



# Wild bee abundance declines with urban warming, regardless of floral density

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## Abstract

As cities expand, conservation of beneficial insects is essential to maintaining robust urban ecosystem services such as pollination. Urban warming alters insect physiology, fitness, and abundance, but the effect of urban warming on pollinator communities has not been investigated. We sampled bees at 18 sites encompassing an urban warming mosaic within Raleigh, NC, USA. We quantified habitat variables at all sites by measuring air temperature, percent impervious surface (on local and landscape scales), floral density, and floral diversity. We tested the hypothesis that urban bee community structure depends on temperature. We also conducted model selection to determine whether temperature was among the most important predictors of urban bee community structure. Finally, we asked whether bee responses to temperature or impervious surface depended on bee functional traits. Bee abundance declined by about 41% per °C urban warming, and temperature was among the best predictors of bee abundance and community composition. Local impervious surface and floral density were also important predictors of bee abundance, although only large bees appeared to benefit from high floral density. Bee species richness increased with floral density regardless of bee size, and bee responses to urban habitat variables were independent of other life-history traits. Although we document benefits of high floral density, simply adding flowers to otherwise hot, impervious sites is unlikely to restore the entire urban pollinator community since floral resources benefit large bees more than small bees.

**Keywords** Bee · Impervious surface · Pollinator decline · Pollinator · Urban heat island · Urban warming

## Introduction

A ubiquitous feature of cities is that they are warmer than surrounding natural areas (Oke 1973). This phenomenon, called the urban heat island effect, is driven largely by impervious surfaces that absorb and reradiate solar radiation (Yuan and Bauer 2007). As small-bodied ectotherms whose metabolism depends on temperature, insects are sensitive to warming (Nooten et al. 2014; Colinet et al. 2015). Indeed, urban warming can alter the physiology, fitness, and abundance of insects in cities (Angilletta et al.

2007; Dale and Frank 2014; Meineke et al. 2014). However, the effects of urban warming vary across taxa, such that some species increase in fitness and abundance whereas others decline (Youngsteadt et al. 2016), making effects on entire communities difficult to predict. Since urban areas are increasingly viewed as having potential to conserve insect diversity and ecosystem services (Hunter and Hunter 2008; New 2015), understanding the effects of urban warming on beneficial insect communities will advance urban conservation and management.

Wild bees are among the insects most often targeted by urban conservation actions, such as installing pollinator gardens (Hall et al. 2016). Bees, as a group, are of conservation concern because they are important pollinators of many crops and wild plants, yet the abundance and range sizes of some wild bees are declining (Bartomeus et al. 2013; Kerr et al. 2015). Despite these declines, relatively diverse bee communities have persisted in cities worldwide, leading to the recognition that cities have a role in pollinator conservation (Baldock et al. 2015; Hall et al. 2016). In some cities, however, bee abundance or diversity declines with urbanization (Bates et al. 2011; Fortel et al. 2014; Geslin et al. 2016), suggesting that cities vary in

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their ability to support their regional bee faunas. Similarly, many studies document changes in bee community composition along urbanization gradients, demonstrating that bee species vary in their urban tolerance (e.g., Bates et al. 2011; Fortel et al. 2014). However, attempts to identify ecological traits, such as body size or nesting habitat, that predict bee responses have yielded mixed results (e.g., Carper et al. 2014; Geslin et al. 2016). We suggest that variability in bee responses to urbanization may arise from unmeasured abiotic factors such as temperature.

Although the effects of urban warming on bees have not been assessed, bees are sensitive to environmental temperature in other contexts. For example, bees that overwinter as adults experience reduced fitness at warmer winter temperatures, likely because of increased metabolism during diapause (Fründ et al. 2013). Warming may also reduce the foraging time available for some (but not all) wild bee species (Rader et al. 2013; Kühnel and Blüthgen 2015). The geographic ranges of northern-hemisphere bumble bees have contracted northward with climate change, suggesting that these bees are particularly intolerant of warming (Kerr et al. 2015). We would expect some variation in bee response to warming to be predicted by morphological and ecological traits. For example, large bees have more thermal mass than small bees (Oyen et al. 2016); ground-nesting bees may be better insulated against high temperatures than are above-ground nesters; and parasitic and oligolectic bees are more sensitive than others to habitat disturbance in general (Winfrey et al. 2011; Sheffield et al. 2013). If such traits are correlated with bee thermal tolerances, they may predict community responses to urban warming.

Here, we investigate how temperature and other habitat variables (impervious surface cover, floral resources) influence wild-bee abundance, diversity, and species composition at sites that vary in urban warming intensity. We predicted that bee abundance and diversity would be independent of temperature, but that community composition would change as warming-tolerant species replace intolerant species in hotter locations. We also expected that floral abundance and diversity would increase bee abundance and diversity, respectively, while impervious surface would reduce bee abundance. If urban warming is an important influence on bee communities, temperature should explain additional variation in bee communities not accounted for by these other predictors. Finally, we asked whether bee response to urbanization depended on body size or other functional traits.

## Materials and methods

### Study sites

We conducted bee community surveys at 15 residential yards and 3 urban natural areas in and around Raleigh, North Carolina, USA. To select study sites, we first solicited

volunteers willing to have bees sampled on their properties. From this pool, we identified sites with a range of thermal conditions using a heat map of Raleigh derived from a Landsat-5 Thematic Mapper band 6 image (image location WRS-2 path 16, row 35; captured August 18, 2007) (Meineke et al. 2013). We overlaid this map with coordinates of potential study sites in ArcMap (ArcGIS Desktop 10; ESRI, Redlands, California, USA), and chose eight warm residential sites, two warm natural sites, nine cool residential sites, and one cool natural site (see the electronic supplementary material Fig. S1). We ultimately excluded two cool residential sites due to heavy shade (>60% canopy cover in the sampling area), yielding the 18 sites presented here.

Residential sites were in yards that ranged in size from 405 to 7487 m<sup>2</sup>. Although the natural areas were larger than residential properties, we limited sampling to 4047 m<sup>2</sup> of each natural site. All sites were more than 2 km apart (Fig. S1, Fig. S2), a distance greater than the foraging distance of most wild bees (Greenleaf et al. 2007).

### Bee sampling

We visited all 18 study sites 6 times each in 2014 and 5 times each in 2015, with sampling dates from May to August (summer) each year. It took 7–11 days to sample all 18 sites at a rate of four sites per day (two hot, two cold). We repeated sampling approximately every two weeks, and rotated the order in which sites were visited during each repetition. At each site on each date we used three collection methods: 12 pan traps (4 white, 4 yellow, 4 blue), 1 vane trap, and 20 min of active netting (Stephen and Rao 2007; Popic et al. 2013). Pan traps were 3.25 oz. soufflé cups (Solo Cup Co., Urbana, IL, USA), left white or painted with yellow or blue fluorescent paint (Guerra Paint & Pigment, New York, NY, USA) and 2/3 filled with soapy water. We placed pan traps 5 m from each other and from floral resources in two X-shaped patterns, varying the pattern as needed to fit the site (Droege et al. 2010). Blue vane traps (SpringStar, Seattle, WA, USA) with 64 oz. jars were filled half full with soapy water and suspended 1 m above the ground in a mostly sunny location. We left traps out for 5 to 7 h between 8:00 and 17:30 and netted between 10:00 and 17:00.

We identified most bees to species using taxon-specific keys (Gibbs 2011; Ascher and Pickering 2014) and by comparison to reference material in the NC State Insect Museum. Experts identified difficult specimens and verified all identifications. We did not separate members of the *Halictus ligatus/poeyi* complex nor *Hylaeus affinis/modestus*. Eight taxa were identified as morphospecies (5 *Lasioglossum*, 1 *Ceratina*, 1 *Nomada*, and 1 *Sphecodes*). To estimate bee body size and foraging ranges, we measured intertegular distances (ITD) of female bees ( $N=1-570$  per species) (as in Cane 1987; Greenleaf et al. 2007). We defined large bees as those with

an ITD of 2 mm or greater (Fig. S3). Finally, we categorized bees by social organization (solitary, eusocial, parasitic), nesting habitat (above or below ground), and dietary specialization (oligolectic or polylectic). We assigned traits by consulting experts and previous studies (Table S1).

### Habitat variables

To measure urban warming intensity, we recorded hourly temperature from May 9 to July 19, 2015 with two iButton temperature loggers (DS1921G, Maxim Integrated, San Jose, CA, USA) per site. To protect iButtons from direct solar radiation, we placed them in radiation shields constructed from white plastic funnels as described by Hubbart (2011) and installed them in shaded locations. Despite these precautions, some iButtons recorded unreasonably high daytime temperatures that did not represent air temperatures. We therefore used only evening temperatures recorded from 19:00 to 21:00. Although these temperatures do not represent all conditions directly experienced by foraging bees, they capture the urban heat island effect without interference from direct solar radiation and place sites on an axis of relative warming (Meineke et al. 2016; Fig. S4). For analysis, we computed the season-long mean evening temperature for each site (range 24.2–26.8 °C).

We quantified the percentage of impervious cover surrounding each site at a local scale (within 200 m) and a landscape scale (within 1000 m) using ArcMap 10 and the 2011 National Landcover Database (Jin et al. 2013). The 200 m radius is expected to encompass most of the activity of small bees at a site (Table S2). Although the largest bees we sampled could have flown more than 1000 m, this radius likely encompasses the majority of their activity (Table S1) (Greenleaf et al. 2007). Impervious surface cover had a range of 0–37.0% at the local scale and 0.4–40.0% at the landscape scale (Fig. S2).

To measure floral diversity at each site, we identified flowers to the lowest taxonomic level possible from photographs (usually species or morphospecies). For analysis, we calculated the mean number of taxa in bloom across sampling dates at each site (range 18–31 taxa). In 2015, we estimated floral abundance by counting the number of entomophilous flowers (or floral units, see below) within a 1 m square quadrat placed in the areas of lowest and highest apparent floral densities at each site on each visit. A floral unit was typically an individual flower, but inflorescences of Asteraceae and of *Trifolium* were also counted as single floral units. Most flowering plants were herbaceous, but woody plants were also included in the estimate; in practice, this included shrubs but not trees (which did not bloom at our sites during the study). We then used these floral counts to inform a site-wide visual estimate of the total (whole-site) floral abundance on a logarithmic scale at each site on each date. We took the mean of these abundances across dates and divided them by site area to obtain floral density estimates (range 1000–200,620 flowers per acre).

### Data analysis

We defined bee abundance as the total number of bees captured at a site using all methods across all 11 sampling dates. To compare species richness across sites independently of bee abundance, we rarefied or extrapolated (at 3 sites) samples to 100 individuals using the package *iNEXT* 2.0.12 in the R 3.1 computing environment for Windows (Gotelli and Chao 2013; R Core Team 2013; Hsieh et al. 2016). For separate analyses of small and large bees, we also rarefied samples to 75 small bees or 25 large bees (with extrapolation at 2 and 5 sites, respectively).

To test predictions about the relationships between temperature and bee abundance and diversity, we constructed a series of linear models, in which temperature was the predictor and bee abundance or bee richness was the response, using the ‘lm’ function in R. To improve distribution of residuals in these linear models, we ln-transformed bee abundance and floral density. We also asked whether temperature was important relative to other, known predictors of bee abundance and richness. To address this question, we explored all possible combinations of the five habitat variables (temperature, local impervious surface, landscape impervious surface, floral density, and floral diversity) as predictors of bee abundance or bee richness using the package *MuMIn* v.1.15.6 (Barton 2016). Multicollinearity of predictor variables was weak, with maximum  $r = 0.61$  (Table S3) and variance inflation factor (VIF) = 1.7 to 2.6 (mean 2.0). We therefore included all predictors in the model selection process (Dormann et al. 2013). To identify the strongest predictor variables and their strongest combinations, we compared AICc (Akaike information criterion corrected for small sample size) for all models and relative importance values for all predictors (Symonds and Moussalli 2011). We used the best model set (all models with  $\Delta AICc < 2$ ) to compute model-averaged parameter estimates. Because bee body size can affect the scale at which species respond to habitat composition (Benjamin et al. 2014), we performed separate analyses for all bees, small bees, and large bees.

To test our prediction that species community composition would shift with warming, we used distance-based redundancy analysis (db-RDA) with Bray-Curtis distances in the R package *vegan* v. 2.4–1 (Oksanen et al. 2016). db-RDA is a multivariate multiple regression in which the environmental variables are the predictors and species’ abundances are the response variables; Bray-Curtis distances make this method more reliable than Euclidean RDA when the dataset includes many zeros (Legendre and Legendre 2012). To determine whether temperature was an important predictor of community composition relative to other habitat variables, we used the ‘ordstep’ function in *vegan* to select the most significant predictors for inclusion in the final db-RDA model. For these analyses, we excluded taxa that occurred at only one site (McCune et al. 2002), and ln-transformed bee counts to improve their linear relationships with predictors.

To determine whether bee ecological traits drive their responses to urbanization, we constructed mixed models in which the response variables were bee abundances and the predictors were environmental variables, bee functional traits (sociality, nesting, dietary specialization, or body size), and their interactions. We also included a random effect of site to account for non-independence of the abundances of bees with different traits at the same site. Significant interaction terms would indicate that bees with different traits respond differently to habitat variables. For each analysis, we excluded species that were uncategorized for the focal trait (that is, 6 species for nesting and sociality and 14 species for lecty), and pooled subsocial and solitary species in the “solitary” category (Table 1). We used the ‘lme’ function in the R package *nlme* v.3.1–128 (Pinheiro et al. 2016) to fit these mixed models, and the ‘r.squaredGLMM’ function in *MuMIn* to obtain marginal and conditional  $R^2$  values for each model. The marginal value ( $R^2_m$ ) quantifies variance explained by fixed effects, whereas the conditional value ( $R^2_c$ ) includes fixed and random effects (Nakagawa and Schielzeth 2013). We ln-transformed bee abundances to improve the distribution of residuals.

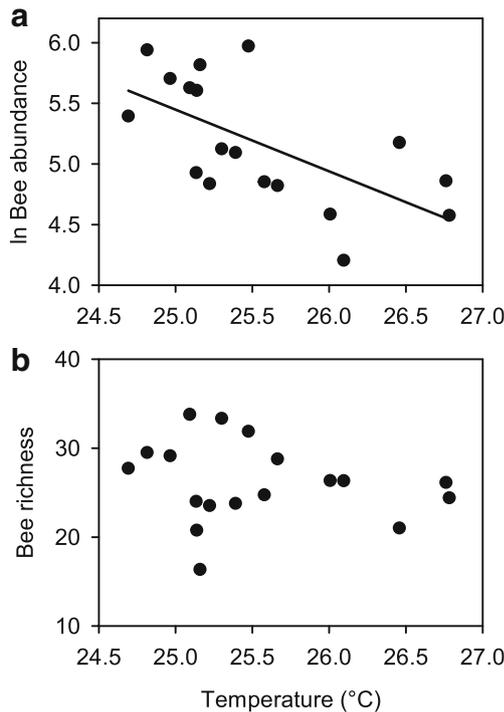
## Results

We collected a total of 3593 bees of 113 species at 18 sites over two years, representing 21% of the species known to occur in the state of North Carolina (J. Ascher, pers. comm.). Each site contributed 67–392 individuals and 22–53 species. Thirty one species (27% of the total) occurred at a single site each; 25 (22%) occurred at half or more of the sites; and four (3.5%) were found at all sites. The majority of individuals belonged to the genus *Lasioglossum* (52%), which also included the three most abundant and ubiquitous species (*Lasioglossum bruneri*, *L. tegulare*, and *L. imitatum*). *Bombus impatiens* also occurred at all sites. Although our sample included bees of diverse ecological traits and life histories (Table 1), the majority of individuals were small, eusocial, ground-nesting, polylectic bees. Additional characteristics of the bee sample are summarized in Table 1.

We predicted that bee abundance would be independent of temperature, but instead total bee abundance declined by about 41% for every °C urban warming (Fig. 1a; ANOVA  $F_{1,16} = 10.3$ ,  $P = 0.005$ ,  $R^2 = 0.39$ , regression parameter estimate  $\pm$  SE =  $-0.51 \pm 0.158$ ). In our multimodel inference procedure, temperature appeared in the best set of models ( $\Delta$ AICc < 2)

**Table 1** Characteristics of the bee sample collected in urban natural and residential areas in Raleigh, NC, USA

	Individuals	Species	% of individuals ( $N = 3593$ )	% of species ( $N = 113$ )
Year				
2014	1876	87	52	77
2015	1717	93	48	82
Method				
Pan trap	2193	79	61	70
Net	1288	92	36	81
Vane trap	112	29	3	26
Bee size				
Small	2788	67	78	59
Large	785	46	22	41
Nesting				
Above ground	614	40	17	35
Below ground	2922	67	81	59
Uncategorized	57	6	2	5
Sociality				
Eusocial	2530	32	70	28
Subsocial	234	8	7	7
Solitary	741	55	21	49
Parasitic	31	12	1	11
Uncategorized	57	6	2	5
Lecty				
Oligolectic	130	13	4	12
Polylectic	3380	86	94	76
Uncategorized	83	14	2	12



**Fig. 1** Effects of urban warming on (a) natural log of bee abundance and (b) bee species richness

for each bee size category. Importance values for temperature were >0.5 in all-bee and large-bee models, interpreted as a greater than 50% probability that temperature is a component of the best model, given the candidate models (Table 2).

Local-scale impervious surface was also a component of the best set of models for abundance of all bee size categories, with a negative effect on bee abundance. In each model, the

importance of impervious surface was similar to, or greater than, that of temperature (Fig. 2a-b). Temperature and impervious surface explained similar amounts of variation in the simplest, single-predictor models (for all bees, temperature  $R^2 = 0.39$  vs. impervious  $R^2 = 0.38$ ; small bees temperature  $R^2 = 0.32$  vs. impervious  $R^2 = 0.38$ ; large bees temperature  $R^2 = 0.39$  vs. impervious  $R^2 = 0.16$ ). In addition, for large bees only, floral density was an important, positive predictor of abundance (Fig. 2c). Individual models in the best-model set for bee abundance are presented in Table S4.

Bee species richness was independent of temperature (Fig. 1b; ANOVA,  $F_{1,16} = 0.6$ ,  $P = 0.438$ ,  $R^2 = 0.04$ , parameter estimate  $\pm$  SE =  $-1.39 \pm 1.743$ ). Instead, multimodel inference indicated that floral density was an important, positive predictor of bee richness across all size categories (Table 2, Fig. 2). In addition, for large bees, impervious surface was an important, negative predictor (Table 2, Fig. 2c). Individual models in the best-model set for bee richness are presented in Table S3.

Bee community composition varied across sites (Bray-Curtis similarities of site pairs ranged from 38 to 72%), and temperature explained 12% of the variation in bee composition (permutation test  $P = 0.017$ ; Fig. 3). Although most variation remained unexplained, stepwise selection also arrived at the temperature-only model as the best predictor of bee community composition. *Lasioglossum pilosum* and *L. tegulare* were among the few species that were more abundant at warmer sites (Fig. 3, left side), while *L. bruneri*, *L. coreopsis*, and *Bombus griseocollis* experienced the strongest declines (Fig. 3, right side).

Given the importance of temperature and impervious surface in predicting bee abundance, we asked whether bee

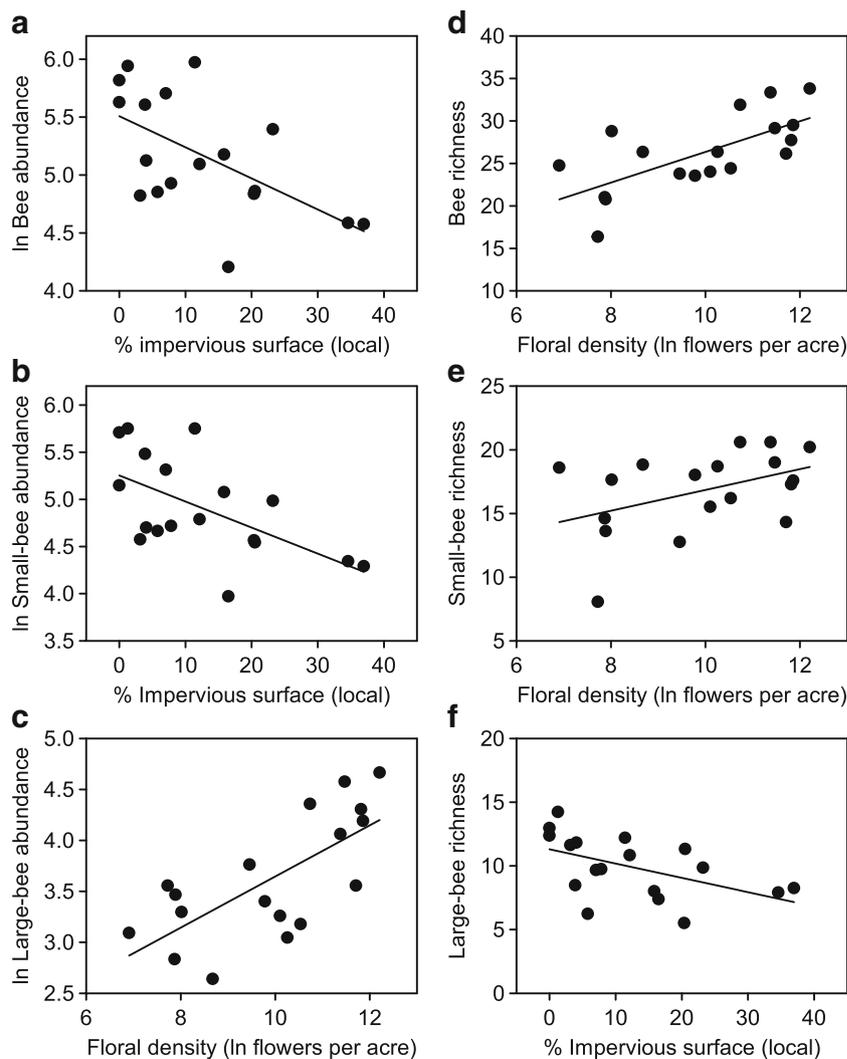
**Table 2** Model-averaged parameter estimates and importance values ( $w_i$ ) for five candidate predictors of abundance and richness of all bees, small bees, and large bees (bold values indicate  $w_i > 0.5$ )

Response	Predictor	Model								
		All bees			Small bees			Large bees		
		Estimate*	S.E.	$w_i$ †	Estimate*	S.E.	$w_i$ †	Estimate*	S.E.	$w_i$ †
ln Abundance	Temperature	-0.21	0.260	0.53	-0.17	0.243	0.42	-0.26	0.234	0.65
	Imperv (local)	-0.02	0.016	0.67	-0.02	0.016	0.72	-0.02	0.014	0.69
	Imperv (landscape)			0.17			0.19			0.11
	ln Floral density	0.03	0.057	0.38			0.19	0.25	0.056	1.00
	Floral diversity			0.16			0.15			0.14
Richness	Temperature			0.15			0.17			0.19
	Imperv (local)	-0.02	0.058	0.30			0.16	-0.13	0.041	0.88
	Imperv (landscape)			0.22			0.19			0.19
	ln Floral density	1.83	0.528	0.98	0.49	0.54	0.55	0.73	0.262	0.80
	Floral diversity			0.15			0.17			0.18

\*Parameter estimates are averaged only across the best-model set; predictors lacking parameter estimates did not appear in that set (Table S3)

†Importance values are interpreted as the probability that a term is a member of the best model, given the candidate models

**Fig. 2** Bee abundance (natural log-transformed; **a–c**) and richness (**d–f**) relative to the single most important predictor of each, as indicated by multimodel inference. All bees (**a, d**), small bees (**b, e**), and large bees (**c, f**) were analyzed separately



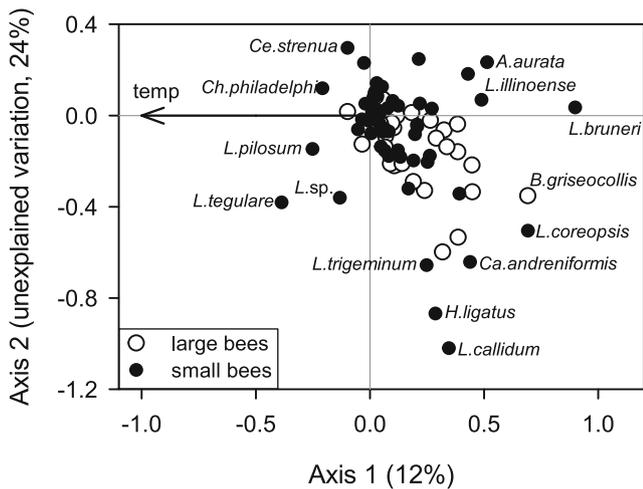
functional traits drove these responses. Main effects were significant in each of the eight resulting models (Table 3, Figs. S5–S6), reflecting the overall decline in bee abundance with temperature and impervious surface; and the greater abundance of dominant trait groups (Table 1, Table 3, Figs. S5–S6). No interaction terms, however, were significant, indicating that all bee groups declined similarly with temperature and impervious surface.

## Discussion

Understanding the effects of environmental warming on organisms is a key challenge in ecology, since habitats are increasingly experiencing urban warming and global climate change. We predicted that urban warming would alter community composition—but not necessarily abundance or diversity—of wild bees. Our results, based on more than 3000 bees collected during two years of sampling at 18 sites, support a role for urban warming in shaping wild-bee communities. Bee

abundance declined with warming, with about 41% fewer bees captured for every °C increase in average site temperature. Multimodel inference also supported temperature as one of the most important predictors of urban bee abundance, demonstrating its relevance alongside other, more widely used predictors (impervious surface at local and landscape scales, floral density, and floral diversity). The effect of warming on bee abundance was independent of bee social organization, nesting habitat, dietary specialization, and body size. We did, however, detect species-level variation in bee responses to warming, and site temperature was the best predictor of bee species composition (Fig. 3). The species ordination results further highlight the diversity of responses within the trait groups we considered. For example, the four strongest responses to warming (two negative and two positive) all occurred in bees that were categorized as eusocial, ground-nesting, polylectic, and small (Fig. 3).

Warming likely affects urban bees through direct and indirect mechanisms. Direct effects could include changes in survival or fitness, driven by the relationship between habitat



**Fig. 3** db-RDA ordination of bee species relative to site temperature (temperature increases to the left, indicated by the arrow aligned with the X-axis). Although bee size was not included in the analysis, large and small bees are symbolized for reference. Most taxa clustered near the center of the plot, indicating insensitivity to temperature; shifts in community composition are driven by the more extreme taxa loaded on the positive and negative extremes of the X-axis. The Y-axis illustrates further variation in community composition, unexplained by the habitat variables we measured

temperature and bee thermal tolerance. Oyen et al. (2016) used physiological tolerance tests in the laboratory to demonstrate that a bumble bee species with a low-altitude (warmer) geographic range tolerated temperatures about 5 °C hotter than did species with high-altitude ranges. Although such laboratory tests are rare in bees, field studies have also demonstrated interspecific variation in apparent thermal optima for pollinators (Rader et al. 2013; Kühsel and Blüthgen 2015). Urban warming could thereby filter the regional species pool by favoring the most heat-tolerant bees. Urban warming could also exert indirect effects on bees via plant stress. Warming or the accompanying water stress often reduce the production of pollen or nectar (reviewed by Scaven and Rafferty 2013), potentially limiting the carrying capacity of hot, urban habitats for insects that depend on flowers.

Local impervious surface cover was also an important, negative predictor of bee abundance and richness. A negative association between impervious surface cover and bee abundance has also been reported in Paris, France (Geslin et al. 2016); Lyon, France (Fortel et al. 2014); and Birmingham, UK (Bates et al. 2011). In those studies, the most urban sites had 64–98% impervious surface within 500 m of sampling sites, whereas our most developed site had only 35% within 500 m. Our results therefore extend the negative relationship between impervious surface and bee abundance to low development intensities. We also provide a potential mechanism through which impervious surface could act, namely, the urban heat island effect. In our study, local impervious surface and temperature were weakly correlated ( $r = 0.61$ ), and each explained a similar amount of variation in bee abundance.

Percent impervious surface is also broadly correlated with land use, air quality, soil quality, soil exposure, and amount of vegetation (Civerolo et al. 2007; Yuan and Bauer 2007; Kaye et al. 2008). Perhaps because it summarizes so many aspects of habitat quality, impervious surface is emerging as a consistent and parsimonious predictor of total bee abundance across continents and development intensities.

Floral density was an important predictor of increasing bee abundance and species richness, although its effect on abundance was limited to large bees (Table 2). The importance of floral density is expected, given that bees depend on floral resources throughout their life cycles. It is well-documented that bee populations are often limited by floral availability (Roulston and Goodell 2011), that floral abundance and diversity structure bee communities (Potts et al. 2003), and that pollinators respond more consistently to floral resources than to other measures of land-use change (Winfree et al. 2011). Our results support these established patterns in an urban habitat.

Two potential predictors never appeared in the best models for bee abundance, richness, or composition: landscape-scale impervious surface and floral diversity. We expected that large (presumably more mobile) bees would be more influenced by landscape-scale impervious surface, and small bees by local impervious surface; instead our results support other findings that local, site-scale factors are important for bees of all sizes (Benjamin et al. 2014; Quistberg et al. 2016). The unimportance of floral diversity was surprising, given known, positive relationships between flower diversity and bee diversity in natural and urban habitats (Potts et al. 2003; Lowenstein et al. 2014; Quistberg et al. 2016). However, these previous studies sampled bees directly from flowers or within designated garden areas, whereas our sampling was broader. In addition to netting at flowers, we placed pan traps on turf lawns even when flowers were sparse to absent. These traps could have captured bees that were “tourists” associated with plants beyond the sampled property. We would expect such spillover to be pronounced in urban areas, where habitat management can vary sharply from one residential property to the next; bee-attractive plant species could be available just over the property line, undetected in our sampling.

Other studies have also asked whether bee ecological traits predict urban tolerance, but consistent patterns have yet to emerge. Some have found that urbanization favors cavity-nesting bees over ground-nesting bees (Cane et al. 2006; Matteson et al. 2008; Geslin et al. 2016), whereas others have not (Carper et al. 2014); some have found that urbanization favors social bees over solitary bees (Kearns and Oliveras 2009; Banaszak-Cibicka and Żmihorski 2012) whereas others have not (Carper et al. 2014; Fortel et al. 2014); and, whereas specialist pollinators are generally more sensitive to land-use change than are generalists (Winfree et al. 2011), studies of bees along urban gradients have found minimal support for

**Table 3** Linear mixed-effects models of bee abundance as a function of urbanization, traits, and their interactions (significant terms are bold)

Habitat factor	Trait	Model term	d.f.	<i>F</i>	<i>P</i>	$R^2_m$ *	$R^2_c$ †
Temperature	Sociality	Whole model				0.90	0.93
		<b>Sociality</b>	2,32	327.29	<0.0001		
		<b>Temp</b>	1,16	10.53	0.005		
		Sociality x Temp	2,32	0.68	0.514		
	Nesting	Whole model				0.73	0.76
		<b>Nesting</b>	1,16	91.80	<0.0001		
		<b>Temp</b>	1,16	11.69	0.004		
		Nesting x Temp	1,16	0.12	0.730		
	Lecty	Whole model				0.84	0.85
		<b>Lecty</b>	1,16	194.18	<0.0001		
		<b>Temp</b>	1,16	6.01	0.026		
		Lecty x Temp	1,16	0.06	0.810		
	Size	Whole model					
		<b>Size</b>	1,16	112.55	<0.0001	0.71	0.83
		<b>Temp</b>	1,16	12.88	0.003		
Size x Temp		1,16	0.34	0.567			
Imperv (local)	Sociality	Whole model				0.90	0.93
		<b>Sociality</b>	2,32	339.44	<0.0001		
		<b>Imperv</b>	1,16	7.67	0.014		
		Sociality x Imperv	2,32	1.30	0.287		
	Nesting	Whole model				0.70	0.76
		Nesting	1,16	91.14	<0.0001		
		Imperv200	1,16	8.24	0.011		
		Nesting x Imperv	1,16	0.01	0.935		
	Lecty	Whole model				0.84	0.85
		<b>Lecty</b>	1,16	194.56	<0.0001		
		<b>Imperv</b>	1,16	5.95	0.027		
		Lecty x Imperv	1,16	0.09	0.766		
	Size	Whole model				0.67	0.83
		<b>Size</b>	1,16	113.46	<0.0001		
		<b>Temp</b>	1,16	7.37	0.015		
Size x Imperv		1,16	0.47	0.501			

\*Marginal  $R^2$  (proportion of variance explained by fixed effects)

†Conditional  $R^2$  (proportion of variance explained by fixed and random effects)

this pattern (Cane et al. 2006; Carper et al. 2014). Our study was conducted in the same urban area as that of Carper et al. (2014), and neither study found trait-based differences in bee responses to urbanization. We suggest that the relatively low-density development in this region has not imposed differential limitations on the trait-groups we examined. Making specific predictions about which kinds of bees thrive or decline in cities remains difficult, and advances will depend on a combination of continued research synthesis and future mechanistic studies that identify more pertinent bee traits.

Urban areas are expanding at unprecedented rates as the human population grows and migrates from rural to urban homes (Seto et al. 2012). Agricultural and natural areas within

and around cities still require pollination services, and conserving pollinator populations is a goal of sustainable urban habitat management. Our results are relevant in this context. Bees appear to respond to local-scale management, such that pollinator gardens, impervious surface reduction, or other heat-island-reduction strategies are worthwhile, even if limited to a single property. However, we also show that components of the bee community respond differently to habitat variables: Large bees benefit more than small bees from high floral density, such that simply providing more floral resources in an otherwise hot and impervious area may attract large bees without restoring the smaller species. Efforts to provide floral resources in cities may be most effective when

targeted to sites with the lowest levels of local impervious surface and urban warming, or when coupled with impervious-surface reduction. To maintain pollinator abundance and diversity, urban insect conservation approaches must address the combined effects of biotic and abiotic factors on different components of the pollinating community.

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**Authors' contributions** ALH and SDF conceived the ideas and designed methodology; ALH collected the data; ALH and EY analyzed the data; ALH and EY led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

#### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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