages in urban environments typically become differentiated from those in less modified habitats (e.g., Vepsäläinen et al. 2008, Savage et al. 2015). Nevertheless, when habitat types were considered as a whole, there was considerable

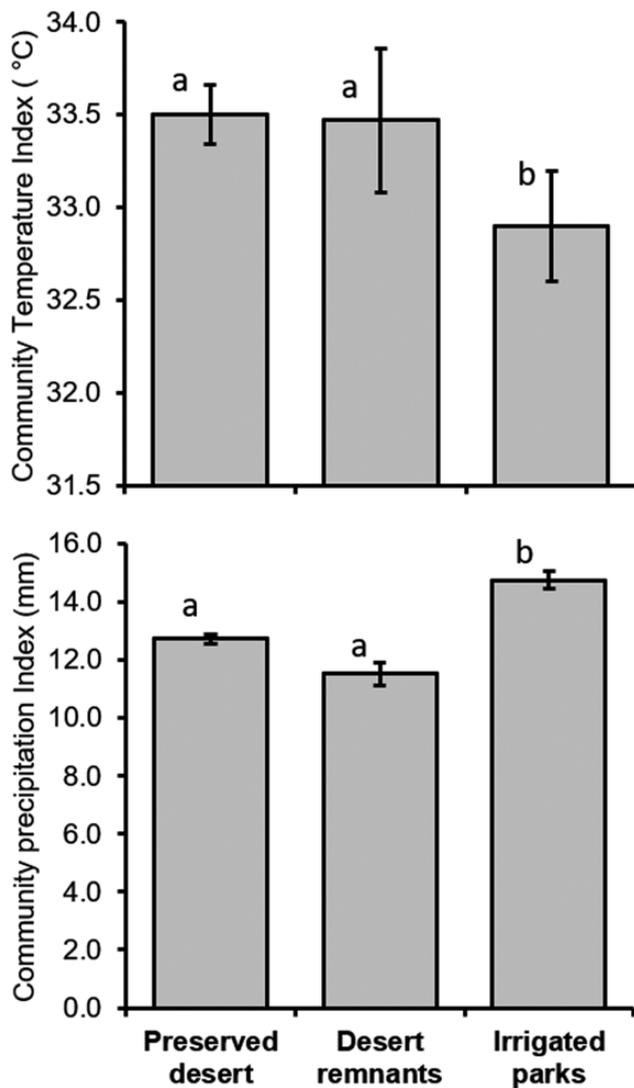


Fig. 6. Average community temperature (top) and community precipitation (bottom) indices by habitat type. The means of bars not labeled with the same letter are significantly different after a Tukey HSD test ($P < 0.5$). Error bars were constructed with the standard deviation.

overlap in the species present in each of them, with few species being exclusive to each habitat and 15 species being shared by all of them. That degree of overlap might hint to a mechanism for source-and-sink dynamics (reviewed by [Leibold et al. 2004](#)) in maintaining the relatively high diversity of ants in irrigated parks and desert remnants. Genetic studies have revealed the high mobility of some ant species in urban environments ([Menke et al. 2010a](#), [Yamamoto et al. 2013](#)), which suggests that urban habitat patches might continuously be exchanging ant species. This flow of species between contrasting habitats would result in greater diversity, even if not all ant species thrive in the new habitats they reach. Although further research is necessary to determine their importance in urban systems, studies considering the mechanisms underlying ant community assembly have found support for this kind of dynamics ([Livingston and Jackson 2014](#), [King and Tschinkel 2016](#)).

Differences in functional group composition among ant assemblages from the habitats sampled suggested that the observed variation in species composition results in part from differences in the climate-related stress and competition dynamics in those habitats.

Although the functional group composition of preserved desert and desert remnants was significantly different, that was mainly due to increased abundance of ants in the Dominant Dolichoderinae and Hot Climate Specialist groups, which point to slight increases in the importance of interspecific competition and hot climate in structuring ant communities in urban desert remnants. In contrast, irrigated parks differed from the other habitats in harboring ant communities with higher proportions of functional groups typical of habitats with high water availability (Generalized Myrmicinae and Tropical Climate Specialists). Overall, the greater abundance of these functional groups suggests that parks resemble mesic or tropical environments more than they do the xeric native habitat. Irrigated parks also had higher abundances of Cryptic species, which might thrive in them thanks to the presence of leaf litter in some areas within parks as a new microhabitat that is absent from the other two habitat types.

Interestingly, only small differences were observed in the abundance of opportunist species across habitats. As a functional group, opportunists are considered disturbance specialists ([Andersen 2010](#)) and are sometimes associated with anthropogenic environments ([Underwood and Fisher 2006](#)). This result suggests that from the point of view of ant colonies, the urban habitats sampled might not be more disturbed than the natural desert environment. Parks, in particular, could be expected to include more opportunists as a result of disturbance caused by higher human activity and regular lawn mowing. The remarkable abundance of some ant species in parks might provide their colonies with some resilience against this disturbance. Larger colonies might be able to rebuild their nests and recover lost territory quickly after a disturbance event, thus preventing the establishment of opportunists. Another possibility is that ant assemblages in the study region might be particularly resilient to disturbance. Studies of the ant diversity in other zones of the arid North American southwest have reported little change in diversity or composition in moderately disturbed areas ([Whitford et al. 1999](#), [Franklin 2012](#)). Franklin hypothesized that this resilience might be a result of the capacity of ants to adapt to disturbance by changing aspects of their colony and nest organization.

Another prominent aspect of the diversity of urban environments is a tendency toward biotic homogenization ([McKinney 2006](#), [Knop 2016](#)) in the form of reduced β diversity among sets of communities. One explanation for urban biotic homogenization is that building, landscaping, and management practices are alike among urban regions, generating habitats that are similar to each other and therefore suitable for similar sets of species ([McKinney 2006](#), [Groffman et al. 2017](#)). Although this mechanism is typically framed in a way that addresses homogenization between groups of cities, it can also be applied to habitats within cities. In this study, ant assemblages from irrigated parks were significantly more similar to each other than those found in urban desert remnants. They also shared landscaping practices and were managed to satisfy the expectations visitors might have of a mesic urban park. Landscaping-related interventions (irrigation, mowing, fertilization, etc.) are likely to have homogenizing effects since one of their purposes is to create similar environments. Conversely, in unmanaged habitats, urbanization might result in environmental changes that differentiate them from one another. For example, they might experience varying degrees of disturbance depending on their accessibility to people or might receive different amounts of water runoff based on their location and the amount of water-impervious surface surrounding them. Therefore, it is not surprising that ant assemblages in irrigated parks would be more similar to each other than those in desert remnants.

An implication of the reduced β diversity in irrigated parks is that each of them makes a comparatively smaller contribution to regional ant biodiversity than a desert remnant of similar size. However, this smaller contribution might be compensated by the relatively high abundance of parks and other irrigated green areas (lawns, gardens, golf courses, etc.) within the urban matrix in most cities. Furthermore, this lower β diversity also makes individual sites redundant so that the survival of species within them is less dependent on the permanence of each habitat patch, which might result in more stable metapopulations.

Our results suggest that the PCI effect can significantly affect the composition of ant assemblages in irrigated urban areas. Ant assemblages in irrigated parks were composed of species typically found in cooler and wetter climates than those from preserved desert locations. Although the magnitude of the PCI effect has not been measured for Tucson, research in nearby Phoenix has estimated a decrease in surface temperatures of 0.8–8.4°C during extreme high-temperature events (Declet-Barreto et al. 2013). The observed mean reduction in the CTI of \sim 0.6°C in irrigated parks with respect to preserved desert sites is close to the lower value of that range. The presence of ant species from milder climates within urban areas of the southwestern United States might be important for their conservation since mesic and riparian environments in that region are projected to diminish in land area as a result of climate change and a continued regional tendency toward greater dryness (Cook et al. 2015). If mesic-adapted species can disperse into green urban habitats, they might be able to survive within them even if their native habitat is diminished or disappears. A similar suggestion has been made about the potential of urban habitats in colder climates to maintain ant species from drier and warmer environments (Menke et al. 2010b). In Tucson, the immediate proximity of several mountainous forested areas (Santa Catalina, Rincon, and Tucson mountains) provides a source of mesic species that can disperse into irrigated habitats inside the city.

Conversely, despite warmer temperatures within the city (Comrie 2000, Scott et al. 2009), ant assemblages in urban desert remnants were not different to those from preserved desert in the climate conditions typically experienced by their species. This is in contrast with previous studies that have found more heat-tolerant assemblages of ants (Menke et al. 2010b), bees (Banaszak-Cibicka 2014), beetles (Piano et al. 2017), and spiders (Meineke et al. 2017) in urban environments. This lack of a difference might be related to the particular nature of the UHI effect in arid regions. Cities in arid regions experience temperature increases due to the UHI effect that are mostly restricted to nighttime temperatures, whereas daytime temperatures tend to be slightly lower than those in surrounding rural areas (Imhoff et al. 2010, Lazzarini et al. 2015). Since most of the stress from high temperatures experienced by an organism happens during the day, this form of the UHI effect is less likely to result in changes in the composition of ant communities.

Overall, our results show that changes related to urbanization have different effects on contrasting urban habitats within an arid region. Ant assemblages from desert remnants resembled preserved desert in parameters of their diversity and abundance. Although there were significant differences in composition, both of those habitats were mostly inhabited by ant species typical of xeric environments. In contrast, ant assemblages in irrigated parks were different from the other two habitats whenever significant differences were detected. These differences suggest that the kind of habitat modification that goes into creating and maintaining parks and other green irrigated areas in arid regions has profound effects on the ecological processes and composition of

communities within them. Although irrigation is likely to be an important driver of these effects (Cook and Faeth 2006), further research is necessary to disentangle its contribution from those of other variables such as human selection of plant species, use of fertilizers, human food inputs, and disturbance resulting from landscaping practices. Notably, the higher prevalence of ant species from cooler and wetter areas within irrigated parks points to the cooling effects of green areas having a previously unrecorded effect on the composition of urban communities. It remains to be determined if similar effects also occur with other groups of organisms besides ants.

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