Ecological Applications, 29(3), 2019, e01869

Multi-scalar drivers of biodiversity: local management mediates wild bee community response to regional urbanization

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Citation: Ballare, K. M., J. L. Neff, R. Ruppel, and S. Jha. 2019. Multi-scalar drivers of biodiversity: local management mediates wild bee community response to regional urbanization. Ecological Applications 29(3):e01869. 10.1002/eap.1869

Abstract. It is critical to understand the specific drivers of biodiversity across multiple spatial scales, especially within rapidly urbanizing areas, given the distinct management recommendations that may result at each scale. However, drivers of biodiversity patterns and interactions between drivers are often only measured and modeled at a single scale. In this study, we assessed bee community composition at three time periods in 20 grassland and 20 agriculture sites located across two major metroplexes. We examined how local environmental variables and surrounding landscape composition impact bee abundance, richness, and evenness, including comparisons between groups with different nesting strategies and body sizes. We collected nearly 13,000 specimens and identified 172 species. We found that levels of regional land use differentially impacted bee abundance and diversity depending on local habitat management. Specifically, within agriculture sites, bee richness was greater with increasing landscape-level seminatural habitat, while in grassland sites, bee richness was similar across landscapes regardless of seminatural habitat cover. Bee evenness at both site types declined with increasing landscape-level habitat heterogeneity, due to an increase of rare species at the grassland sites, but not in the agricultural sites, further indicating that diversity is driven by the interaction of local habitat quality and landscape-level habitat composition. We additionally found that agriculture sites supported higher abundances, but not richness, of small-bodied and below-ground nesting bees, while grassland sites supported higher abundances of above-ground nesting bees, and higher richness of large-bodied species. Increased levels of local bare ground were significantly related to multiple metrics of bee diversity, including greater below-ground nesting bee abundance and richness. Local floral richness was also significantly related to increases of overall bee abundance, as well as the abundance and richness of small bees. Overall, we suggest that local land managers can support bee abundance and diversity by conserving areas of bare soil and promoting native floral diversity, the latter especially critical in highly urban agricultural spaces. Our results provide the first documentation of significant interactions between local habitat management and landscape composition impacting insect communities in urban systems, indicating that bee conservation practices depend critically on land use interactions across multiple spatial scales.

Key words: community ecology; gardens; habitat fragmentation; landscape complexity; land use gradients; native bees; remnant grasslands; Texas; urban farms.

INTRODUCTION

Across the globe, terrestrial ecosystems are increasingly altered and fragmented by human-modified habitat, whereby anthropogenic land use, including agricultural, industrial, peri-urban, and urban development, can occur within the heart of natural habitat. Landscape modification, which typically results in the loss and fragmentation of natural habitat, is one of the main drivers of biodiversity decline (Fahrig 2003, Fischer and Lindenmayer 2007), often resulting in altered species compositions with dominance of a handful of urban-adapted species (Grimm et al. 2008, Geslin et al. 2013) and decreased ecological function (Hooper et al. 2005, Wardle et al. 2011). Human-dominated landscapes are particularly important places to investigate biodiversity patterns, not only because these landscapes continue to expand in size and number with human population growth (Vitousek et al. 1997), but also because they can act as model systems to understand the impacts of disturbance and habitat heterogeneity on biodiversity at multiple spatial scales (McDonnell and Pickett 1990).

Manuscript received 27 February 2018; revised 13 November 2018; accepted 19 December 2018. Corresponding Editor: Alison K. Brody.

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Despite this, biodiversity patterns in urban areas are not well understood and are often only investigated at the local scale, even though theoretical and empirical work indicate that local habitat composition likely interacts with landscape-level processes to influence species composition (Hille Ris Lambers et al. 2012). For example, some researchers have hypothesized that complex regional landscapes (typically defined as landscapes with high amounts of seminatural habitat) may positively impact species richness in structurally simple local habitats (i.e., agricultural or industrial areas) via dispersal from the regional landscapes. In contrast, complex local habitats (i.e., remnant natural habitat patches) may not benefit as much by the same landscape-level complexity given that high species diversity is already locally supported (Tscharntke et al. 2012, Lichtenberg et al. 2017). While tests of this "landscape-complexity hypothesis" (Tscharntke et al. 2012) have been useful for interpreting biodiversity patterns in agricultural systems (Batáry et al. 2007, Rundlof et al. 2008, Carvell et al. 2011, Jonsson et al. 2015), its relevance has yet to be explored in other areas, such as urban ecosystems. Further, there is increasing evidence that biodiversity underlies a number of key ecosystem services in urban areas (Schwarz et al. 2017); thus, it is vital to understand the mechanisms regulating the community composition of key ecosystem-service providing organisms within urban ecosystems.

One particularly critical ecosystem service is pollination, where wild and managed bees are the most economically important pollinators in both managed and natural landscapes (Losey and Vaughan 2006, Gallai et al. 2009). In urban systems, farmers and gardeners are often entirely dependent on wild bee pollination services, given the many legal and financial restrictions on honey bee management in city limits (Salkin 2011). Further, given the national and global declines of bee species (Bartomeus et al. 2013, Goulson et al. 2015), the increases in urban agriculture (Lin et al. 2015), and the increased cultivation of pollinator dependent crops worldwide (Aizen et al. 2008), there is increased concern over the pollination services received by both wild and cultivated plants in urbanized landscapes (Threlfall et al. 2015, Quistberg et al. 2016). Although urbanization can threaten biodiversity, there are a few local habitat types within urban ecosystems that can support bee communities and are also uniquely sensitive to reductions in wild pollination services; two of these include (1) urban agricultural spaces (e.g., community gardens, urban farms) and (2) remnant grassland patches (e.g., nature preserves, natural parkland). Urban farms and gardens have been shown to provide important habitat for bees and other taxa (Matteson et al. 2008, Lin et al. 2015), and the maintenance of urban prairies is becoming an increasingly common way to turn vacant lots into biodiversity refuges (Goddard et al. 2010, Gardiner et al. 2013). However, it is currently unknown how the surrounding urban landscape composition interacts with local agriculture and prairie management to impact bee community composition.

Past research has indicated that landscape processes can influence bee community composition, but the key landscape drivers have been distinct in many past study systems. At landscape scales (i.e., ≳2 km), some studies have documented negative impacts of increasing regional urban cover on regional bee abundance and diversity (reviewed in Winfree et al. 2009), while others have found relatively high bee diversity in highly urbanized areas (Fortel et al. 2014, Baldock et al. 2015). One reason for this discrepancy may be the investigation of different landscape drivers in the past studies, where some studies have focused exclusively on landscape-level seminatural habitat cover as a major predictor of bee abundance and diversity (Steffan-Dewenter 2003, Williams et al. 2010), while others have focused on habitat heterogeneity or other land-cover types (e.g., agricultural land; Holzschuh et al. 2007). Second and relatedly, because distinct bee groups require different habitats for nesting and foraging (Westrich 1996, Steffan-Dewenter et al. 2002, Franzén and Nilsson 2009), responses to land use and landscape diversity may also vary within distinct functional groups (Williams et al. 2010), and differences may not be captured in studies that only focus on metrics for the entire bee community. For example, bees with different maximum foraging distances (possibly correlated with body size; Greenleaf et al. 2007) may vary in their ability to colonize local sites from surrounding land use. Community composition of bees has been shown to shift towards larger-bodied bees in intensive agricultural landscapes (Steffan-Dewenter and Tscharntke 1999, but see Larsen et al. 2005), and greater persistence of pollinator species with longer dispersal abilities has previously been documented in habitats fragmented by human land use (Wood and Pullin 2002, Jauker et al. 2009).

Local habitat features may also differentially influence species colonization patterns (Williams and Kremen 2007, Hille Ris Lambers et al. 2012), and thus may additionally regulate the response of the whole community to landscape-level habitat cover (Tscharntke et al. 2005). For example, local habitats with higher levels of disturbance may support higher abundances of common and generalist species, as seen in previous bee studies (Threlfall et al. 2015) and in other taxa (Devictor et al. 2008, Mangels et al. 2017). Local management may also structure bee communities based on functional trait differences, for example different nesting strategies (Williams et al. 2010). Eighty percent of bee species nest underground and it is hypothesized that ground-nesting bees experience decreased nest site availability because of increased impervious surface and/or frequent soil disturbances in cities (Ahrné et al. 2009). In contrast, some studies have shown that above-ground nesting species can be more abundant in urban areas than in surrounding continuous natural habitat (Cane et al. 2006, Matteson et al. 2008), presumably due to increased local nest site availability in human-associated materials such as firewood and built structures. Thus, investigations of landscape interactions with local management may be important for understanding responses of the whole bee community, as well as the distinct responses of body-size and nesting-based functional groups.

To assess this, we compared bee community composition in urban grassland and agricultural fragments and investigated how local habitat management and landscape-level habitat composition affected the abundance, species richness, and evenness of all bees; we then specifically compared these drivers for above- and belowground nesting species, and for species of both small and large body size classes. Although richness and abundance are the typical indices for assessments of native bee diversity, recent studies have shown that evenness is an important aspect to measure separate from richness, as richness is often strongly confounded with abundance, and high richness is often driven by increases in rare species (Lichtenberg et al. 2017). While it has been reported that common species provide the majority of pollination services in some agricultural systems (Kleijn et al. 2015), it is likely that the presence of rare species contributes to ecosystem resilience and functional redundancy (Mouillot et al. 2013). This is especially important in human-dominated ecosystems where local habitats are often dominated by large abundances of a small handful of disturbance-tolerant or “weedy” species. Therefore, patterns of diversity in urban ecosystems must be investigated using several metrics to truly address how local management and landscape context may affect ecosystem functioning across urban areas. Specifically, we asked the following three questions. (1) Does urban bee community composition differ between agriculture and grassland management? (2) What local habitat features most correlate with abundance, species richness, and evenness of (a) the full bee community, and (b) bees with different nesting preferences and body sizes? (3) Does landscape context interact with local management to differentially affect abundance, species richness, and evenness of the full bee community and of the distinct nesting- and body-size-based functional groups?

METHODS

Study area

We conducted this research in 40 study sites within a ~350-km corridor from Central to Northeastern Texas, spanning two of the fastest growing cities in the United States (Fig. 1): 20 sites in each of Dallas-Ft. Worth (centroid: 97.096429° W, 32.805049° N) and Austin (centroid: 97.890679° W, 30.329448° N). Dallas-Ft. Worth is located in north-central Texas, and is the fourth largest metropolitan area in the United States (Population Division 2017). The Austin metroplex is located on the southern end of the corridor, with an estimated 2.0 million people, and is currently the second fastest growing city in the United States, exhibiting an increase in over 19% of the human population from 2010 to 2016 (Population Division 2017). Current land use is comprised of urban, suburban, cropland, pasture, and seminatural habitats.

At the local scale, sites were categorized based on two main management styles: (1) grassland sites (20 sites total), which are herbaceous plant communities managed as wildlife refuges, state or city parks, or private grassland habitats and (2) agriculture sites (20 sites total), which are herbaceous plant communities managed as small-scale farms or community gardens (Appendix S1: Fig. S1, Table S1). Grassland sites were dominated by native vegetation and had minimal disturbance regimes, including little to no human disturbance except for infrequent mowing (occurring zero to two times per year). In contrast, agriculture sites were dominated by nonnative species including crop and horticultural species, and much higher levels of local disturbance including frequent soil tillage, plant cultivation, and vegetation removal (occurring two to five times per month), typical of a small-scale farm or garden. Both management types were represented across the gradient of developed land, occurring in rural, peri-urban, and central urban areas (Fig. 1). Sites were located a minimum of 2 km apart to reflect bees’ typical maximum foraging distance (Greenleaf et al. 2007). At each site, we established a 50 × 50 m study plot, where all insect collection and vegetation surveys were conducted. To document bees and flowering plants throughout the late spring growing season, we surveyed study plots three times in 2013; in the first weeks of May, June, and July. Although central and northeastern Texas exhibits a roughly bimodal bloom period extending from February to October, we sampled during the late spring period only as this period has the least variable rainfall from year to year (Bomar 1995; J. L. Neff, *unpublished data*), and therefore, sampling during this time is likely to produce the most representative sample of the typical bee community.

Bee collection

Bees were collected across sites through a combination of standardized pan traps (Potts et al. 2005) and blue vane traps (LeBuhn et al. 2003, Stephen and Rao 2007) in each of the three sampling periods. Pan traps were made from 3.25 ounce Solo® polystyrene plastic soufflé portion cups (model number: P325W-0007, Urbana, IL, USA). 1 ounce = 29.57 mL), either painted fluorescent blue or yellow Guerra Paint & Pigment Corporation, New York, NY, USA) or left white and filled with soapy water (as per LeBuhn et al. 2003). Vegetation above each trap was cleared to ensure traps were visible to flying insects. A total of 50 pan traps were placed one meter apart in an “X” formation at the center of each plot, alternating blue, white, and yellow traps (as per LeBuhn et al. 2003), and were collected after 24 h. Immediately after the completion of pan trapping, four blue vane traps were suspended from a wooden stand 1 m above the ground in the center of the plot for 5 d. Upon collection from both pan and blue vane traps, bees were

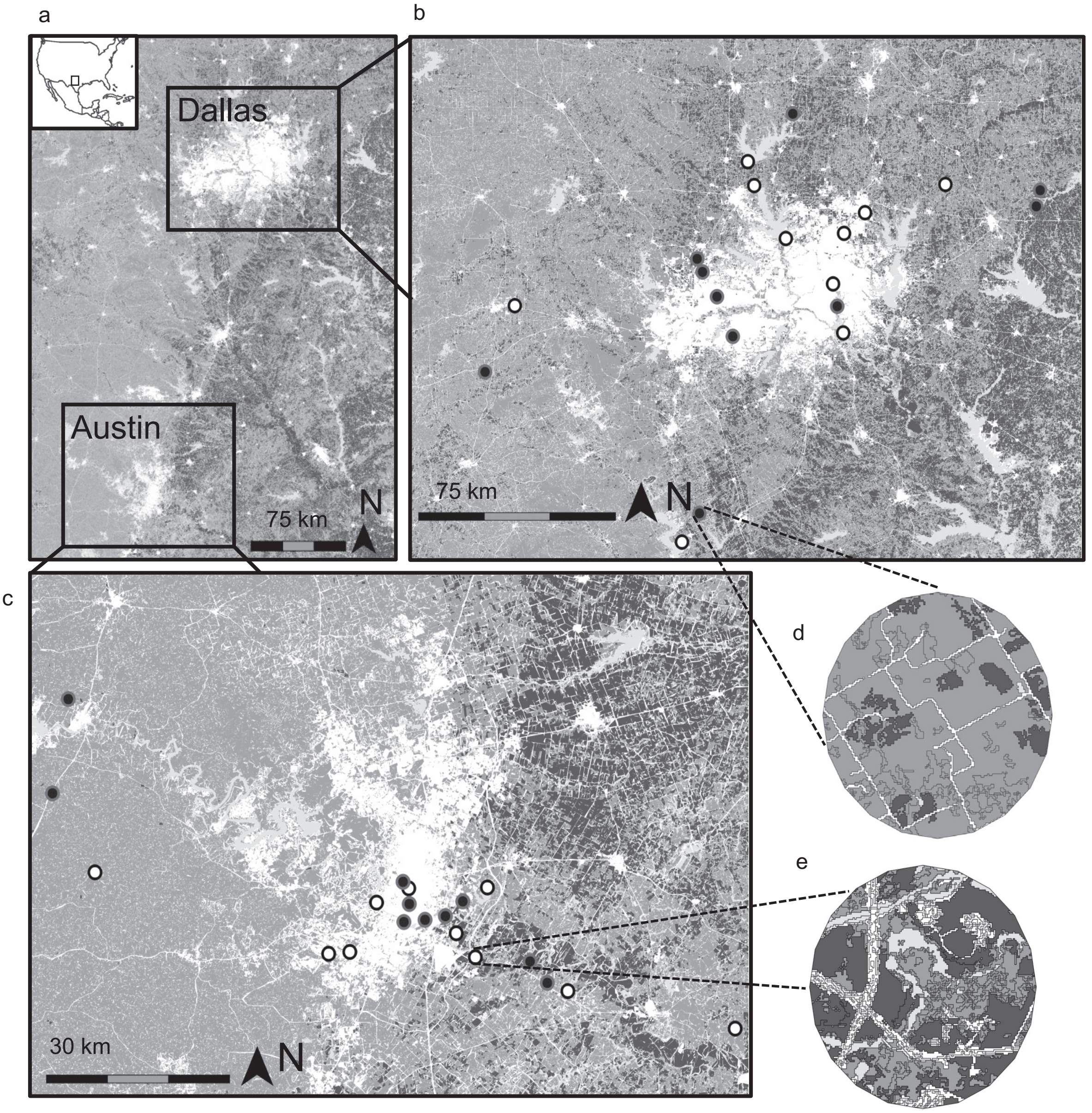

Fig. 1. Map of study sites (a) in Texas, N. America (inset) showing broadly defined land use categories (white is developed, light gray is seminatural, and dark gray is pasture and crop). The location of (b) 20 study sites in the Dallas city region (centroid: 97.096429° W, 32.805049° N) and (c) 20 study sites in the Austin city region (centroid: 97.890679° W, 30.329448° N), where agriculture sites are shown as black circles, and grassland sites are shown as white circles. An example of a 2-km buffer at site with (d) low landscape heterogeneity and (e) high landscape heterogeneity, where patches of different NLCD land-cover types are outlined in black.

preserved in 100% EtOH, and later washed gently with soap and water, pinned, dried, and identified to species or morphospecies level. Bees were classified as either above- or below-ground nesting based on information from published literature (Michener 2000) and taxonomic experts (J. L. Neff, *personal communication*). As per Benjamin and Reilly (2014), bees were classified into one of two body size groups based on measured intertegular distance (ITD); either small (<2.25 mm) or large (≥2.25 mm). Mean ITD per species was calculated from measurements of five pinned specimens in our collection or the maximum number available. Intertegular distance is a commonly used metric of bee body size (Cane 1987) that is likely correlated with maximum foraging and dispersal distance (Greenleaf et al. 2007).

Local vegetation surveys

During the three sampling periods, each plot was surveyed for local ground cover, canopy cover, and floral cover to provide information on potential foraging and nesting habitat. Specifically, these three types of cover were surveyed in 30 1 × 1 m quadrats, sampled in three transects of 10 quadrats, which ran north-south in each plot, located at 10, 25, and 40 m from the northwest corner of the plot (as per Ritchie et al. 2016). Within each of the 30 quadrats per plot, the following was assessed: number of inflorescences, percent cover live vegetation, percent cover dead vegetation/leaf litter, percent cover bare ground, percent cover rocky or impervious ground, and percent tree canopy cover. All inflorescences of forb or woody plant species in flower (grasses were not counted) were identified to species or morphospecies level.

Landscape characterization

Landscape buffers were created with a radius of 2 km to reflect most bee's maximum foraging distance around each sampled site in qGIS v. 2.14 (QGIS Development Team 2014) using the most up-to-date publicly available land use layers from the National Land Cover Database (NLCD; Homer et al. 2012), which provides land classification at a 30-m resolution. To analyze the impact of landscape-level land cover, the percentage area of 11 land use types in the 2-km buffers was summed into three land cover categories representing broad differences in bee nesting and foraging habitat (as per Ritchie et al. 2016): (1) *developed*, comprised of high intensity developed, medium intensity developed, low intensity developed, and developed open space (NLCD categories 21–24); (2) *pasture and crop,* comprised of pasture/hay and agriculture crops (NLCD categories 81–82); and (3) *seminatural*, comprised of deciduous forest, evergreen forest, mixed forest, grassland/herbaceous, and shrub/scrub (NLCD categories 41–43, 71, 52). This combination also facilitated statistical analyses as these three terms were not highly collinear, unlike many of the individual land use variables, allowing for early variable reduction. Additionally, preliminary *t* tests indicated that the amounts of each of these landscape types did not differ significantly between management types. In general, across all sites, developed land cover ranged from 0% to 98% within a 2-km radius of the sampling point. As per Ritchie et al. (2016), we did not include the areas of open water, barren land, or inundated habitats (NLCD categories 11, 31, 90, 95) in these broad habitat categories, as these are not typically suitable bee nesting habitats, and made up <5% of land use within the buffers. Finally, to acknowledge the potential role of habitat heterogeneity, in addition to the coverage of the three summed land cover categories, we quantified heterogeneity as the total number of land use patches of all 15 possible NLCD land use types within each 2-km buffer, calculated using qGIS. This metric ranged from 376 total patches in the most homogenous buffer to 5,206 patches in the most heterogenous buffer (also see Fig. 1 for examples). This metric of heterogeneity is analogous to other measures of landscape heterogeneity (i.e., edge density), and is useful for describing gradients of habitat diversity in urban systems, especially when combined with class-level indices that describe the relative contributions of different land uses (Luck and Wu 2002).

Data analysis

All analyses were completed using R v 3.4.1 (R Core Team 2015).

Bee community composition in agriculture and grassland management.—Differences in the bee community between the two management types were tested using permutational MANOVA (PERMANOVA, adonis function, R package vegan) and visualized using nonmetric multidimensional scaling (NMDS) using a Bray-Curtis similarity index (NMDS function, R package vegan), following the recommended procedure in Minchin (1987). PERMANOVA has been shown to be a more powerful tool than other ordination methods (i.e., ANOSIM or Mantel tests) to detect changes in community structure of real ecological data in balanced designs (Anderson and Walsh 2013). Because of low sample sizes at certain sites and sampling dates, we first pooled all bees collected at each site across the three sampling periods (as per Baldock et al. [2015], 40 total samples), and then conducted the analyses using data from bee species that were present in more than one site. Preliminary analyses of log-transformed abundances showed that bee communities were significantly different between city regions (PERMANOVA, $P = 0.001$), and so city was included as a stratum in the PERMANOVA analysis to account for the nested structure of the data. We then conducted the same analysis twice: first, using $\log(x + 1)$-transformed raw abundance data, and second, using only presence absence data to further reduce biased contributions of the more abundant species (Clarke 1993). The contribution of each species to the Bray-Curtis dissimilarity between management types, and the probability of each species occurring in either agriculture or grassland sites, was analyzed using a similarity percentage analysis (SIMPER, Clarke 1993) using $\log(x + 1)$ abundance and presence absence data with 1,000 permutations (simper function, R package vegan). SIMPER performs pairwise comparisons of species collected at each site and finds the average contributions of each species to overall Bray-Curtis dissimilarity, as well as the likelihood of each species occurring in one site type over another. To mitigate the tendency of SIMPER to preferentially detect more variable species as having between-group effects (Warton et al. 2011), we only considered species as significant drivers of community difference if they were significant in both the presence-absence and $\log(x + 1)$ abundance transformations, and interpreted these species not as single drivers of community difference, but rather as indicator species of bee groups with different habitat preferences.

Effects of local environmental drivers and landscape context on bee abundance and diversity in agriculture and grassland management.—To understand how different management types impact bee communities at multiple scales, we used linear mixed models (LMMs; R package lme4) to examine differences between agriculture and grassland sites, as well as their local and landscape environmental conditions. Specifically, we examined effects on bee abundance, bee species richness (Chao1; Chao 1984), and evenness (E_{var}, Smith and Wilson 1996) for (1) the total bee community, (2) above- and belowground nesting bees, and (3) small- and large-bodied bees. Chao1 is an extrapolated measure of species richness, which accounts for potential undersampling by estimating higher species richness for samples with more rare taxa present (Chao 1984). E_{var} ranges from 0 (one taxon present/dominant) to 1 (equal abundance for all taxa). Lower levels of E_{var} indicate a greater difference in abundance of common and rare taxa (i.e., lower evenness), and higher levels of E_{var} indicate a lower level of difference between the abundance of common and rare taxa (i.e., higher evenness; Smith and Wilson 1996). Evenness was only analyzed for samples where we collected at least three species (as per Lichtenberg et al. 2017). We used a normal distribution for all models, after $\log(x + 1)$ transforming bee abundance and richness. In all models, we included the random effect of site nested within city to account for overdispersion and potential community differences based on geography of regions and individual sites (Zuur et al. 2009). For these LMMs, we analyzed bees collected at each site and sampling period as a separate sample (120 samples, 3 samples at each of 40 sites), with sampling date included as an additional random effect to account for the natural decline of floral abundance and diversity over the course of the season (J. L. Neff, *unpublished data*). The three response variables were modeled as a function of explanatory variables including management type (grassland or agriculture) and two sets of environmental variables: local variables (plot level) or landscape variables (within 2 km of the center of the plot). Local variables included measurements of floral availability, ground cover, and canopy cover (Table 1; Appendix S1: Fig. S3) and were included in the model as single terms to understand how local environmental variation affected bee communities regardless of the management type. To specifically investigate the landscape-complexity hypothesis within our urban system, landscape variables were included as interaction terms with management (sensu Batáry et al. 2007, Rundlof et al. 2008) to analyze potential differences in the effect of surrounding landscape composition for the two management types. These included percentage of different land uses and measures of habitat heterogeneity (Table 1). All continuous variables were standardized using the scale function in R. The same explanatory variables were included in starting models for all response variables. We tested for multiple collinearity using variance inflation scores (Fox and Weisberg 2014), eliminating variables from the model with VIF scores higher than three. In each model, percentage of developed land had a high VIF score and was colinear with percentage of seminatural land. The local variables percentage of dead vegetation and percentage of rocky ground also showed high VIF scores within each model. After removing these three explanatory variables from the initial models, all remaining variables showed VIF scores of approximately two or lower, and so we proceeded constructing initial models including all remaining variables. All model residuals conformed to a normal distribution and did not show evidence of spatial autocorrelation. We then tested all combinations of the explanatory variables and conducted model selection via Akaike's information criterion (AIC) using the MuMIn package. We constructed our final models by averaging all models within $\Delta\text{AIC} < 2$ of the top model (Grueber et al. 2011) also using MuMin. We report the full model average, which incorporates relative variable importance

TABLE 1. List of measured variables for linear mixed model analysis, indicating scale, type of effect (either fixed or random), and whether or not each was included in the initial model.

Measured variable	Type of effect	Included in initial models?
Site scale		
Management type (grassland or agriculture)	fixed	yes
Local scale, retained		
Floral abundance		
Floral species richness		
Percentage of live vegetation		
Percentage of bare ground		
Percentage of canopy cover		
Landscape scale, retained		
Percentage of seminatural land × management type		
Percentage of crop/pasture × management type		
Heterogeneity × management type		
Not related to scale		
Sample date	random	
Local scale, dropped		
Site nested within city region	random	
Percentage of dead vegetation	fixed	no
Percentage of rocky or impervious ground		
Landscape scale, dropped		
Percentage of developed land		

Notes: Agriculture management was the intercept (i.e., reference category) in all models. After running models with all measured variables included, we dropped four explanatory variables (bottom four rows) from the initial models based on high variance inflation factor (VIF) scores (>3): percentage of dead vegetation and percentage of rocky ground were dropped because they were highly negatively correlated with percentage of live vegetation, percentage of developed land within 2 km was dropped due to high negative correlations with percentage of seminatural land.

to the averaged model, and is therefore a more conservative estimate of significant model factors than the conditional average, which does not incorporate variable weights (Burnham and Anderson 2003).

Finally, because low evenness can be caused by the outsized presence of rare or common species (Hillebrand et al. 2008), we conducted two separate post-hoc LMM's for each resulting significant variable from the averaged model outputs for evenness. The response variables for these models were (1) the $\log(x + 1)$ number of rare species and (2) the $\log(x + 1)$ number of common species in a sample. Following Lichtenberg et al. (2017), we classified a species as rare if abundance was <5% of total abundance for a sample, and common if ≥5% of a sample. All post-hoc models consisted of one response variable and one explanatory variable from the evenness output and included the same random effects as described above.

Results

We collected, preserved, and identified 12,654 bee specimens across the 40 sites, consisting of 172 species, 44 genera, and six families (Appendix S1: Table S2). We collected between 2 and 43 species and 6 and 1,095 individuals at each site and sampling period. We found 39 species that were represented by a single specimen in the entire collection. Although European honey bees (*Apis mellifera*) were observed at some sites, the vast majority of specimens collected in traps were native species, with honey bees making up <1% of all bees collected ($n = 68$). The most abundant species collected were *Lasioglossum coactum* (3,703), *Lasioglossum hudsoniellum* (1,076), and *Melissodes tepaneca* (796). The most abundant genera were *Lasioglossum* and *Mellissodes*, representing 61% and 12% of all specimens, respectively. The most speciose genera were *Lasioglossum* (44 species) and *Megachile* (18 species). Twenty species were morphospecies; 19 of these in the genus *Lasioglossum,* primarily in the subgenus *Dialictus*- a notoriously difficult group to assign taxonomy, and whose species have not yet been fully revised for Texas. Among the species we collected, 134 species were below-ground nesting (94% total specimens) and 34 species were above-ground nesting (5%), with the remaining four species' nesting location classified as unknown or variable between above- and below-ground habitats. These four species (<1%) were not included in nesting analyses. Small-bodied bees represented 83 species (68%), and large-bodied bees 87 species (32%).

Bee community composition in agriculture and grassland management

PERMANOVA showed that bee community composition was significantly different between grassland and agriculture sites, both with $\log(x + 1)$ transformed abundance data ($P = 0.003$) and presence absence data ($P = 0.004$). Visual separation of communities in NMDS analyses was similar between $\log(x + 1)$ transformed abundance and presence–absence data (Appendix S1: Fig. S2), and stress levels using two dimensions were slightly above 0.2 for both data sets. SIMPER analysis on transformed bee abundance and presence absence data did not reveal any species that contributed >4% to overall dissimilarity between communities of agriculture and grassland sites; thus no single species had a major disproportionate influence on the differences in communities between the two management types. However, some species were significantly more likely to be more abundant or occur in either agriculture or grassland sites. Specifically, in both presence–absence and abundance analyses, the representation of six species (including one morphospecies) was consistently significantly different between grassland and agriculture sites (See Appendix S1: Table S3 for each species' relative contribution to dissimilarity and significance for each analysis): *Lasioglossum longifrons*, *Lasioglossum* sp. TX-18, *Perdita ignota crawfordi*, and *Xenoglossa strenua* were significantly more likely to be both present and abundant in agriculture sites, while *Osmia subfasciata* and *Xylocopa virginica* were significantly more likely to be present and abundant in grassland sites.

Effect of local environmental drivers and landscape context on bee abundance and diversity in agriculture and grassland management

Across response variables, model selection resulted in multiple models with $\Delta\text{AIC} < 2$; these top models were averaged incorporating the relative importance of each variable in the final averaged model (see Table 2; Appendix S1: Tables S4–S5).

Abundance.—Mean overall bee abundance (±SE) across all sites was 105.45 ± 11.17. Overall mean abundance at the agriculture sites was 125.11 ± 19.05, and at the grassland sites was 85.78 ± 11.21, but this difference was not significant in the averaged model ($P = 0.648$, Fig. 2a), as local and landscape factors were better predictors of overall abundance than management type. At the local scale, across both management types, sites with higher levels of percentage of bare ground ($z = 3.369$, $P = 0.001$, Fig. 3a) and species richness of flowers ($z = 2.502$, $P = 0.012$) had significantly higher overall bee abundance. At the landscape scale, overall bee abundance was significantly positively affected by the amount of heterogeneity within 2 km surrounding sites, but only at the grassland sites ($z = 2.710$, $P = 0.007$, Fig. 4a), with a marginally significant negative effect on bee abundance at the agriculture sites ($z = -1.817$, $P = 0.069$, Fig. 4a).

Mean above-ground nesting bee abundance (±SE) was 5.73 (±0.69), and mean below-ground nesting bee abundance was 99.51 (±11.12). Above-ground nesting

Table 2. Full results of averaged linear mixed models for the full bee community with AIC <2 for abundance, species richness (Chao1 index), and evenness (E_{var} index), as well as the number of models (N) in which each variable was included.

	Abundance: N total models = 9					Species richness: N total models = 11					Evenness: N total models = 15				
Variable	Estimate	SE	z	Pr(>|z|)	N	Estimate	SE	z	Pr(>|z|)	N	Estimate	SE	z	Pr(>|z|)	N
Management: Agriculture† (intercept)	4.267	0.171	24.684	<0.001*	9	3.191	0.071	44.665	<0.001*	11	0.489	0.023	20.621	<0.001*	15
Management: Grassland†	−0.098	0.212	−0.457	0.648	9	0.01	0.107	0.098	0.922	9	0.057	0.034	1.71	0.087	15
Floral abundance†	−0.009	0.036	−0.256	0.798	2	−0.001	0.012	−0.033	0.974	1	−0.001	0.005	−0.192	0.847	2
Floral species richness†	0.215	0.085	2.502	0.012*	9	−0.001	0.014	−0.047	0.963	1	−0.008	0.014	−0.536	0.592	5
Percentage of vegetation†	0.027	0.069	0.391	0.696	3	0.124	0.07	1.759	0.079	10	0.002	0.009	0.259	0.796	3
Percentage of bare ground†	0.296	0.087	3.369	0.001*	9	0.197	0.06	3.275	0.001*	11	−0.026	0.018	−1.420	0.156	12
Percentage of canopy cover†					0	−0.023	0.046	−0.487	0.626	3	−0.001	0.005	−0.101	0.919	2
Percentage of seminatural land × agriculture‡	0.106	0.112	0.943	0.346	6	0.18	0.065	2.742	0.006*	11					0
Percentage of pasture and crop × agriculture‡	0.022	0.061	0.36	0.719	2	0.145	0.056	2.591	0.010*	11	0.0003	0.004	0.098	0.922	1
Heterogeneity × agriculture‡	−0.595	0.325	−1.817	0.069	9	0.099	0.105	0.931	0.352	9	0.055	0.041	1.323	0.186	15
Percentage of seminatural land × grassland‡	0.003	0.048	0.053	0.958	1	−0.188	0.126	−1.478	0.139	9	−0.001	0.007	−0.070	0.944	1
Percentage of pasture and crop × grassland‡					0	−0.004	0.029	−0.140	0.889	1					0
Heterogeneity × grassland‡	0.783	0.286	2.71	0.007*	9	0.018	0.077	0.233	0.816	2	−0.100	0.042	−2.314	0.021*	15

Notes: AIC, Akaike's information criterion; SE, standard error. Agriculture management served as the reference category (intercept) for all models.

*$P < 0.05$.

† Local scale.

‡ Landscape scale.

bees had significantly higher abundance at the grassland sites as compared to the agriculture sites ($z = 2.414$, $P = 0.016$, Fig. 2b). At the local scale across management types, higher floral species richness had a significant positive relationship with abundance of both above- ($z = 2.230$, $P = 0.026$, Fig. 3b) and below-ground nesting bees ($z = 2.327$, $P = 0.020$), and below-ground nesting species also had higher abundance with higher levels of percentage of bare ground ($z = 3.488$, $P < 0.001$). Below-ground nesting bees at the grassland sites had significantly higher abundance with higher levels of surrounding landscape heterogeneity ($z = 3.265$, $P = 0.001$, Fig. 4b) but, at agriculture sites, they had significantly lower abundance with higher levels of surrounding landscape heterogeneity ($z = -2.310$, $P = 0.021$, Fig. 4b).

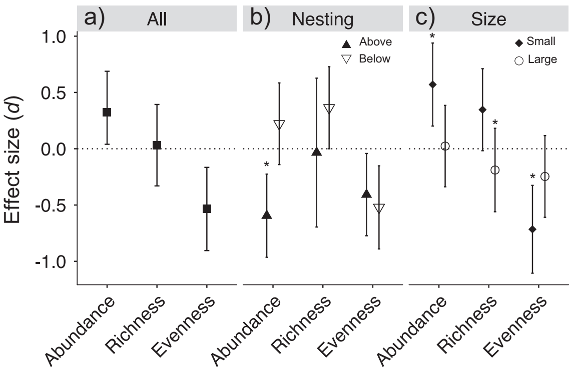

FIG. 2. Effects of local habitat management on mean bee abundance, species richness (Chao1 index), and evenness (E_{var}). Cohen's d effect size with 95% CI of agriculture management for (a) the full bee community, (b) above- and below-ground nesting bees, and (c) small and large bees. An asterisk above an effect size denotes a significant ($P < 0.05$) difference found between agriculture and grassland management in linear mixed-effects models (Appendix S1: Tables S2–S4).

Mean small bee abundance was 71.53 ± 10.21 and mean large bee abundance was 33.92 ± 3.72. Small bees were significantly less abundant at the grassland sites than at the agriculture sites ($z = -2.139$, $P = 0.032$, Fig. 2c). At the local scale across management types, small bees were significantly more abundant at sites with higher levels of bare ground ($z = 2.629$, $P = 0.009$) and floral species richness ($z = 2.830$, $P = 0.005$). Large bees were also significantly more abundant with higher local levels of bare ground ($z = 2.697$, $P = 0.007$, Fig. 3c). Small bees were significantly more abundant with a higher percentage of seminatural land, but only at agriculture sites ($z = 2.056$, $P = 0.040$), and were significantly more abundant if surrounded by higher levels of heterogeneity, but only at grassland sites ($z = 2.506$, $P = 0.012$). At the landscape scale, large bees were more abundant at sites with higher levels of surrounding pasture and cropland, but only in agriculture sites ($z = 2.638$, $P = 0.008$, Fig. 4c).

Species richness.—Mean species richness (±SE) across all sites was 26.74 ± 1.36. Species richness at agriculture sites was 26.97 (±1.87), and at grassland sites was 26.50 ± 2.01. At the local scale across management types, species richness increased significantly with increased bare ground ($z = 3.275$, $P = 0.001$, Fig. 3d), and exhibited a marginally significant increase with percentage of live

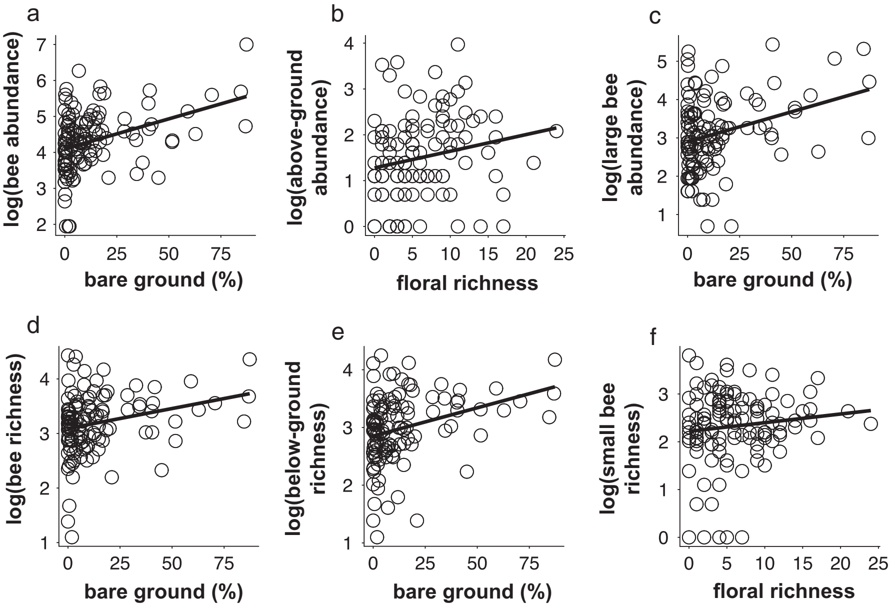

FIG. 3. Selected significant local effects on (a–c) bee abundance and (d, e) bee richness for the full bee community (a, d), nesting groups (above- or below-ground nesting bees; (b, e) and size groups (large or small bees, measured by intertegular distance; (c, f). Trendlines were made from the linear model relationship between the two variables (R package ggplot2).

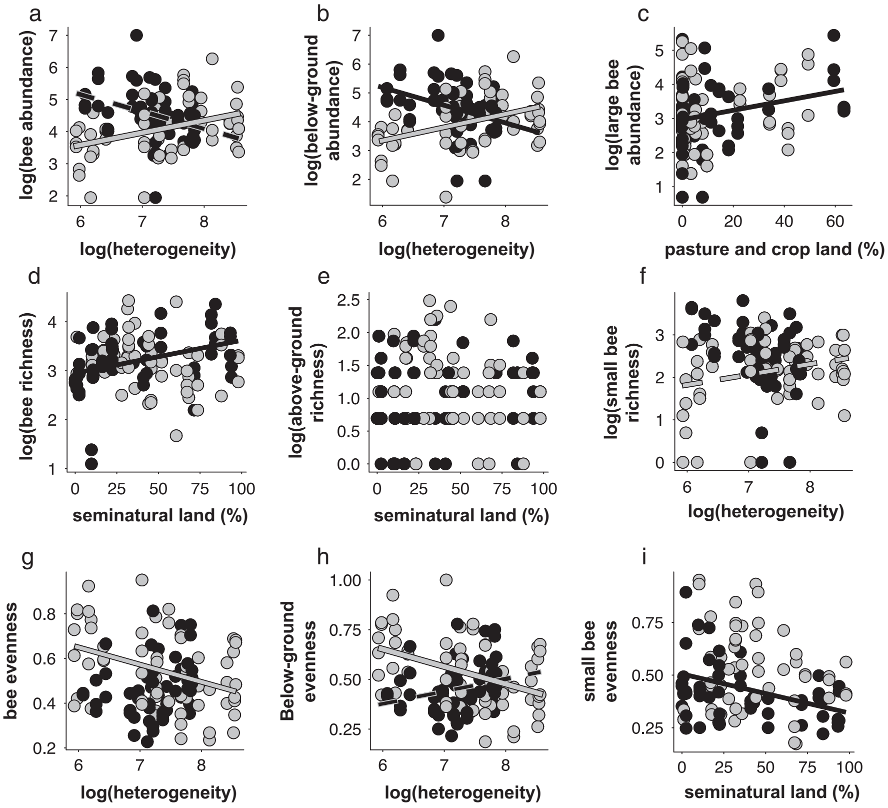

FIG. 4. Selected landscape effects on (a–c) bee abundance, (d–f) species richness, and (g–i) bee evenness for the full bee community (a, d, g), nesting groups (above- or below-ground nesting bees; (b, e, h), and size groups (large or small bees; c, f, i). Grassland management is shown in gray and agriculture management is shown in black. Trendlines are shown for significant ($P < 0.05$, solid line) and marginally significant ($P < 0.10$, dashed line) relationships, and made from the linear model relationship between the two variables (R package ggplot2); Heterogeneity (total number of land use patches) was log-transformed for plot visualization but was not transformed in the models.

vegetation ($z = 1.759$, $P = 0.079$). At the landscape scale, there were significantly more species with higher levels of surrounding percentage of seminatural land ($z = 2.742$, $P = 0.006$, Fig. 4d), and percentage of pasture and crop ($z = 2.591$, $P = 0.010$), but only at the agriculture sites. There was not a significant difference in species richness with any landscape variable at the grassland sites.

Mean above-ground nesting species richness (±SE) was 2.67 ± 0.21, and mean below-ground nesting species richness was 22.02 ± 1.18. No local or landscape variables were significantly correlated with species richness of above-ground nesting bees (Fig. 4e). At the local scale across management types, below-ground nesting bees had higher species richness at sites with higher levels of percentage of bare ground ($z = 4.357$, $P < 0.001$, Fig. 3e) and percentage of live vegetation ($z = 2.684$, $P = 0.007$).

Mean species richness of small bees was 11.77 ± 0.73 and of large bees was 12.82 ± 0.77. Species richness of both size classes was mainly affected by local factors. Specifically, at the local scale across management types, small bees had significantly higher species richness with higher levels of floral species richness ($z = 2.878$, $P = 0.004$, Fig. 3f), and bare ground ($z = 2.352$, $P = 0.019$). There was a marginally significant positive effect on small bee species richness surrounded by higher levels of landscape heterogeneity, but only at the grassland sites ($z = 1.799$, $P = 0.072$, Fig. 4f). Large bees had higher species richness at grassland sites ($z = 2.695$, $P = 0.007$, Fig. 2c), and at sites with higher levels of bare ground ($z = 3.448$, $P = 0.001$, Fig. 3c). There was a marginally significant positive effect of surrounding pasture and crop on large bee richness at the agriculture sites ($z = 1.926$, $P = 0.054$).

Evenness.—Mean evenness (±SE) across all sites was 0.505 ± 0.014; evenness at agriculture sites was 0.464 ± 0.016, while evenness at grassland sites was 0.545 ± 0.022, with grassland sites exhibiting marginally more evenness than agriculture sites ($z = 1.710$, $P = 0.087$). None of the local variables significantly affected overall evenness at the $P < 0.05$ level. At the landscape scale, evenness was significantly lower with higher levels of surrounding heterogeneity, but only at the grassland sites ($z = -2.314$, $P = 0.021$, Fig. 4g). Post-hoc LMM's for evenness found that there were marginally significantly more rare species at the grassland sites with increased landscape heterogeneity (df = 20.00, $t = 1.987$, $P = 0.060$, Fig. 5a), but there were not significantly more common species (df = 20.20, $t = -0.731$, $P = 0.473$, Fig. 5a).

Mean evenness of above-ground nesting bees was 0.82 ± 0.03, and of below-ground nesting bees was 0.49 ± 0.01. There were no significant local or landscape predictors of above-ground nesting evenness in the averaged model. At the local scale across management types, below-ground nesting bees had significantly lower evenness with higher amounts of bare ground ($z = -2.043$, $P = 0.041$). Across management types, post-hoc LMM's for evenness showed that sites with higher levels of bare ground had significantly more rare species (df = 56.400, $t = 3.057$, $P = 0.003$), and no difference in common species (df = 50.390, $t = -0.537$, $P = 0.593$). At the grassland sites, below-ground nesting bees also had significantly lower evenness with higher levels of surrounding heterogeneity ($z = -2.735$, $P = 0.006$, Fig. 4h), but did not have significantly more rare (df = 7.03, $t = 0.516$, $P = 0.621$) or common below-ground nesting species (df = 20.00, $t = -0.955$, $P = 0.351$). There was a marginally significantly higher level of evenness of below-ground nesting bees at the agriculture sites ($z = 1.667$, $P = 0.095$, Fig. 4h). This was caused by agriculture sites with higher levels of landscape heterogeneity having significantly lower levels of rare below-ground nesting species (df = 18.30, $t = -3.31$, $P = 0.004$), but there was no significant effect on number of common below-ground nesting species (df = 19.51, $t = -0.22$, $P = 0.828$).

Mean evenness of small bees was 0.47 ± 0.02, and of large bees was 0.68 ± 0.02. There were no significant predictors of evenness for large bees in the averaged models. For small bees, grassland sites had significantly higher evenness than agriculture sites ($z = 3.794$, $P < 0.001$, Fig. 2c). Post-hoc LMM's indicated that the grassland sites had significantly fewer rare small species than agriculture sites (df = 33.58, $t = -3.552$, $P = 0.001$), but there was no significant difference in common small species between the two management types (df = 24.38, $t = 1.60$, $P = 0.123$). Small bees had significantly less even communities with higher levels of surrounding seminatural land ($z = -3.729$, $P = 0.001$, Fig. 4i) and landscape heterogeneity ($z = -2.518$, $P = 0.012$), but only at the agriculture sites. Post-hoc LMM's indicated that agriculture sites with higher levels of seminatural land had significantly more rare small species (df = 21.28, $t = 2.532$, $P = 0.0193$, Fig. 5c), while there was no difference in number of common small species (df = 25.96, $t = -1.21$, $P = 0.237$, Fig. 5c). In contrast, post-hoc LMM's indicated that agriculture sites with higher levels of landscape heterogeneity had significantly fewer small rare species (df = 13.99, $t = -2.717$ $P = 0.0167$, Fig. 5b), but no significant effect of heterogeneity on the number of common species (df = 15.442, $t = 1.143$, $P = 0.270$, Fig. 5b).

DISCUSSION

Our results provide the first documentation of significant local and landscape interactions in urban ecosystems. We found that the abundance and diversity of communities in locally simple habitats responded positively to landscape-level habitat complexity, while communities in locally complex habitats did not (as per Tscharntke et al. 2012). In particular, we show that levels of surrounding seminatural land, cropland, and habitat heterogeneity differentially impact bee abundance and diversity depending on the local habitat management as an agriculture or grassland site. We additionally found that local management type structured the bee community within different functional groups, and that floral richness and bare ground positively influenced bee abundance and diversity regardless of management type.

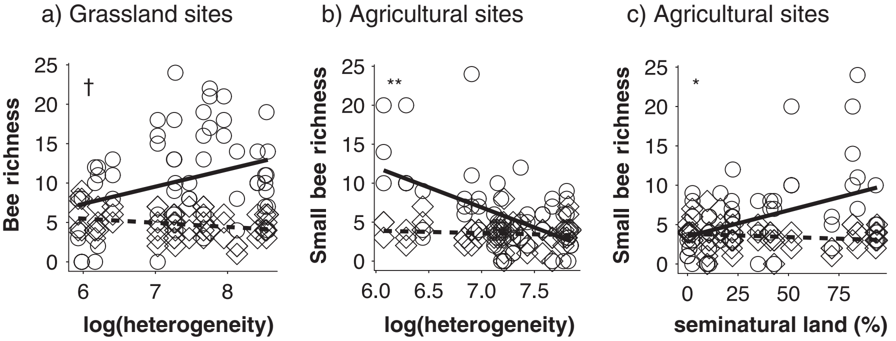

FIG. 5. Select results of post-hoc linear mixed model tests on landscape factors contributing to decreases in evenness of (a) total bees, b,c) small bees. Richness of rare species (open circles, solid trendline) and common species (open diamonds, dashed trendline) is shown for each group. Symbols indicate a significant (**$P < 0.01$, *$P < 0.05$) or marginally significant (†$P < 0.10$) relationship for number of rare species. There were no significant relationships found between any variable and number of common species. Trendlines were made from the linear model relationship between the two variables (R package ggplot2).

Landscape context mediates bee abundance and diversity differently for agriculture and grassland habitats

In theory, local disturbance regimes may mediate the effects of landscape composition on species diversity, whereby local differences in resource availability can determine the species capable of successfully colonizing from the surrounding landscape (Hille Ris Lambers et al. 2012, Tscharntke et al. 2012). There is increasing evidence that local management interacts with landscape complexity to affect insect abundance and diversity in agricultural systems (Williams and Kremen 2007, Carvell et al. 2011, Kennedy et al. 2013, Lichtenberg et al. 2017), but similar studies in urban landscapes have been lacking. Past urban studies have instead often highlighted the importance of local habitat characteristics to bee communities, while documenting little to no impact of landscape-level habitat composition (Matteson and Langellotto 2010, Quistberg et al. 2016).

Our results show that the species richness of the overall bee community was greater in landscapes with a higher percentage of seminatural land, but only in sites where the local management was agriculture. This pattern suggests that agriculture sites likely have reduced local resources that limit the number of species able to persist without recolonization from seminatural habitat. Although agricultural areas can provide floral resources for native bees, including crop flowers and weeds (Westphal et al. 2003, Saunders et al. 2013), these areas are less likely to provide adequate habitat for bee species that nest in or collect pollen and nectar from seminatural habitats (Westrich 1996). Our result reflects other studies that have also suggested that areas with limited rather than high quality resources at the local scale have more positive responses in pollinator diversity to landscape-level natural habitat availability (Kleijn and van Langevelde 2006, Lichtenberg et al. 2017). We also documented a greater abundance of small-bodied bees in agriculture sites with larger amounts of surrounding seminatural land. Small bees are believed to have lower dispersal abilities (Greenleaf et al. 2007, but see Castilla et al. 2017), and therefore may be more likely to nest closer to foraging resources (Jauker et al. 2009, Carrié et al. 2017), which are often located in seminatural habitat. Interestingly, in our agriculture sites, we also found that increases in seminatural land led to decreases in the evenness of small-bodied bees, which was due to an increase in the representation of rare species, highlighting a mechanism by which seminatural land influences bee communities in urban agriculture. A recent meta-analysis suggests a similar mechanism, where agricultural landscapes with higher levels of natural area supported less even pollinator communities, driven specifically by increases in the numbers of rare species (Lichtenberg et al. 2017). Although levels of resource specialization are not known for many of the species in our study, past studies have shown that specialists, which are often rare, tend to decline or are more rare in urban areas (Hernandez et al. 2009) and thus may be more dependent on seminatural habitats for foraging and nesting resources (Harrison et al. 2017).

We found that surrounding pasture and cropland positively impacted overall bee species richness and large bee abundance, but again only at the agriculture sites. Much of the pasture and cropland present in our system was comprised of livestock grazing land, likely containing valuable floral forage for bees including native and nonnative forb species and flowering trees. Low-intensity agriculture, such as minimally grazed grasslands or heterogeneous cropland, has been shown to promote biodiversity at a landscape scale (Freemark et al. 2002, Tscharntke et al. 2005, Fahrig et al. 2015), and our results support this pattern, indicating that some types of agricultural land use can provide important habitat for bees, especially for larger species.

In our study, landscape-level habitat heterogeneity had somewhat contrasting effects on bee communities between the two local habitat management types, especially in regards to bee evenness. We found that the patterns of lower evenness in the grassland sites were driven by an increase in the abundance of a few common species, as well as an increase in richness of rare species. Although higher levels of habitat heterogeneity suggest a more fragmented landscape, both common and rare bee species persisting in high-quality local habitat such as natural grasslands may benefit from the multiple land use types in heterogeneous surrounding landscapes, as bees frequently use distinct habitat types for nesting and foraging (Westrich 1996, Winfree et al. 2007). Some studies have found that moderate increases in human-dominated land use can increase abundance and species richness due to greater resource breadth that covers the diet and nesting requirements of more pollinator species, including rare species (Cane et al. 2006, Winfree et al. 2007, Matteson et al. 2008).

In contrast, increased habitat heterogeneity surrounding agriculture sites led to a less even community for both below-ground nesting and small-bodied species, but this was not due to an increase in rare species at these sites; instead, the richness of rare below-ground nesting and small-bodied species *declined*. These sites were instead dominated by a few common species and had few or no rare species. For small-bodied bees, most of which also nest underground, this result may be driven by the combined force of lower local habitat quality in the agriculture sites and fragmented surrounding habitat that small species may not as easily penetrate, preventing recolonization of the agriculture sites by a more diverse bee community (sensu Hillebrand et al. 2008). Our results provide evidence that rarer small bees may be particularly sensitive to regional losses in seminatural habitat and/or increases in habitat fragmentation, especially in agricultural areas that are more disturbed and have less diverse local habitat resources. Because rare taxa are likely important to ensure functional redundancy and resilience in ecosystem functions and services (Mouillot et al. 2013), our results suggest that urban farms and community gardens may be more vulnerable to losses in pollination service than more rural farms or grassland habitats across landscape gradients.

Bee community composition is differentially influenced by agriculture and grassland management, but similar local environmental drivers influence bee abundance and diversity across sites

Results from both LMM and community ordination analyses support the hypotheses that agriculture and grassland sites differ in their ability to provide resources for bees across a range of nesting preferences and body sizes. Both species that were more likely to occur in grassland sites were above-ground nesting species: *Xylocopa virginica* is a large species that excavates nests in sound wood (Michener 2000), and *Osmia subfasciata* is a small species that makes its nests in pre-formed cavities (Neff and Simpson 1992). These results suggest that grassland sites may contain more resources to support bee species that utilize above-ground resources than the agriculture sites. Indeed, grassland sites had less frequent removal of woody debris and other potential nesting material, as well as higher levels of live vegetation as compared to the agriculture sites. Williams et al. (2010) similarly found that above-ground nesting bees were less abundant at more highly disturbed sites with higher levels of vegetation removal. Other studies have similarly shown that different land use practices can produce different bee communities in urban environments worldwide (Pardee and Philpott 2014, Threlfall et al. 2015), and that this is often driven by nest site availability (Neame et al. 2013).

The majority of the species in our collection are small and nest below-ground, and our regression analyses indicate that the availability of below-ground nesting habitat (represented by percentage of bare ground) was consistently a significant predictor of bee abundance and diversity across both agriculture and grassland management. However, agriculture sites tended to have higher levels of bare soil, and SIMPER analyses showed that all four species significantly more likely to occur in agriculture sites nest below ground (*Lasioglossum longifrons*, L. sp. TX-18, *Perdita ignota crawfordi*, *Xenoglossa strenua*). This indicates that, despite having higher levels of surface-level soil disturbance, agriculture sites are able to provide crucial nesting habitat for below-ground nesting bees. Our finding is consistent with other studies, which have shown that increased bare soil is significantly related to abundance and species richness of bees in urban community gardens (Quistberg et al. 2016).

Floral species richness also had a significant positive effect on overall bee abundance, abundance of bees of both nesting groups, and the abundance and species richness of small bees across both management types. Floral pollen and nectar are the primary food resources for bees at both adult and larval life stages (Michener 2000). Sites that have a more diverse flora may have more consistent pollen and nectar availability throughout the blooming season and between years, providing essential food resources that support greater offspring provision and contribute to a more abundant bee fauna (Roulston and Goodell 2011, Blaauw and Isaacs 2014). Our results are also in line with previous studies in urban systems, which have shown that bee abundance in urban areas was most positively correlated with local habitat characteristics including floral diversity (Matteson and Langellotto 2010, Hennig and Ghazoul 2012, Pardee and Philpott 2014, Quistberg et al. 2016).

Conservation implications and management recommendations

Our data add to the growing literature showing that urban areas can provide important bee habitat (Hall et al. 2017), and highlight the great potential that local- and landscape-specific management practices have to enhance urban bee biodiversity and conservation. Specifically, our study indicates that the best practices for supporting higher abundance and diversity of bees differs substantially depending on the local management goals as well as the landscape context. While bee diversity levels in grassland sites were similar across the urban/natural landscape gradient, agriculture sites did not support as diverse of a bee community when located in highly developed areas. Therefore, farms located within a more seminatural landscape context may be able to leverage adjacent seminatural habitat fragments to augment wild bee communities and pollination service, while community gardens and farms with less seminatural landscape context should focus on efforts to augment local habitat resources in order to support bee abundance and diversity in these areas.

Our results also show that both urban grasslands and agriculture sites have the opportunity to make small changes to their local habitat management that can have large impacts on the bee community. First, a diversity of floral forage with a variety of blooming phenologies should be encouraged in both management types to ensure consistent nectar and pollen resources are available throughout the blooming season. Gardens and farms should include some native floral species in their plantings as this has been shown to promote bee diversity in urban gardens (Pardee and Philpott 2014). While we did not find a local environmental driver for above-ground nesting bee abundance other than grassland management, above-ground nesting habitat can generally be created by reducing or eliminating mowing, and by retaining some dead woody vegetation such as logs and shrub stems. Although artificial nest boxes may also be added where above-ground nesting resources are more scarce, the true utility of these may vary regionally and among species (MacIvor and Packer 2015). We also strongly encourage the practice of maintaining patches of untilled, un-mulched, and non-compacted soil within urban green space to provide critical nesting habitat for below-ground nesting bees, the most common bee nesting type. Encouraging the maintenance of native floral forage, vegetation, and non-mulched areas of pervious soil can also benefit a wide variety of taxa in addition to bees in urban areas (McKinney 2002). City governments can implement these recommendations in both planned and existing urban green spaces to attract a more diverse group of bee pollinators with different life history traits. Given the global increases in human population size, expanding patterns of urban agriculture, and increased cultivation of pollinator-dependent crops, it is essential to manage urban green spaces for pollinator conservation in order to safeguard biodiversity and the associated ecosystem services it provides.

Acknowledgments

We would like to thank individual landowners, Texas State Parks, the Lower Colorado River Authority, as well as the cities and community gardens of Austin, Dallas, and Fort Worth for allowing access to properties. We thank C. Glinka, A. Ritchie, A. Kusmik, S. Cunningham, K. Merrill, and B. French for assistance with field collection of insects and vegetation surveys, as well as N. Vojnovich, M. Rolbiecki, T. Ortega, L. Stevens, and N. Fogel for assistance with insect preservation and curation. We thank N. Pope, S. Cusser, M. O'Connell, and E. Lichtenberg for their assistance and advice on the data analysis and comments on the original manuscript, and two reviewers for extremely helpful suggestions for the final manuscript. K. Ballare received support for this research from Texas Parks and Wildlife Department, Texas Ecolabs, and the Graduate Program in Ecology, Evolution, and Behavior at the University of Texas at Austin. Additional support to S. Jha and K. Ballare was provided by the National Science Foundation and the U.S. Army Research Office.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1869/full

DATA AVAILABILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.pf68071