SHORT NOTES

Idiosyncrasies in cities: evaluating patterns and drivers of ant biodiversity along urbanization gradients

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Abstract

Urbanization is expected to reduce biodiversity. However, an increasing number of studies report urban biodiversity comparable to that of surrounding nonurban areas, leaving open the question: what maintains biodiversity in cities? We characterized patterns of ant biodiversity across urbanization gradients of three major cities in the Midwestern United States and evaluated the support for two mechanisms underlying the maintenance of biodiversity in cities, specifically via introduced non-native species and differential phenology of communities along each urbanization gradient. We observed idiosyncrasies in ant species diversity such that each city displayed either increased, decreased or no change in biodiversity across the urbanization gradient. We found partial support (one of the three cities) for the hypothesis that non-native species can contribute positively to overall species diversity in cities, though even with introduced species removed from consideration, native ant biodiversity was maintained along the urbanization gradient. We found no support for systematic differential phenology across urbanization gradients, although species diversity did vary over time across all sites. Our results further challenge the assumption of biodiversity loss in cities, as two of our three cities exhibited maintained species diversity along the urbanization gradient. Most importantly, our study demonstrates that urban biodiversity can be maintained entirely by native communities.

Key words: Formicidae, urban biodiversity, land-use change, global change, phenological shifts, non-native species

Introduction

For decades, cities have been viewed as barren ecosystems that negatively affect biodiversity (Davis 1978; Denys and Schmidt 1998). This assumption is supported by multiple studies, many of which observed urban communities composed of only a few, but highly abundant species (Holway and Suarez 2006; Thompson and McLachlan 2007; McKinney 2008; Luck and Smallbone 2010; Buczowski and Richmond 2012; Tagwireyi and Sullivan 2015). However, as the field of urban ecology continues to grow, some studies have challenged the idea that biodiversity is lost in cities, finding comparable or even modest increases in biodiversity to that of the surrounding nonurban areas (Magura, Lövei, and Tóthmérész 2010; Ives et al. 2013; Saari et al. 2016).

One straightforward explanation for the maintenance or increase of biodiversity in cities is the presence of introduced, non-native species, especially early after their introduction and before they can cause potentially negative effects on native biodiversity (Gaertner et al. 2017; Ricotta et al. 2017). This pattern and mechanism is seen in plant communities, for which greater biodiversity is observed in urban areas compared with the surrounding areas due to the high frequency of deliberate non-native species introductions by humans (Fig. 1a; McKinney 2008; Faeth, Bang, and Saari 2011). While urban plant community composition is often the result of intense human intervention, community composition in many other taxa is not (Faeth, Bang, and Saari 2011). In many invertebrate systems, biodiversity is resilient to urban land-use change, with diversity...
Within these extreme responses, patterns for sites of intermediate ISA values would be expected to fall. For simplicity, the number of native species (gray bars) may be higher at low percent-developed ISA sites, the added number of non-native species (purple bar) introduced to high ISA sites (either direct or indirectly) may initially positively contribute to the overall number of species (though negative effects of introduced species on native biodiversity can arise later; see main text). (b) Hypothetical pattern of differential phenologies between biological communities at sites of 80 and 0% developed ISA. If communities at sites with 80% developed ISA (red line) experience warmer temperatures and initiate activity earlier in the year (earlier Julian day) compared with communities at 0 ISA sites (blue line), the number of species may appear to be greater in cities if sampling only occurs early in the activity season (within the vertical dashed lines). For simplicity, depicted ISA values represent the extremes of our study design. Species diversity patterns for sites of intermediate ISA values would be expected to fall within these extreme responses exhibiting little change or even modest increases across urbanization gradients (Niemelä and Kotze 2009; Hill et al. 2016, 2017) while also retaining assemblages predominantly composed of native species (Barratt et al. 2015; Barbato et al. 2017). The question therefore remains: what maintains biodiversity in cities, particularly in invertebrate systems?

An alternative hypothesis to explain the (apparent) maintenance of urban biodiversity is differential phenological patterns in communities along the urbanization gradient. Species phenology is often controlled by seasonal environmental fluctuations in critical climatic parameters including temperature (Scranton and Amarasekare 2017; Tonkin et al. 2017). Cities generate elevated environmental temperatures compared with nearby nonurban areas (the urban heat island effect; Imhoff et al. 2010), and while warming-induced shifts in the timing of emergence and other population dynamics such as the timing of peak abundance and the duration of activity periods are well documented (Parmenter 2006; Diez et al. 2012), most comparisons across urbanization gradients are performed at only a few or single time point (Sanso 2016). This focus on a limited number of temporal samples may obscure the signal of urban-driven changes in total biodiversity. For example, if urban communities experience warmer temperatures and reach peak abundance earlier in the year compared with nonurban communities, biodiversity may appear to be greater in cities due to altered phenologies, even when total urban biodiversity is in fact lower (Fig. 1b).

To uncover whether and how urban species diversity might be maintained in invertebrate communities, we first describe overall patterns of species diversity change in a ubiquitous invertebrate taxon, ants (Hymenoptera, Formicidae), across three urbanization gradients of major cities within the same ecoregion (Midwestern United States). Second, we evaluate two alternative hypotheses for maintained or increased species diversity in cities. Our study asks: (1) whether ant biodiversity increases, decreases or is maintained across urbanization gradients; (2) whether patterns of ant biodiversity along urbanization gradients are influenced by the presence of introduced, non-native species at sites with greater urban development and (3) whether patterns of ant biodiversity along urbanization gradients are influenced by differential patterns of phenology or temporal turnover of communities.

**Methods**

**Study area and sampling design**

We sampled ant assemblages across urbanization gradients at three major cities in the state of Ohio, USA, including Cleveland (41.4993° N, 81.6944° W), Columbus (39.9612° N, 82.9988° W), and Cincinnati (39.1031° N, 84.5120° W). We used ants as a focal taxon, as they are geographically widespread, abundant in cities and vary in species composition along natural environmental gradients of key climatic variables such as temperature and aridity (Dunn et al. 2010) that are known to be altered as a function of urbanization (see below). Our focal cities of Cleveland, Columbus and Cincinnati are all located in the Midwestern United States and are roughly comparable in size and age; the cities were constructed between 1816 and 1836 and have population sizes between 2,057,009 and 2,190,209, throughout the metropolitan area (US Census Bureau, Population Division 2018). Importantly, our sampling design that uses percent-developed impervious surface area (ISA) to quantify the degree of urbanization along each of the three gradients, allowed us to make direct comparisons across each city. ISA is the percentage of surface area covered by artificial surfaces such as pavement, roads and building infrastructure with larger percentages indicating increased urban development. Percent-developed ISA is a commonly used proxy for urbanization (Raciti et al. 2012; Bounoua et al. 2018) as it correlates with changes in temperature (Imhoff et al. 2010), soil chemistry (Pouyat et al. 2008; Raciti et al. 2012; Bettez and Groffman 2013), water quantity and quality (Martin and Stabler 2002; Weitzell et al. 2016) and air pollutants (Gregg, Jones, and Dawson 2003; George et al. 2017). As confirmation of the transferability of ISA across each of the three urbanization gradients, our ground-based sensor network showed a very repeatable temperature difference between the most urbanized sites (~80% ISA) and the least urbanized sites (~0% ISA). The differences ranged from 2.7°C in Cleveland to 1.86°C in Columbus and 1.44°C in Cincinnati (Supplementary Fig. S1). All percent-developed ISA data were derived from the
In each city, we established five sites along a continuous percent-developed ISA gradient extending out from the city center in increments of ~20% ISA (~80, 60, 40, 20 and 0% ISA; Fig. 2; Supplementary Table S1). Although we took multiple samples from each site in a transect design, we did not have multiple, independent replicates of the same ISA increments within each city. Therefore, we cannot estimate the repeatability of diversity patterns within each ISA increment for each city. Rather, our experimental design harnesses the power of exploring diversity patterns across relatively fine-scale ISA increments for each city, and allows us to compare these ISA-diversity relationships among cities. Under this experimental design, even nonrepresentative diversity estimates at one or even more ISA increments should be compensated by exploring the diversity trend across the entire set of five ISA increments for a given city. Thus, our design allows us to compare ant diversity changes across three urbanization gradients in a manner comparable to well-studied biogeographic diversity patterns along elevation or latitudinal clines (Dunn et al. 2010).

The extent of our sampling design exceeded the grid size of the NLCD data. Therefore, we estimated site-level ISA by taking the mean of all percent-developed ISA values within a 90-m buffer using the Focal Statistics function in ArcMap v. 10.3. Because percent-developed impervious surface only describes the degree of urban development rather than land cover type (e.g., 0% ISA could equally describe a forest as an agricultural field), we were also careful to match general habitat features, such as the presence of parking lots, pathways, roads and active public use, within and between our different urbanization gradients. Furthermore, urban ant diversity and community composition are known to be affected by habitat type (Uno, Cotton, and Philpott 2010). We avoided selecting sites at vacant lots, community gardens, forest remnants and private residences. Within a given urbanization gradient, we selected seminatural recreational park habitat, with parking lots, pathways and roads, as the ~0% ISA site, and similar, but more heavily developed areas with increased amounts of parking lots, pathways and roads as the higher ISA-valued sites (Supplementary Fig. S2). We kept this assignment the same across the different urbanization gradients to ensure comparability of ISA categories across the three cities (Supplementary Table S1).

We sampled each site from May to September of 2015 (with the exception of two sites in Columbus, each sampled from July to September and one site in Cincinnati that was not sampled in July). Due to the mosaic of impervious surfaces and natural land-use fragments at each site, it was nearly impossible to establish a linear sampling transect, where we could reliably set (dig) traps at a given increment of space. We determined the number and spatial coverage of traps from previous studies that successfully sampled ant communities in urban environments (Gibb and Hochuli 2002; Clarke, Fisher, and LeBuhn 2008; Pecarević, Danoff-Burg, and Dunn 2010; Menke et al. 2011). Additionally, we increased the temporal resolution of the sampling effort from the above-mentioned studies to capture the seasonal components of biodiversity. Every 30 days, we placed five pitfall traps spaced ~20-m apart in a semilinear transect, and allowed them to operate for 48-h. Traps consisted of an open specimen cup (52 mm in diameter and 60 mm in height) buried so the lip was flush with the ground, allowing easy access to ground foraging invertebrates such as ants. We partially filled traps (approximate volume, 50 ml) with 70% ethanol solution as a preservative. This ethanol solution does not attract or repel ants (Greenslade and Greenslade 1971; Bestelmeyer et al. 2000), and a sufficient amount of ethanol solution to preserve all captured ant specimens remained in all pitfall traps after the 48-h sampling period. In addition, we performed a mini-Winkler extraction, which consisted of vigorously sifting a 1-m² sample of surface material (mulch, leaves, litter) through a 1-cm grid sieve. The resulting siftate was then loaded into a mesh bag suspended within a larger funnel-shaped enclosure (Winkler extractor) for 48-h. Invertebrates that dropped out of the mesh bag were collected in a small specimen cup filled with ethanol placed at the bottom of the funnel. With this overall sampling design, we aimed to minimize potential biases in species body-size, foraging-range and natural history (Gotelli et al. 2011), while maintaining adequate coverage of the site. Voucher specimens are retained at the Diamond Lab Entomology Collection at Case Western Reserve University.

**Ant species assemblages and diversity**

All ant specimens collected from the urbanization gradients were counted and identified at least to species group using regional identification keys (Coover 2005; Ellison et al. 2012). Owing to their eusocial organization, estimating numerical abundance of ants can be challenging since individuals collected within a single trap likely originate from the same colony (Gotelli et al. 2011). To alleviate potential biases from this constraint, we used species incidences across sampling units per time point as our measure of abundance instead of raw individual counts (Gotelli et al. 2011). Thus, the maximum ‘abundance’ any ant species can have at a site is six (five pitfall traps plus one Winkler extraction). We quantified ant species diversity using the first two Hill numbers (Hill 1973; Jost 2006), which are weighted measures of species richness that take relative abundance (species incidences) into account. Hill numbers are recommended for comparative biodiversity studies as they report in units of ‘effective number of species’ and are appropriate for comparing diversities across communities (Chao et al. 2014). The first Hill number (Hill.1) is equal to the exponent of the Shannon index (Shannon and Weaver 1949) and weighs each species according to its abundance in the community, representing the number of common species (Jost 2006). The second Hill number (Hill.2) is equal to the inverse of the Simpson index (Simpson 1949) and places less weight on rare species, and can be interpreted as the number of highly abundant species in the community. Using both Hill numbers, we can evaluate the contribution of rare versus common species in the overall diversity patterns.

**Statistical analyses**

**Characterizing biodiversity patterns across urbanization gradients**

To evaluate how well our sampling procedures were able to detect each species within the ant community of each city (sampling completeness), we generated species accumulation curves based on sampling incidence (i.e. the presence or absence of an ant species in a sample) using the program EstimateS (Colwell 2013). Curves reaching a plateau at values of maximum sampling effort indicate that the number of sampled species likely represents the actual number of species within each city (Soberon and Llorente 1993).

To examine the patterns of ant species diversity across space (sites along the urbanization gradient) and time (from the beginning to the end of the activity season) in our three focal cities, we constructed linear regression models with the main
effects and interaction effects (up to the three-way interaction) of percent-developed ISA (continuous variable, the five sampling sites in increments of 20% ISA), Julian Day (continuous variable, the \( \text{30-day sampling interval points from May to September} \)) and City (the three focal cities of Cleveland, Columbus and Cincinnati). We modeled City as a fixed effect (rather than a random effect) as we were specifically interested in the question of whether our three focal cities harbored similar or different relationships between diversity and urbanization, rather than the cross-city overall trend. We performed separate models with Hill.1 and Hill.2 as the response variables. In the case of significant interaction effects including the City term, we used this as justification to analyze species diversity responses to percent-developed ISA and Julian Day for each city separately in subsequent analyses. This modeling framework allowed us to evaluate whether biodiversity is maintained in cities (significance of the percent-developed ISA term), whether biodiversity is stable across the activity season (significance of the Julian Day term), whether biodiversity patterns are similar among the urbanization gradients in different cities (significance of the City \( \times \) percent-developed ISA interaction term), whether biodiversity patterns are similar among time in different cities (significance of the City \( \times \) Julian Day interaction term), and whether biodiversity patterns among sites with different percent-developed ISA values depend on time and/or City (significance of the percent-developed ISA \( \times \) Julian Day and/or percent-developed ISA \( \times \) Julian Day \( \times \) City interaction terms).

In addition to overall patterns of biodiversity, we examined how species composition was influenced by urbanization over the course of the activity season. We used permutational multivariate analysis of variance (PERMANOVA) based on species incidence, Bray–Curtis dissimilarity matrices, with percent-developed ISA,
Evaluating the mechanisms of urban biodiversity patterns

To explore whether non-native species were driving our observed patterns of ant biodiversity along urbanization gradients, we reran our above-described models of diversity while excluding all non-native species. We then compared the results of the analyses using the full suite of species and those using only native species to assess the influence of non-native species on our observed diversity patterns. To explore an alternative mechanism, specifically, whether differential phenologies along the urbanization gradient could explain our observed patterns of ant biodiversity, we examined the significance of the percent-developed ISA × Julian Day interaction term from the diversity models described above. If urban heat islands drive phenological advancement of ant peak abundance and activity leading to spurious patterns of the maintenance of urban biodiversity, we would expect a significant percent-developed ISA × Julian Day interaction such that higher biodiversity would be associated with sites with higher percent-developed ISA values, earlier in the season (Fig. 1b). All statistical analyses were performed using R version 3.4.2 (R Core Team 2018) unless otherwise specified.

Results and discussion

Numerous studies have challenged the assumption of biodiversity loss in cities, finding comparable levels of biodiversity to that of the surrounding nonurban areas (Magura, Lövei, and Tóthmérey 2010; Saari et al. 2016; Hill et al. 2017). Yet, how frequently and by what mechanism biodiversity is maintained in cities remains largely unknown. Although habitat type appears to play an important role in structuring urban biodiversity (Gibb and Hochuli 2002; Uno, Cotton, and Philpott 2010; Nielsen et al. 2014; Aronson et al. 2017), it is unclear how, given the same general habitat type embedded within increasing amounts of impervious surfaces, species introductions or differences in phenology could drive the maintenance of biodiversity in cities. In this study, we used fine-scale spatio-temporal mapping of diversity patterns of ant communities within and among three major cities in the Midwestern United States to explore the maintenance of biodiversity in urbanized areas. We found that in two out of three cities, biodiversity was maintained along the urbanization gradient, from nonurban to heavily urbanized areas, and that neither non-native, introduced species nor altered seasonal activity were responsible for these patterns. As a consequence, urban ant biodiversity was maintained throughout the typical activity season by native communities.

Positive, but mixed support for the maintenance of urban biodiversity in ants

Species accumulation curves generated for each city demonstrate that the number of sampled ant species increased with sampling effort and began to level at maximum sampling effort (Supplementary Fig. S5). Additional sampling effort or alternative methods such as baiting and/or hand collecting may be required for a complete inventory of ant species at each city, but it is important to note that collecting all species at a site is highly unlikely (Longino, Coddington, and Colwell 2002; Groc et al. 2007). Indeed, our sampling protocol may have been biased towards ground-dwelling species; however, outside of tropical systems, there are no strict arboreal species (Gotelli et al. 2011), and previous work has shown that the combination of these two methods effectively inventories ant communities in temperate systems (Martelli, Ward, and Fraser 2004; Groc et al. 2007). Therefore, few additional species would have been collected with additional sampling effort.

Adding to a growing body of work (Niemelä and Kotze 2009; Ives et al. 2013; Hill et al. 2016; Saari et al. 2016), we find that urbanization does not consistently reduce biodiversity. Instead, we observed idiosyncratic responses among our three focal cities. A significant interaction between percent-developed ISA and City (Supplementary Table S2) motivated us to perform separate models of diversity (Hill.1 and Hill.2) as a function of ISA for each city (Table 1). We effectively found three different patterns of biodiversity across the urbanization gradients in the three cities, though importantly, in the majority of cases (Columbus and Cincinnati), we found that biodiversity was at least maintained from nonurban into highly urbanized sites (Fig. 2; Table 2). Specifically for Cincinnati, we observed a non-significant (though positive-trending) relationship between Hill.1 species diversity (species weighted by relative abundance) and percent-developed ISA (Table 2). However, for Hill.2 (more weight on common species), we found a significant positive relationship where species diversity was highest at more urbanized sites (Table 2). Together, these results suggest that communities at lower percent-developed ISA may be composed of numerous species, but only a few of these species are common, whereas at high percent-developed ISA sites, the ant communities are composed of numerous species that are all equally abundant, with only a few rare species. Only Cleveland exhibited the widely assumed pattern of decreased biodiversity with increasing levels of urbanization (Fig. 2; Table 2). Thus in a majority of our cities (two out of three), we do not find support for the expectation of urban-driven biodiversity loss. The critical question then becomes: what mechanisms maintain urban biodiversity? Indeed, few studies have evaluated the mechanistic drivers of biodiversity patterns in cities (Shochat et al. 2006; Diamond et al. 2015), though arguably to predict current and future consequences for urbanization impacts on biodiversity, we need to understand why biodiversity patterns arise (Diamond et al. 2015).

Non-native species introductions can contribute positively to species diversity, but do not entirely explain the maintenance of urban biodiversity

Humans can modify species diversity in cities through direct introductions of non-native species. In some cases, this mechanism underlies patterns of maintained or increased species diversity relative to the surrounding undeveloped areas (Fig. 1a; Hope et al. 2003; Faeth, Bang, and Saari 2011). When we removed non-native species from our analyses, we found that our results were unchanged in Cleveland and Columbus (decreased and maintained diversity, respectively, Table 2, Supplementary Table S3). In contrast, in Cincinnati, exclusion of the non-native species changed the previous interpretation of increased urban
biodiversity (Hill.2) to one of maintained urban biodiversity. Our analysis revealed nonsignificant differences in species diversity across percent-developed ISA (Table 2; Supplementary Table S3). These results suggest that in Cincinnati, non-native species were highly abundant at the most urban sites, contributing positively to Hill.2 species diversity.

Beyond the numerical contribution to biodiversity in Cincinnati, it is worthwhile asking what the broader effects of the non-native ant species are on the native ant community. Although introduced species can contribute positively to biodiversity immediately after their introduction, given sufficient time to interact with native species, introduced species could eventually have negative effects on native ant biodiversity (Sanders et al. 2003; Holway and Suarez 2000; Wittman 2014; Wills and Landis 2018). For example, introduced ant species could plausibly outcompete native species for food and nest resources (Bertelsmeier, Blight, and Courchamp 2016). However, this scenario appears to be unlikely in our particular study system. The two non-native species sampled in our study (Nylanderia flavipes and Tetramorium immigrans), while numerically abundant in urban habitats (Bruder and Gupta 1972; Lessard and Buddle 2005; Ivanov and Milligan 2008; Pecarević, Danoff-Burg, and Dunn 2010; Ivanov et al. 2011), may only have marginal effects on native ant communities (Pecarević, Danoff-Burg, and Dunn 2010). *Nylanderia flavipes* avoids aggressive interactions with native ants, and is quickly displaced at food resources (Ivanov 2016). *Tetramorium immigrans* has been labeled as an urban exploiter, and while its abundance can be negatively correlated with local ant species richness (Steiner et al. 2006, 2008; Ivanov 2016; Gipper et al. 2017), it is primarily aggressive towards conspecifics (Kwon et al. 2014, personal observation), and has been observed to lose control of baits to native ant species (Menke et al. 2010).

Furthermore, while we find that these introduced ant species currently have a positive effect on total biodiversity and are unlikely to have later negative effects on native biodiversity, it is possible that the introduced species biodiversity could collapse in the future. This phenomenon has been documented in several introduced ant species including *Anoplolepis gracilipes*, *Pheidole megacephala* and *Linepithema humile*. Each of these species have been found to rapidly decline or collapse following an initial population expansion (Cooling et al. 2012; Wetterer 2012; Cooling and Hoffmann 2015; and see Lester and Gruber 2016) for a recent possibility in Lasius neglectus). In our study system, although *T. immigrans* is a relatively old introduction (Suarez, McGlynn, and Tsutsui 2010), *N. flavipes* was recorded for the first time in Cleveland in 2005 (Ivanov and Milligan 2008), and specimens from this study represent its first observation in Columbus. We are still learning the ecology of *N. flavipes* outside its native range (Ivanov et al. 2011; Ivanov 2016), so it is unclear if this introduced species will continue to contribute positively to urban biodiversity or whether it will undergo extirpation in urbanized environments. In a broad sense, the effects of non-native ant species on native ant biodiversity are rather complex. Whether non-natives numerically bolster biodiversity or actively reduce biodiversity appear to largely depend on the nature of their interactions with other species and the time elapsed since their introduction, rather than their status as non-natives per se.

### Table 1: Linear model summary table for species diversity (Hill.1, Hill.2) modeled as a function of percent-developed Impervious Surface Area (ISA), Julian Day and their interaction for each city considered separately (Cleveland, Columbus and Cincinnati)

| City     | Response | Term          | F     | P       |
|----------|----------|---------------|-------|---------|
| Cleveland | Hill.1   | ISA           | 10.817| 0.004   |
|          |          | Julian Day    | 0.696 | 0.493   |
|          |          | ISA × Julian Day | 12.828| 0.002   |
|          | Hill.2   | ISA           | 2.659 | 0.123   |
|          |          | Julian Day    | 0.916 | 0.346   |
|          |          | ISA × Julian Day | 1.076 | 0.296   |
| Columbus | Hill.1   | ISA           | 3.081 | 0.086   |
|          |          | Julian Day    | 1.402 | 0.255   |
|          |          | ISA × Julian Day | 0.796 | 0.372   |
| Cincinnati | Hill.1 | ISA            | 7.667 | 0.009   |
|           |          | Julian Day    | 0.201 | 0.667   |
|           |          | ISA × Julian Day | 0.933 | 0.337   |

Sample sizes were Cleveland = 25; Columbus = 20; and Cincinnati = 24. The numerator degrees of freedom for each term was 1, as each term was modeled as a continuous predictor. Significant P-values are in bold.

### Table 2: Estimates, standard errors, test statistics and P-values from linear models of the relationship between species diversity (Hill.1, Hill.2) and percent-developed Impervious Surface Area (ISA)

| Data subset                  | City       | Response | Estimate | SE    | t     | P     |
|------------------------------|------------|----------|----------|-------|-------|-------|
| All species (native and introduced non-native species) | Cleveland | Hill.1  | −0.037   | 0.011 | −3.262 | 0.003 |
|                              |            | Hill.2  | −0.036   | 0.010 | −3.566 | 0.002 |
|                              | Columbus   | Hill.1  | −0.017   | 0.010 | −1.667 | 0.113 |
|                              |            | Hill.2  | −0.010   | 0.008 | −1.737 | 0.256 |
|                              | Cincinnati | Hill.1  | 0.014    | 0.008 | 1.748  | 0.095 |
|                              |            | Hill.2  | 0.019    | 0.007 | 2.825  | 0.002 |
| Native species               | Cleveland  | Hill.1  | −0.037   | 0.011 | −3.387 | 0.003 |
|                              |            | Hill.2  | −0.034   | 0.010 | −3.459 | 0.002 |
|                              | Columbus   | Hill.1  | −0.017   | 0.010 | −1.772 | 0.083 |
|                              |            | Hill.2  | −0.010   | 0.008 | −1.227 | 0.236 |
|                              | Cincinnati | Hill.1  | 0.004    | 0.008 | 0.452  | 0.656 |
|                              |            | Hill.2  | 0.085    | 0.007 | 1.239  | 0.228 |

Separate models are performed for each diversity metric (Hill.1 and Hill.2), for each city and for data subsets including all species versus only native species. Data are pooled across the non-significant term of Julian Day. Significant P-values are in bold.
No indication of differential phenologies in communities along urbanization gradients

Timing of peak abundance and the duration of activity periods often follows seasonal environmental fluctuations in abiotic factors such as temperature (Scranton and Amarasekare 2017; Tonkin et al. 2017). Owing to urban heat islands, urbanization may create differential phenological patterns in communities along urbanization gradients (Shochat et al. 2006). This difference in timing may lead to spurious inferences regarding total biodiversity when limited temporal samples are taken (Fig. 1b). However, we failed to find any support for this hypothesis: while we observed variable spatial patterns of species diversity along each urbanization gradient, temporally, we found no significant interaction between percent-developed ISA and Julian Day (Table 1). This indicates that along each gradient, biodiversity did not display any systematic temporal pattern across sites with different percent-developed ISA values. Our analyses of community composition further support these results. NMDS ordinations revealed spatial differences in species composition along each urbanization gradient (Cleveland Columbus and Cincinnati), demonstrated by the clear distinction between ant communities in high and low percent-developed ISA values. However, along the activity season, we found clustering of points within Julian Day. These results show that while composition changed significantly along each of our three urbanization gradients, composition was invariant over time (Fig. 3; Table 3).

While we sampled across a typical activity season for temperate North American ant species (Herbers 1985, 1989), it is possible that if we were to extend the sampling interval across the entire year, we may then observe differential patterns of phenology among sites with different percent-developed ISA values. A wide array of organisms show phenological advancement in cities such as plants (Neil and Wu 2006), birds (Deviche and Davies 2014) and scale insects (Meineke, Dunn, and Frank 2014), though the opposite pattern has also been found in butterflies (Diamond et al. 2014). Recent work in the study area has shown that urban heat islands can advance reproductive phenology for the ant species Temnothorax curvispinosus by ~1 month (Chick et al. 2019). Overall, however, we know very little about urban-driven phenological shifts in ants as biodiversity studies are overwhelmingly based on sampling during a typical activity season, with few contributions focused on early season, late season or overwintering.

Table 3: PERMANOVA summary table examining differences in ant communities across percent-developed Impervious Surface Area (ISA), Julian Day and their interaction for each city (Cleveland, Columbus, and Cincinnati)

| City     | Term         | F    | R²   | P    |
|----------|--------------|------|------|------|
| Cleveland | ISA          | 3.676| 0.140| 0.001|
|          | Julian Day   | 1.014| 0.039| 0.419|
|          | ISA×Julian Day| 0.614| 0.023| 0.773|
| Columbus | ISA          | 4.617| 0.204| 0.001|
|          | Julian Day   | 1.329| 0.059| 0.002|
|          | ISA×Julian Day| 0.692| 0.031| 0.698|
| Cincinnati| ISA         | 8.746| 0.272| 0.001|
|          | Julian Day   | 2.583| 0.080| 0.018|
|          | ISA×Julian Day| 0.987| 0.027| 0.496|

Sample sizes were Cleveland = 25; Columbus = 20; and Cincinnati = 24. The numerator degrees of freedom for each term was 1, as each term was modeled as a continuous predictor. Significant P-values are in bold.

Figure 3: Two-dimensional nonmetric multidimensional scaling (NMDS, Bray-Curtis dissimilarity matrix) ordination of the sampled ant communities across percent-developed impervious surface area (ISA) and Julian Day for the cities of Cleveland, Columbus and Cincinnati. Final stress of 0.18 for Cleveland, 0.16 for Columbus and 0.17 for Cincinnati, signifying good representation of the variance of species assemblages in the reduced dimensions. Symbols and colors correspond to sampled species composition at each (a) ISA site and (b) Julian Day of each sampling point. Ellipses represent 95% confidence interval around the centroid of points.
responses (Santos 2016). Although the question of year-round phenological change in cities merits further study, our main focus was on whether the timing of sampling along the urbanization gradient could lead to the apparent maintenance of biodiversity in cities (Fig. 1b). At least for ants sampled during the typical activity season, this possibility appears unlikely; however, it remains to be seen how generalizable our temporal patterns of ant biodiversity are across other systems.

Study limitations and future directions

Our study finds support for the maintenance of urban ant biodiversity in some cities, but not all, and therefore, it is important to consider how differences among cities themselves might contribute to this variation in biodiversity patterns. We selected cities within the same geographic region (the Midwestern United States), and with relatively similar city ages and sizes. However, among our focal cities, potential sources of inter-city variation include differences in background climate and proximity to large bodies of water, with Cleveland having cooler mean annual temperatures and positioned adjacent to Lake Erie. These factors have been shown to interact with urbanization gradients to influence ant physiology and behavior (Warren, Bayba, and Krupp 2018) and may play a role in structuring communities by facilitating or preventing the movement of certain species into cities. At a broader scale, future research involving syntheses of multiple urban biodiversity studies might be able to find general patterns in how variation among cities, with respect to size, age, and many other factors (McDonnell et al. 1997; Grimm et al. 2008; McIntyre, Knowles-Yañez, and Hope 2008), contributes systematically (or not) to urban biodiversity patterns.

Urban biodiversity is increasingly recognized for maintaining ecosystem function and social and cultural well-being (Müller and Werner 2010). Our study found that cities can maintain or even increase levels of biodiversity relative to the surrounding nonurban areas. From a conservation standpoint, the maintenance of ant urban biodiversity may facilitate ecosystem function as ants perform key ecosystem services including decomposition, soil aeration and seed dispersal (Del Toro, Ribbons, and Pelini 2012). While we find that introduced non-native ant species can contribute positively to urban biodiversity, a pattern and mechanism seen in urban plant communities, in the majority of cities we examined, the main- tenance of biodiversity was driven by responses of native ant communities. This suggests that ants may be resilient to some forms of anthropogenic change including urbanization. Moving forward, uncovering the degree to which different components of native biodiversity are affected by urbanization, such as functional trait diversity, are ripe areas for future research and will further aid in understanding the mechanisms driving community structure and species diversity in cities.

Data availability

Data included in the manuscript is available on request.

Supplementary data

Supplementary data are available at JUECOL online.

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