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Temperature and not landscape composition shapes wild bee communities in an urban environment

Costanza Geppert[1] | Andree Cappellari[1] | Daria Corcos[1,2] | Valerio Caruso[2] | Pierfilippo Cerretti[2] | Maurizio Mei[2] | Lorenzo Marini[1]

[1]Department of Agronomy, Food, Natural resources, Animals and Environment, University of Padova, Legnaro, Padova, Italy

[2]Department of Biology and Biotechnology "Charles Darwin", Sapienza University of Rome, Rome, Italy

Correspondence
Costanza Geppert, Department of Agronomy, Food, Natural resources, Animals and Environment, University of Padova, Viale dell'Università 16, 35020 Legnaro, Padova, Italy.
Email: costanzageppert@gmail.com

Abstract

1. More than half of the world's population lives in urban areas, a proportion that is expected to increase. Even if urbanisation is widely regarded as a major threat to global biodiversity, recent research highlighted the potential ecological importance of cities for pollinators. Key determinants of cities' ability to sustain pollinators are the presence of green areas and the connectivity between them. However, also temperature is expected to be of primary importance for pollinator activities.

2. Here, we aimed at disentangling the effects of temperature, open habitat cover, and distance from the city centre on wild bee communities in the city of Rome (Italy). We selected 36 sites along two statistically independent gradients of temperature and open habitat cover, and we sampled wild bee communities using pan-traps for 4 months. Then, we measured functional traits of wild bee species, that is, body size, social behaviour, nesting strategy, and diet breadth.

3. Temperature emerged as the main driver of wild bee communities, with communities richer in species and individuals at warmer temperatures. We found little species replacement between cold and warm sites. In addition, with increasing temperatures, bee communities were dominated by polylectic and small-bodied species.

4. Here, we showed that in a highly urbanised environment, temperature shapes pollinator communities irrespective of other landscape metrics. Even if warming seemed beneficial for urban pollinator abundance and richness, it might strongly homogenise bee communities by selecting for those traits that make species more easily adaptable.

KEYWORDS
Apoidea, biodiversity, body size, climate change, foraging, functional traits, pollinator, Rome, sociality, urban ecology

INTRODUCTION

Globally, urban areas are expanding, while natural habitats shrink and become more remote (Grimm et al., 2008). Today, more than half of the world's population lives in urban landscapes, a proportion that is expected to increase to 85% by 2100 (OECD, 2015). Urbanisation is widely regarded as a major threat to global biodiversity (Grimm et al., 2008; Sala, 2000); however, high levels of biodiversity may also thrive inside cities (Beninde et al., 2015). In particular, recent research highlighted the ecological importance of cities for pollinators (Hall et al., 2017; Theodorou et al., 2020; Wenzel et al., 2020). Urbanisation generally enhanced pollinator diversity compared to more intensified agricultural landscapes (Wenzel et al., 2020). Moreover, urbanisation appeared to shift the functional diversity of bee assemblages (Fournier et al., 2020). Over the last years, it has been well established that insect pollinators are declining worldwide, mostly due to habitat fragmentation, loss and land-use intensification (Kennedy et al., 2013; Potts et al., 2010). In this context, understanding the potential role of cities as pollinator refuge becomes fundamental.

Key determinants of cities' ability to sustain pollinators are often related to the amount of green areas that are rich in nesting and food resources and to the connectivity between green fragments (Beninde et al., 2015; Biella et al., 2022; Wenzel et al., 2020). Moreover, besides the well-known positive effects of flower availability and high landscape connectivity, temperature is expected to be of primary importance for pollinator activities (Kühsel & Blüthgen, 2015). As for ectotherms in general, temperature is one of the main drivers of insect pollinators' activities (Bale et al., 2002; Kühsel & Blüthgen, 2015). Warmer environments are expected to be associated with higher growth rates, reduced development time, and increased probability of survival (Zuo et al., 2012). However, excessive climate warming can also lead to negative effects such as increased desiccation impairing insect growth, reproduction, and survival (Dale & Frank, 2018; Hamblin et al., 2018). For pollinators, changes in climate are also expected to cause spatial and temporal mismatches with their food plants (Papanikolaou et al., 2017). The urban heat island effect makes cities warmer than surrounding natural areas (Oke, 1973), providing an ideal system to study warming effects.

Considering the high diversity of bee life-history strategies, different species might respond to environmental changes in different ways (Bale et al., 2002). Because certain traits can be favoured in different environmental conditions, pollinator communities are likely to exhibit shifts in functional group composition in response to urbanisation and warming. Usually, under warming temperatures, organisms show a smaller body size because warmer temperature increases metabolic rates and the associated costs for a given body size (Brown et al., 2004; Eggenberger et al., 2019). However, responses to increasing temperatures can be different from taxon to taxon, for example, bumblebees and halictids showed dissimilar thermal limits and desiccation tolerances (Burdine & McCluney, 2019). In contrast, the relationship between wild bees' traits and urbanisation is more variable. However, most studies highlighted that urban areas act as strong environmental filter on wild bees and that some functional traits are particularly beneficial to thrive in urban areas (Buchholz & Egerer, 2020; Gathof et al., 2022). For example, cavity-nesting and polylectic species seemed to profit more from urbanisation than ground-nesting and oligolectic species (Sexton et al., 2021; Wenzel et al., 2020).

In this study, we aimed at disentangling the effects of temperature, open habitat cover, and distance from the city centre on wild bee communities in the metropolitan city of Rome (Italy). Mediterranean ecosystems are among the most vulnerable to climate change and belong to the world biodiversity hotspots for wild bees (Orr et al., 2021). In particular, Italy hosts an incredible diversity of bee species: more than half of the species listed for the entire Europe (Quaranta et al., 2018). However, few studies focus on Mediterranean bees and even less on bees in Mediterranean urban environments. Here, we selected 36 sites along two statistically independent gradients of temperature and open habitat cover and we sampled bee communities using pan-traps for 4 months. We then measured several functional traits of pollinator species. We hypothesised that wild bee diversity and abundance would increase with warmer temperatures and with a higher cover of open habitat at the landscape scale. In addition, we expected that communities would be dominated by species adapted to warm conditions at higher temperatures. In particular, we hypothesised traits to be filtered by the environment, with small bees being favoured at warmer temperatures near the city centre and below ground nesters and oligolectic bees in areas with a higher cover of open habitat.

MATERIALS AND METHODS

Study area

The study area was the metropolitan city of Rome (Italy, 41°53′ N, 12°29′ E) (Figure 1a), defined as the territory circumscribed by the great motorway ring (c. 360 km^2). Rome is the third most populated city in the European Union, with a population estimated at 3.8 million, and a density of 2232 people/km^2 in 2016 (World Population Review, 2016). The climate is temperate, with mild wet winters and warm summers. From 1970 to 2000, maximum mean annual temperature was 21.4°C, minimum mean annual temperature was 9.1°C, and mean precipitation was 140.9 mm. Over the last 40 years in Italy, summer temperature increased on average by 0.52°C every 10 years (Fioravanti et al., 2020). Approximately 54% of the study area is represented by urban areas (residential, industrial, and commercial areas), 16% by urban green areas (non-agricultural green areas, both artificial and semi-natural, including historical and archaeological sites, public parks and gardens, grasslands, shrublands, and forests), and the remaining 30% is covered in agricultural lands, pastures and water.

Sampling design

We selected 36 sampling sites with open grassland vegetation with 2 km minimum and 26 km maximum distance from each other (Figure 1b and
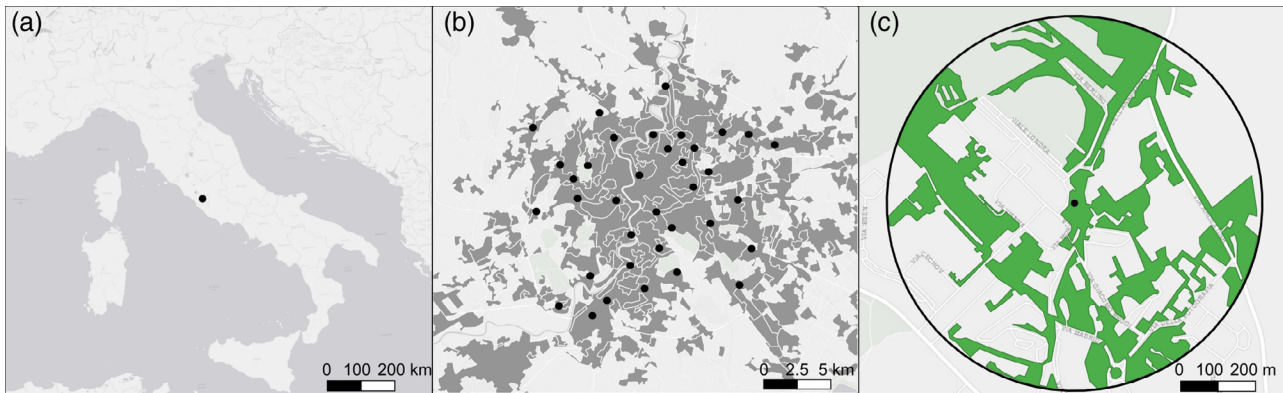
FIGURE 1 Study area in the city of Rome, Italy (a); spatial distribution of the 36 selected sampling sites (black points) along a gradient of urbanisation (shaded) (b); and example of open green habitat cover (in green) in a 500 m buffer (c). The centroid of the buffer is the point where pan-traps were placed. *Source*: Maps were obtained from OpenLayers Plugin, QGIS.

Table S1). Sampling sites were chosen along two independent gradients: a gradient of median surface temperatures from 34 to 43°C, and a gradient of open habitat cover in a buffer of 500 m radius spanning from 4% to 53%. We selected a 500 m radius because it emerged from several studies as the most appropriate landscape scale for wild bees (Gathmann & Tscharntke, 2002; Steffan-Dewenter et al., 2002).

To obtain surface temperatures, we extracted the radiative skin temperature of the land surface, using Landsat 8 images with 30 m resolution. For each pixel, we calculated the median of the temperatures recorded over the sampling period, from June to September 2016, using Google Earth Engine (Ermida et al., 2020). This temperature metric is considered very relevant for insects and it has been used as a source of temperature data in several insect population models (Blum et al., 2015; Chuang et al., 2012).

To quantify the cover of the main habitat categories in a radius of 500 m around each sampling site, we identified urban, woody, and open habitat areas (i.e. covered in herbaceous vegetation) and digitised polygons in Google Earth Pro manually (Google Earth 7.1.5.1557, 2015). Then, with a field survey, we validated the habitat classification obtained digitised polygons (Figure 1c).

Moreover, we calculated the distance of each site from the city centre, that is, the Colosseum (41°53′24″ N, 12°29′32″ E). For Rome, this variable is a good proxy of decreasing disturbance along an urban–rural gradient (Fattorini, 2014), as suburban areas are richer in semi-natural habitats than the central areas (Figure 1b). Lastly, we assessed collinearity between all landscape variables, that is, land surface temperature, open habitat cover, urban cover, woody habitat cover, and distance from the city centre (Figure S1a).

Wild bee sampling

At each sampling site, we collected wild bees (Apoidea: Anthophila) using a set of six yellow pan-traps, composed of plastic cups (750 ml, Ø 12.5 cm, h 4.5 cm) filled with a solution of water and 2% biodegradable dish detergent. As the vegetation in the sampling sites was below

50 cm, we placed pan-traps on the ground approximately 10 m apart, in two parallel lines of three pan-traps each. Due to the well-documented relationship between pollinator diversity and flower cover, we chose our sampling sites to reflect a similar amount of flower availability, allowing us to focus on the broader landscape context, that is, open habitat cover and temperature. We placed the pan-traps in small patches of open grassland vegetation characterised by similar plant composition and similar vegetation height (between 20 and 50 cm). Field work was carried out every 2 weeks from mid-June to mid-September 2016, for a total of seven sampling rounds. For each sampling round, pan-traps were set out for 48 h. We excluded honeybees from this study because in our sampling area most honeybees are managed; therefore, their abundance strongly depends on beehive presence. The material was sorted by D.C. and identified by M.M. using identification keys (additional references in the Supplementary Information S1) and the reference collection of the Museum of Zoology of Sapienza, University of Rome. Species names follow Discover Life (Perlmutter, 2010). Specimens are preserved at the Museum of Zoology of Sapienza, University of Rome.

Pan-trap sampling is a well-established method of collecting Hymenoptera and it usually captures a greater diversity of bee species compared to netting (Boyer et al., 2020). Even if the potential bias was constant across all sites, by using pan traps to sample wild bees we may have under-sampled certain taxa (Prendergast et al., 2020), in particular larger bees (Roulston et al., 2007). In addition, several studies assessed colour preference in Hymenoptera, showing that trap colour affects the diversity of sampled bees and that, in most cases, yellow pan traps collected the largest numbers of bees (Buffington et al., 2021; Krahner et al., 2021). To evaluate the completeness of our sampling effort, we estimated the rarefaction curves using a coverage-based method (Chao et al., 2020) (Figure S2a,b). With a few exceptions, the curves presented similar slopes and did not cross indicating that our species richness estimates were comparable across sites. However, the quick saturation showed by most curves stressed again that some groups of bees might have been under-sampled (Prendergast et al., 2020).

Wild bee functional traits

To investigate how life history and ecological characteristics mediate bee response to temperature, open habitat cover, and distance from the city centre, we sorted all recorded species based on functional traits. For each bee species, we collected (1) body size, (2) social behaviour (solitary or social), (3) nesting strategy (above ground or below ground), and (4) diet breadth (oligolectic or polylectic) (Table S2; additional references in Supplementary Information S1). We selected the most informative functional traits in predicting bee responses to environmental change according to current literature and our knowledge (Williams et al., 2010). For body size, we measured body length of pinned specimens from head to metasoma end using graph paper. We measured one to five individuals, proportionally to how many specimens we collected in the field. For each species, whenever possible, we measured at least one female and one male. We then calculated the mean body size value for each species. We considered semi-social, social, and eusocial bees as social. Concerning nesting strategies, nesting categories were collapsed to below-ground and above-ground nesting to increase sample size and provide greater generality (Williams et al., 2010). Above-ground nesting bees included those species which build their nests in stems or pre-existing cavities. For diet breadth, we classified as oligolectic those bee species that are specialised to forage on one specific plant taxon, for example, one single plant family (Cane, 2021). Finally, we assessed collinearity between all functional traits of wild bees (Figure S1b).

Statistical analyses

First, we estimated the effects of surface temperature, open habitat cover, and distance from the city centre on wild bee abundance, species richness, and community evenness. We calculated wild bee community evenness using the R package 'codyn' (Hallett et al., 2016) with the default settings that calculate evenness as Evar (Smith & Wilson, 1996). Then, we fitted three linear regressions using surface temperature, open habitat cover, distance from the city centre, and their two-way interactions as fixed factors and wild bee abundance, species richness, and community evenness as response variables. We used a natural logarithmic transformation of wild bee abundance and species richness to meet the assumption of normally distributed residuals. Pan-traps were placed in herbaceous open habitats that are considered to be the most influential habitat types for wild bees (Michener, 2000; Winfree et al., 2011). However, some oligolectic species, in particular the ones nesting in wood, might be associated with trees. Therefore, we tested also for the effect of woody cover on wild bees and wood-nesting bees, separately. As woody cover was negatively correlated with surface temperature ($r = -0.49$, $p = 0.002$), we could not test for the effect of both variables in the same models. Woody cover did not affect the abundance, species richness, and community evenness of either wild bees or wood-nesting bees (Table S3). Therefore, we decided to present in the main text only models testing for the effects of open habitat, surface temperature and distance from the city centre on all wild bees.

Second, we measured changes in the community composition. Based on presence/absence community data, we calculated richness and replacement, the two components of pairwise Jaccard dissimilarity, using the function 'betadiver' of the R package 'vegan' (Oksanen et al., 2019). Then, we generated a temperature distance matrix, a habitat cover distance matrix, and a distance from the city centre distance matrix using the 'vegdist' function with Euclidean distance, and a geographical distance matrix using the R package 'geosphere' (Hijmans, 2019). To test the effects of temperature, open habitat cover and geographic distance on wild bee community dissimilarity, we performed multiple regressions on the obtained distances using the 'MRM' function in the 'ecodist' package with 1000 permutations

TABLE 1 Results from the four linear models testing the effect of temperature, open habitat cover, and distance from the city centre on wild bee abundance (a), species richness (b), and community evenness (c)

| Response variable	Explanatory variable	R^2	Estimate	SE	t	p
(a) Abundance	Intercept	0.2	0.278	1.775	0.157	0.877
	Temperature		0.107	0.045	2.389	0.023
	Open habitat cover		−0.011	0.009	−1.164	0.253
	Distance from the city centre		0.015	0.041	0.362	0.72
(b) Species richness	Intercept	0.25	1.154	0.765	1.509	0.141
	Temperature		0.048	0.02	2.418	0.016
	Open habitat cover		−0.007	0.004	−1.814	0.081
	Distance from the city centre		<0.001	0.018	−0.015	0.988
(c) Community evenness	Intercept	0.1	1.07	0.366	2.919	0.006
	Temperature		−0.015	0.009	−1.567	0.127
	Open habitat cover		−0.004	0.008	−0.512	0.612
	Distance from the city centre		0.001	0.002	0.715	0.48

Note: Wild bee abundance and species richness were logarithmically transformed to meet the assumption of normally distributed residuals. No significant interactions were found ($p < 0.05$).
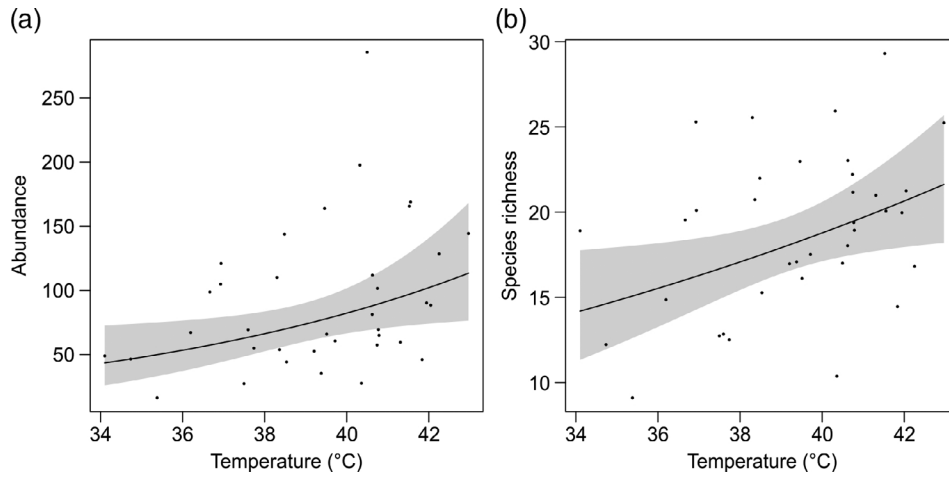
FIGURE 2 Effect of surface temperature on abundance (a) and species richness (b) of wild bees. The line indicates model predicted values, and the shaded area shows the 95% CI.

TABLE 2 Results from multiple regression models on distance matrices testing the effects of temperature distance, open habitat cover distance, and geographic distance on wild bee composition dissimilarity components, that is, (a) richness dissimilarity and (b) replacement dissimilarity

Response variable	Explanatory variable	R^2	Estimate	p
(a) Richness dissimilarity	Intercept	0.05	<0.001	0.823
	Temperature distance		0.015	0.027
	Open habitat distance		<0.001	0.764
	Distance from the city centre		−0.004	0.524
	Geographic distance		<0.001	0.701
(b) Replacement dissimilarity	Intercept	0.01	<0.001	0.682
	Temperature distance		−0.001	0.910
	Open habitat distance		<0.001	0.923
	Distance from the city centre		0.004	0.571
	Geographic distance		<0.001	0.451
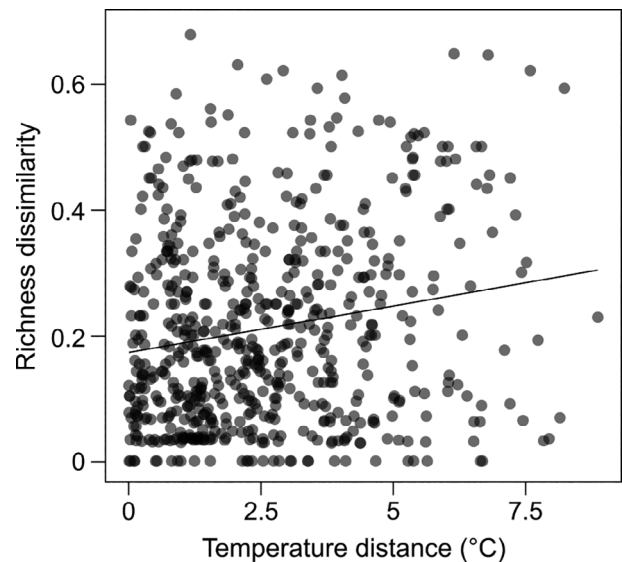
FIGURE 3 Effect of temperature distance on richness dissimilarity of wild bee communities among sites. Composition dissimilarity was calculated using the richness component of Jaccard index (Legendre 2014). The line is estimated from a multiple regression model on distance matrices.

(Goslee & Urban, 2007). We used richness and replacement dissimilarities as response variables.

Third, to measure functional diversity, we used functional dispersion (FDis) and functional evenness (FEve). Functional dispersion represents the dispersion of bee species in a multi-dimensional trait space, that is, the distance of species to the centroid of all species in the community, weighted by their abundance (Laliberté & Legendre, 2010). Functional evenness describes the regularity of

species distribution in the trait space weighted by their abundance. First, we created a distance matrix using Gower distance for traits. Then, we calculated both indices based on abundance data and Gower distances for traits using the R package 'FD' (Laliberté et al., 2014). Finally, we fitted two linear models using functional dispersion and functional evenness as response variables and surface temperature, open habitat cover, distance from the city centre, and their two-way interactions as fixed factors.

Fourth, to assess shifts in trait values within communities due to environmental selection, we used community-weighted means (CWMs), which allow extracting community-level trait values weighed by species abundances. CWMs are particularly useful as the

TABLE 3 Results from the two linear models testing the effect of temperature, open habitat cover, and distance from the city centre on functional dispersion (a), and functional evenness (b) of wild bee communities

| Response variable	Explanatory variable	R^2	Estimate	SE	t	p
(a) Functional dispersion	Intercept	0.12	0.359	0.119	3.004	0.005
	Temperature		−0.003	0.003	−0.848	0.403
	Open habitat cover		−0.001	0.001	−1.183	0.245
	Distance from city centre		−0.003	0.003	−1.024	0.314
(b) Functional evenness	Intercept	0.18	1.19	0.223	5.338	<0.001
	Temperature		−0.014	0.006	−2.488	0.018
	Open habitat cover		0.001	0.001	0.737	0.467
	Distance from city centre		0.001	0.005	0.289	0.774

Note: No significant interactions were found ($p < 0.05$).

distribution of traits is one of the best methods to describe the community functional composition (Moretti et al., 2009). We calculated CWM for all wild bee functional traits, expanding nominal traits, that is, social behaviour, nesting strategy, and diet breadth, into binary traits (Podani, 2005). Then, we fitted four linear regressions using surface temperature, open habitat cover, distance from the city centre, and their two-way interactions as fixed factors and CWMs for each of the four traits as response variables. We excluded kleptoparasite species from all models of functional traits, as they lack pollen collecting structures and do not build their nests, and morphospecies from social behaviour and diet breadth models, as we lack these data. Moreover, when analysing nesting strategy, we excluded one site because it contained extreme values of above ground-nesting bees compared to all other sites, distorting our analysis (Grubbs test for outliers $p < 0.001$), and violating assumption of residuals' normality.

Starting from each of the full linear models, we used a backward deletion procedure, removing one-by-one the interactions with $p > 0.05$, and re-ran the model with all main effects to avoid overfitting and to correctly interpret the main effects. Moreover, in all models, we estimated variance inflation factors (VIFs) to assess possible collinearity issues between fixed effects. All VIF values were close to 1, indicating very little collinearity among predictors (Akinwande et al., 2015). Model assumptions were visually evaluated using diagnostic plots of model residuals (Figure S3). All analyses were run with R 3.5.1 (R Core Team, 2017).

Multi-model inference

To evaluate the uncertainty of model selection, we also performed a multi-model inference analysis and compared the fit of all possible candidate models nested within each of the full models presented above. Within each set, models were ordered based on their second-order Akaike information criterion (AICc), with the best-fitting model showing the lowest AICc. For each model, we calculated the difference between the model AICc and the lowest AICc of the entire set of models ($\Delta AICc_i = AICc_i - AICc_{MIN}$). A model in a set can be considered plausible if its $\Delta AICc$ is below 2. Multi-model inference analyses
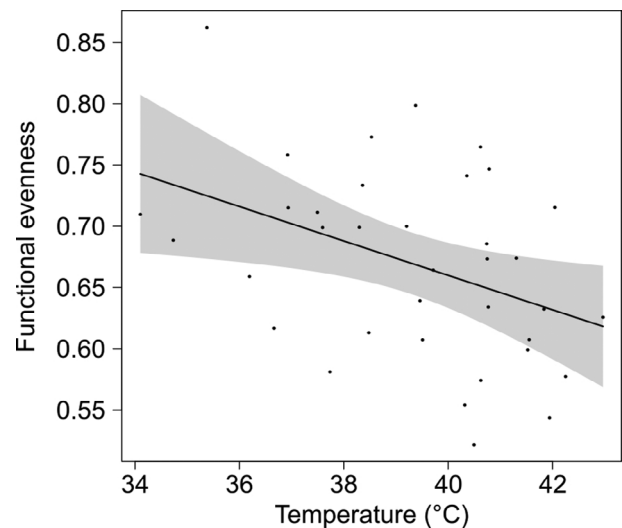
FIGURE 4 Effect of surface temperature on functional evenness of wild bee communities. The line indicates model predicted values, and the shaded area shows the 95% CI.

were performed with the 'MuMIn' package (Barton, 2020; Burnham et al., 2010). Final models selected according to the backwards stepwise deletion were consistent with the ranking of the plausible models based on AICc (Tables S4 and S5). Hence, we presented the results of the reduced models from the backward deletion procedure in the main text and reported the multi-model inference analyses only in the Supporting Information S1.

RESULTS

Overall, we collected 3280 individuals of 96 species and morphospecies of wild bees (Figure S4, Table S2). The most abundant species was *Lasioglossum malachurum* (Kirby, 1802) ($n = 897$ individuals), followed by *Lasioglossum glabriusculum* (Morawitz, 1853) ($n = 456$ individuals) and *Halictus gemmeus* Dours, 1872 ($n = 275$ individuals). Among the collected species, 77% were polylectic bees, 22% showed a social lifestyle and 38% nested above ground.

TABLE 4 Results from the linear models testing the effect of temperature, open habitat and distance from the city centre on CWMs for body size (a), nesting strategy (above ground) (b), diet breadth (polylecty) (c), and social behaviour (sociality) (d) of wild bee communities

Response variable	Explanatory variable	R^2	Estimate	SE	t	p
(a) Body size	Intercept		10.892	1.826	5.965	<0.001
	Temperature		−0.117	0.046	−2.524	0.017
	Open habitat cover	0.24	<0.001	0.009	0.05	0.941
	Distance from the city centre		0.096	0.042	2.284	0.031
(b) Nesting strategy (above ground)	Intercept		<0.001	<0.001	0.574	0.57
	Temperature		<0.001	0.003	0.036	0.972
	Open habitat cover	0.06	−0.001	0	−1.302	0.203
	Distance from the city centre		<0.001	0.002	−0.186	0.854
(c) Diet breadth (polylecty)	Intercept		0.533	0.28	1.903	0.066
	Temperature		0.007	0.002	3.71	0.001
	Open habitat cover	0.29	0.001	0	1.578	0.128
	Distance from the city centre		−0.001	0.002	−0.283	0.602
(d) Social behaviour (sociality)	Intercept		−0.041	0.436	0.095	0.925
	Temperature		0.015	0.011	1.36	0.174
	Open habitat cover	0.18	0.004	0.002	1.83	0.077
	Distance from the city centre		0.007	0.01	0.717	0.496

Note: No significant interactions were found (*p* < 0.05).
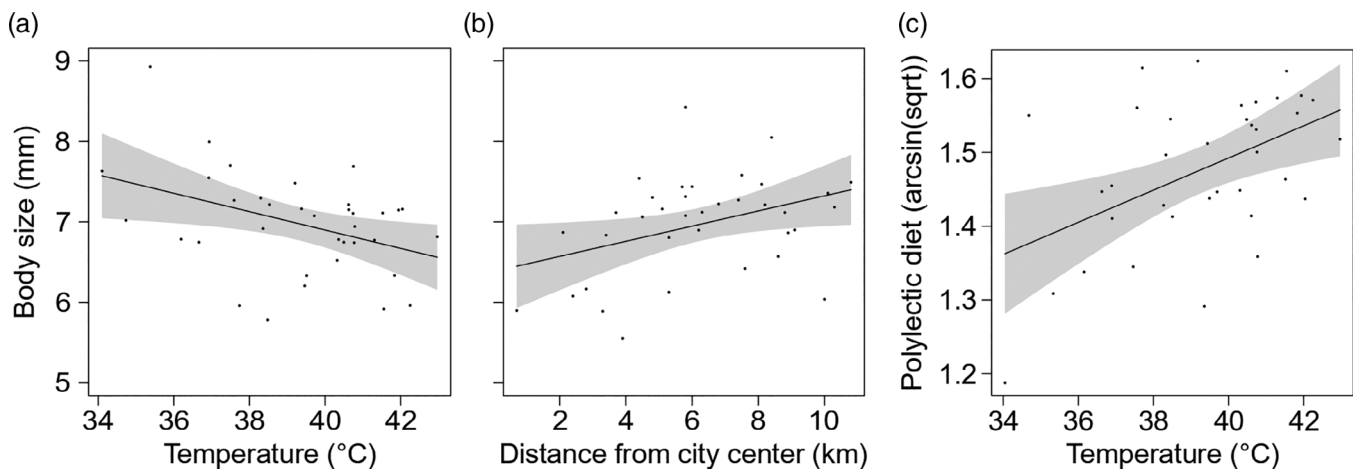
FIGURE 5 Effects of temperature (a), distance from the city centre (b) on community-weighted mean (CWM) body size and effect of temperature on CWM diet breadth (polylecty) (c). The line indicates model predicted values, and the shaded area shows the 95% CI. CWMs for diet breadth were arcsine square root transformed to obtain normally distributed residuals.

Surface temperature was the only factor affecting wild bee abundance and richness (Table 1). Both abundance and species richness increased with increasing temperatures (Figure 2a,b), while community evenness did not respond. Open habitat cover and distance from the city centre did not affect wild bee abundance, species richness, and community evenness (Table 1).

Multiple regressions on distance matrices showed that temperature distance affected only community dissimilarity related to species richness difference (Table 2). Species richness difference increased with increasing temperature distance, that is, sites with similar temperatures shared a subset of the occurring species and showed more similar bee communities (Figure 3). In contrast, the species replacement component was not affected by temperature. In addition, open habitat distance, distance from the city centre and geographic distance did not have any effect on both richness and replacement components (Table 2).

Functional diversity analyses showed that functional evenness decreased at higher temperatures (Table 3, Figure 4) while it was not affected by open habitat cover or distance from the city centre. Functional dispersion did not respond to temperature, open habitat cover or distance from the city centre.

By analysing CWMs for body size, social behaviour, nesting strategy, and diet breadth, we found that communities were functionally

diverse depending on temperature and distance from the city centre (Table 4). Communities were characterised by smaller individuals when they were close to the city centre or when temperatures were warmer (Figure 5a,b). Moreover, bee communities showed a higher proportion of individuals of polylectic species with warmer temperatures (Figure 5c). In contrast, CWMs for nesting strategy and social behaviour did not respond to surface temperature, open habitat cover or distance from the city centre. However, we found a positive trend between sociality and open habitat cover (Figure S5).

DISCUSSION

Here, we showed that in a highly urbanised environment, temperature was the key driver of wild bee diversity, abundance, composition and functional diversity, shaping pollinator communities irrespective of the cover of open habitat and the distance from the city centre. Warmer sites showed communities richer in individuals and species but dominated by similar traits. In response to warming and distance from the city centre, bee assemblages exhibited clear shifts in functional composition.

Temperature as the main driver of wild bee communities

Both wild bee abundance and species richness were driven by temperature, with a positive effect of warmer temperatures. In addition, temperature was the only factor filtering community composition and, even with a very high variability, it led to communities that differed because of the number of species, and not because of species turnover. Warm temperatures are often beneficial to insects, as they might increase growth rate and survival, and reduce development time (Zuo et al., 2012). Most studies investigating the relationship between temperatures and pollinators found that warm temperatures increased insect activities, abundance, diversity or biomass (Burdine & McCluney, 2019; Kühsel & Blüthgen, 2015; Schürch et al., 2016; Welti et al., 2021, but see Casanelles-Abella et al., 2021; Hamblin et al., 2018; Papanikolaou et al., 2017). However, the reported positive effect of warming should be taken with caution. Large deviations from long-term temperature averages were found to negatively affect flying insects, as rapid temperature rises may exceed locally established tolerance (Welti et al., 2021). To assess more precisely temperature warming effects on bees, we should gain knowledge on mid- and long-term effects of temperature and on species thermal optima. However, little is still known on bee thermal and humidity limits, besides that they could strongly differ from species to species and even from one population to another (Burdine & McCluney, 2019; Martinet et al., 2021; Sánchez-Echeverría et al., 2019).

Cities usually experience much warmer temperatures than nearby rural or semi-natural areas because of heat absorbing and impervious building materials (Oke, 1973). In contrast, increasing vegetation cover decreases temperatures (De Frenne et al., 2013). Also in this study, we found a negative correlation between temperature and tree cover, that is, warmer sites were embedded in highly urbanised landscapes, while colder sites showed a lower percentage of urbanisation (Figure S1a). Besides increasing local temperatures with a potentially positive effect on bee growth and survival, high urbanisation might provide locally a large amount of floral resources, for example, in parks, gardens and roadsides, therefore sustaining a high number of species and individuals (Baldock et al., 2019; Hall et al., 2017; Wilson & Jamieson, 2019). However, in our study, wild bee abundance and diversity did not respond to open green habitat cover and distance from the city centre. Therefore, it is likely that different sites offered a similar amount of floral resources irrespective of the amount of open habitat in the landscape. Another hypothesis is that all sampled species had been already selected for intensive anthropogenic habitat types (Corcos et al., 2019). In cities, wild bee communities should be the result of centuries of human disturbance and therefore, they might be composed mostly of species adapted to an urban environment. Many studies revealed that only a subset of species, consisting in the most tolerant to anthropogenic activities, is able to survive in highly disturbed environments (Banaszak-Cibicka & Żmihorski, 2012; Fournier et al., 2020; Gámez-Virués et al., 2015). In particular, it has been found that insect diversity increases with the age of an urban settlement (Sattler et al., 2010), as its insect fauna has probably been selected for high tolerance to fragmentation and colonisation potential.

Warm urban communities are dominated by specific functional traits

Our results show that in warmer sites, functional evenness decreased. This means that at high temperatures, the most abundant species shared similar traits different from the rest of community. Probably, few species characterised by specific traits can cope better with warm conditions. As a consequence, these few dominant species may be better adapted to future climate change scenarios, while others, characterised by different traits, may disappear. By analysing community mean traits, we were able to identify which traits seemed beneficial with increasing temperatures. Community mean trait values shifted depending on temperature and distance from the city centre. As expected, we found that mean body size decreased with increasing temperatures, that is, communities adapted to warm conditions showed on average smaller individuals. Similar results were reported for spiders, beetles, and aquatic taxa in urban environments (Merckx et al., 2018). It is well known that usually smaller animals dissipate heat better (Burdine & McCluney, 2019). Larger wild bee species might be therefore negatively affected by increasing temperatures in cities (Wilson & Jamieson, 2019). In addition, mean body size increased further away from the city centre, irrespective of the cover of open habitat. Similar results were reported in other studies, where mean body size of several invertebrate species increased with increasing distance from the city centre regardless of local site characteristics (Braschler et al., 2021;

Tóth & Hornung, 2020). For ground-dwelling arthropods, the decrease in body size has been related to a combination of reduced soil moisture and increased soil contamination (Braschler et al., 2021). However, for mobile flying organisms such as wild bees, this result is probably linked to foraging distances. Larger bee individuals forage further away, while smaller individuals travel closer to their nest (Greenleaf et al., 2007). Cities seem to favour smaller-bodied species because small bees may be more likely to use local and isolated floral spots in the city centre (Braschler et al., 2021; Prendergast et al., 2022). An additional possible explanation is that smaller species require a much limited amount of resources compared to larger species (Eggenberger et al., 2019; Winfree et al., 2011).

Besides filtering for smaller body size, warm temperatures increased the number of individuals of polylectic species in the community. In our study, all wild bee communities showed a high level of generalisation, with most species having a polylectic diet. This is typical of highly urbanised environments, where oligolectic species are usually uncommon (Casanelles-Abella et al., 2022; Lizee et al., 2011). Polylectic wild bee species are better able to exploit resources in urban areas as they can access and forage on a great variety of flowers. In this study, the few oligolectic species occurring at colder temperatures disappeared at warmer temperatures. A possible explanation for this might be that specialised species strongly depend on a particular range of conditions and are, consequently, more vulnerable to habitat disturbance in general and warming in particular (Hopfenmüller et al., 2014; Martinet et al., 2021; Winfree et al., 2011). It might also be that the abundance of the favoured host plants of some oligolectic species decreased at warmer temperatures but, unfortunately, we lack the data to confirm this hypothesis.

Finally, we did not find any effect of temperature, open habitat cover, and distance from the city centre on nesting strategy and social behaviour, except for a positive trend between sociality and open habitat cover (Figure S5). Williams et al. (2010) also found that social species responded strongly to the amount of natural habitat. In our study, most social species nested below ground (Figure S1b) and, therefore, the availability of bare ground in open areas might have been a key resource for them.

CONCLUSIONS

In a highly urbanised environment, such as the metropolitan city of Rome, wild bee abundance and diversity did not change in response to open habitat cover or distance from the city centre. In contrast, temperature was the main driver shaping wild bee communities. Under future global warming, we expect that heat-tolerant wild bee species will benefit from increasing temperatures in urban settlements and that warm temperature communities will be dominated by polylectic and small-bodied bees. Further research is needed to understand the potential role of cities as pollinator refuge under global change, focusing not only on wild bees, but even on other fundamental pollinator taxa such as Coleoptera, Diptera, and Lepidoptera.

AUTHOR CONTRIBUTIONS

Costanza Geppert: Formal analysis (equal); writing – original draft (lead); writing – review and editing (equal). **Andree Cappellari:** Formal analysis (equal); writing – original draft (equal); writing – review and editing (equal). **Daria Corcos:** Data curation (equal); writing – review and editing (supporting). **Valerio Caruso:** Data curation (equal); writing – review and editing (supporting). **Pierfilippo Cerretti:** Project administration (lead); writing – review and editing (supporting). **Maurizio Mei:** Data curation (equal); writing – review and editing (supporting). **Lorenzo Marini:** Conceptualization (lead); formal analysis (equal); funding acquisition (lead); writing – original draft (equal); writing – review and editing (equal).

CONFLICT OF INTEREST

All authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study will be openly available in Zenodo upon acceptance of the manuscript. https://zenodo.org/record/6979676#.YvUJXPhByUl

ORCID

Costanza Geppert https://orcid.org/0000-0003-1970-4131

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Supporting Information.