





ARTICLE

Functional diversity of farmland bees across rural–urban landscapes in a tropical megacity

Gabriel Marcacci¹  | Ingo Grass²  | Vikas S. Rao³ | Shabarish Kumar S⁴ | K. B. Tharini³ | Vasuki V. Belavadi³ | Nils Nölke⁵ | Teja Tschardtke^{6,7}  | Catrin Westphal^{1,7} 

¹Functional Agrobiodiversity, Department of Crop Sciences, University of Göttingen, Göttingen, Germany

²Ecology of Tropical Agricultural Systems, University of Hohenheim, Stuttgart, Germany

³Agricultural Entomology, University of Agricultural Sciences, Bangalore, India

⁴Department of Apiculture, University of Agricultural Sciences, Bangalore, India

⁵Forest Inventory and Remote Sensing, Faculty of Forest Sciences and Forest Ecology, University of Göttingen, Göttingen, Germany

⁶Agroecology, Department of Crop Sciences, University of Göttingen, Göttingen, Germany

⁷Centre of Biodiversity and Sustainable Land Use (CBL), University of Göttingen, Göttingen, Germany

Correspondence

Gabriel Marcacci

Email: gabriel.marcacci@uni-goettingen.de

Funding information

Deutsche Forschungsgemeinschaft, Grant/Award Numbers: 493487387, 405945293, 289781364

Handling Editor: Claudio Gratton

Abstract

Urbanization poses a major threat to biodiversity and food security, as expanding cities, especially in the Global South, increasingly compete with natural and agricultural lands. However, the impact of urban expansion on agricultural biodiversity in tropical regions is overlooked. Here we assess how urbanization affects the functional response of farmland bees, the most important pollinators for crop production. We sampled bees across three seasons in 36 conventional vegetable-producing farms spread along an urbanization gradient in Bengaluru, an Indian megacity. We investigated how landscape and local environmental drivers affected different functional traits (sociality, nesting behavior, body size, and specialization) and functional diversity (functional dispersion) of bee communities. We found that the functional responses to urbanization were trait specific with more positive than negative effects of gray area (sealed surfaces and buildings) on species richness, functional diversity, and abundance of most functional groups. As expected, larger, solitary, cavity-nesting, and, surprisingly, specialist bees benefited from urbanization. In contrast to temperate cities, the abundance of ground nesters increased in urban areas, presumably because larger patches of bare soil were still available beside roads and buildings. However, overall bee abundance and the abundance of social bees (85% of all bees) decreased with urbanization, threatening crop pollination. Crop diversity promotes taxonomic and functional diversity of bee communities. Locally, flower resources promote the abundance of all functional groups, and natural vegetation can maintain diverse pollinator communities throughout the year, especially during the noncropping season. However, exotic plants decrease functional diversity and bee specialization. To safeguard bees and their pollination services in urban farms, we recommend (1) preserving seminatural vegetation (hedges) around cropping fields to provide nesting opportunities for aboveground nesters, (2) promoting farm-level crop diversification of beneficial crops (e.g., pulses, vegetables, and spices),

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2022 The Authors. *Ecological Applications* published by Wiley Periodicals LLC on behalf of The Ecological Society of America.

(3) maintaining native natural vegetation along field margins, and (4) controlling and removing invasive exotic plants that disrupt native plant–pollinator interactions. Overall, our results suggest that urban agriculture can maintain functionally diverse bee communities and, if managed in a sustainable manner, be used to develop win–win solutions for biodiversity conservation of pollinators and food security in and around cities.

KEYWORDS

alien species, Bangalore, bee diversity, crop diversity, flowering resources, functional diversity, impervious area, India, specialization, urban agroecosystems, urban farming, urbanization

INTRODUCTION

Urbanization poses one of the greatest threats to biodiversity and associated functions and services (Faeth et al., 2011; Piano et al., 2020; Wagner et al., 2021). It represents one of the most severe and persistent forms of land-use change and is associated with other stressors for biological communities, such as urban warming, pollution, or invasive species (Grimm et al., 2008). Already 4.2 billion people—more than half of the world’s population—are considered urban dwellers, and current projections predict that 2.5 billion will be added to this number by 2050, with 90% of this increase taking place in Asia and Africa (United Nations, 2018). Urban agriculture has recently received a growing interest and is already playing a major role for food security (Cabannes & Pasquini, 2008; Orsini et al., 2013; Thebo et al., 2014; Zezza & Tasciotti, 2010). On the other hand, expanding cities in the Global South—where most of the ongoing and projected future urbanization hotspots are located—increasingly compete for fertile agricultural lands, threatening food security (Gu et al., 2019; van Vliet et al., 2017). A major challenge is how to feed the urban population in a sustainable manner (Armanda et al., 2019).

One third of global crops depend on animal pollination (mostly bees; Klein et al., 2007), and this dependency is increasing (Aizen et al., 2019), especially in countries from the Global South (e.g., China, India) where pollination benefits are the highest (Potts et al., 2016). In addition, bee pollination improves crop quality and commercial value (Bartomeus et al., 2014; Klatt et al., 2013), and functional diversity of bee pollinators increases crop yield (Hoehn et al., 2008; Martins et al., 2015). However, pollinators are declining globally, and the causes are multiple, ranging from land-use change and intensification and loss of flowering resources and nesting sites to pathogens and invasive plant species (Potts et al., 2010, 2016). It is therefore essential to understand how urbanization is driving pollinator communities in urban agricultural systems to safeguard their biodiversity and associated ecosystem services.

A recent review showed contrasting responses of pollinators to urbanization, depending on the type of urban transformation (i.e., urban sprawl vs. urban densification) and the baselines used for comparison (i.e., intensive agriculture vs. natural habitats; Wenzel et al., 2020). Some studies found that urban areas could be hotspots for bees (Baldock et al., 2015; Theodorou et al., 2020), but others found that they contributed to their decline (Bates et al., 2011; Geslin, Le Féon, et al., 2016; Pereira et al., 2021). Within urban areas, bee communities are affected by different biotic and abiotic drivers, such as urban warming and pollution (Hamblin et al., 2018) and other environmental factors ranging from local to landscape scales (Birdshire et al., 2020). Within their local habitats, flower cover and floral richness enhance their diversity (Bates et al., 2011; Hülsmann et al., 2015; Theodorou et al., 2017). Exotic plants (e.g., introduced, ornamental, or invasive) are not necessarily less attractive to pollinators than native species (Garbuzov et al., 2015). However, they can disfavor specialized bee species and increase the dominance of generalists (Banaszak-Cibicka & Żmihorski, 2012; Grass et al., 2013). In addition, exotic plants can also negatively affect the functional diversity of pollinators (Grass et al., 2014). Urban gardens, urban parks, and seminatural areas promote bees’ richness in the wider landscapes (Lanner et al., 2020; Marín et al., 2020), whereas their responses to impervious area (e.g., sealed surface, such as buildings) are guild specific (Geslin, Le Féon, et al., 2016; Wilson & Jamieson, 2019) and largely depend on their functional traits (Buchholz & Egerer, 2020). For instance, cavity-nesting bees occur in high density in urban areas where they can nest in buildings and constructions (Fortel et al., 2014; Pardee & Philpott, 2014). By contrast, urbanization often reduces the availability of habitats for ground-nesting bees (Banaszak-Cibicka & Żmihorski, 2012; Hinners et al., 2012). In addition, social and larger bees may also perform better in cities because they can travel longer distances between nesting and foraging habitats in these fragmented landscapes (Crowther et al., 2014). Other

studies found the opposite and argued that the food resources provided by the small habitat patches in the urban matrix are not sufficient to sustain large bees (Banaszak-Cibicka et al., 2018; Banaszak-Cibicka & Żmihorski, 2012). Yet, despite the recent growing interest in studying pollinators in urban ecosystems (Silva et al., 2021), studies investigating bee functional traits and functional diversity are still scarce, making conservation recommendations challenging (Buchholz & Egerer, 2020).

So far, only a few studies on bee communities have been conducted in urban or suburban agricultural systems, despite their major importance for crop pollination (Frankie et al., 2013; Potter & LeBuhn, 2015; Silva et al., 2021; Wenzel et al., 2020). In rural agricultural systems, bees are threatened by intensified farming practices, which often employ detrimental agrochemicals, such as pesticides (e.g., neonicotinoids), and result in landscape simplification (e.g., by expanding monocultures), thereby reducing food availability and nesting opportunities (Potts et al., 2010). Increasing crop and landscape diversity (i.e., landscape compositional heterogeneity) and reducing field sizes (i.e., increasing landscape configurational heterogeneity) can buffer the negative effects of agriculture at the landscape scale (Hass et al., 2018; Sirami et al., 2019). Such complex landscapes provide complementary food resources across the seasons (Grass et al., 2021; Martins et al., 2018; Sutter et al., 2017). Wild flower strips, field margins, or other seminatural habitats, such as hedges, increase flower resources and nesting sites, which further promote bee communities at the local and landscape scales (Beyer et al., 2021; Ganser et al., 2021). The same measures could likely mitigate the potential negative effects of urbanization, thereby enhancing vital pollination services for urban farmers.

However, despite the fact that most urbanization hotspots are located in tropical regions from the Global South, the vast majority of studies are conducted in temperate countries from the Global North (Silva et al., 2021; Wenzel et al., 2020). Furthermore, most of these studies were conducted in urban gardens and urban parks but without considering urban agriculture along urbanization gradients (Wenzel et al., 2020). Finally, urban agriculture in cities from the Global South differs from that of cities located in the Global North. Indeed, though in the Global North urban agriculture comprises residential and community gardens (allotments) or rooftop gardening (Lin et al., 2015), urban agriculture in the Global South often consists of smallholder farms or homestead gardens whose production is sold in local markets or used for self-subsistence, thereby contributing to food security (De Zeeuw et al., 2011; Zezza & Tasciotti, 2010).

In this study, we addressed these research gaps and investigated how urbanization modifies bee communities, functional composition, and functional diversity in

agricultural systems across rural–urban landscapes. To do so, we surveyed bee communities in 36 vegetable-producing farms spread along a continuous urbanization gradient in Bengaluru, an Indian tropical megacity. Keeping the focal habitat constant (i.e., vegetable-producing farms) while varying the landscape context (i.e., urbanization intensity) allowed us to disentangle the true effect of urbanization. Because we expected temporal variations in bee communities, we repeated our surveys every month for a year, thus encompassing three seasons (i.e., dry, monsoon, cropping). We evaluated the following hypotheses. First, bees' responses to urbanization (i.e., amount of gray/impervious surface) are guild specific. We predict positive effects on cavity-nesting, social, and larger bees, whereas ground-nesting and specialized bees are negatively affected. Second, flower resources (i.e., flower cover) and farm-level crop diversity (i.e., crop Shannon diversity) promote wild bee communities, independently of their functional traits. Third, exotic plant species favor generalist over specialist species. Fourth, we hypothesize that urbanization reduces functional diversity (i.e., functional dispersion), thereby acting as an environmental filter.

METHODS

Study area

This study was conducted in Bengaluru (formerly Bangalore), a South Indian megacity located in the state of Karnataka (Figure 1). According to the latest *UN World Urbanization Prospects* (United Nations, 2018), Bengaluru has a population of 12.8 million inhabitants and is considered the second fastest growing city in India after New Delhi. The city is embedded in an ancient agricultural landscape composed of small-scale farms interspersed with seminatural habitats such as forest remnants, bushes and hedges, tree lines, coconut and eucalyptus plantations, permanent fallows, and wetlands. However, the rapid urban expansion, both from the city's edges and around satellite towns and rural villages (i.e., polycentricity, see Steinhübel & von Cramon-Taubadel, 2020), increasingly competes with agricultural and seminatural lands.

Bengaluru is situated on the Deccan Plateau at an elevation of 920 m above sea level and with a moderate tropical climate, with temperatures ranging between 12 and 38°C and annual precipitation of about 800 mm. Additionally, Bengaluru experiences three distinct seasons: a mild and mostly dry winter (October–January, the postmonsoon season), a hot and dry summer (February–May, the dry season), and the monsoon season (June–September). Most farming activities are concentrated during the monsoon (i.e., Kharif crops) and

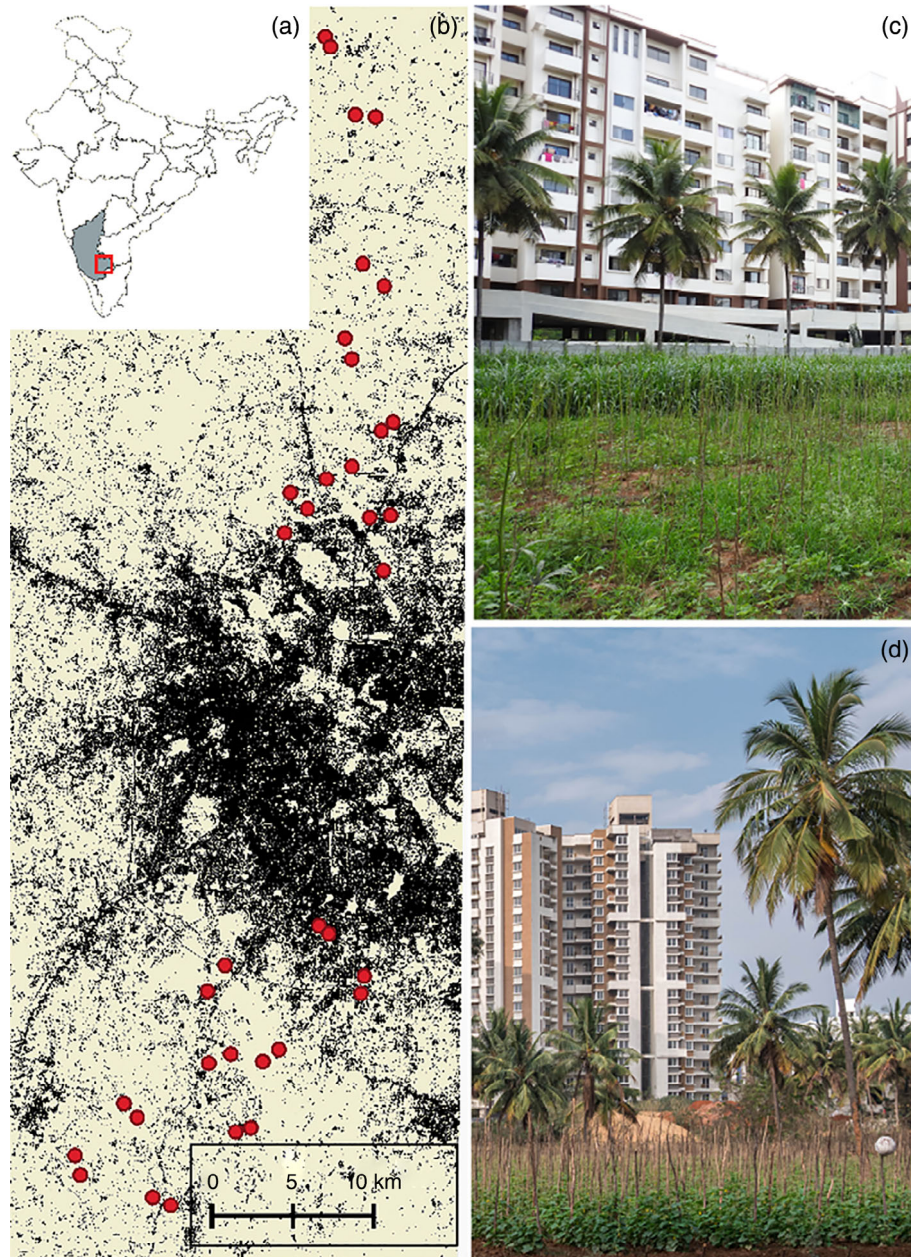


FIGURE 1 Study area. (a) Map of India with Karnataka highlighted in gray and the study region by the red square. (b) Map of study area with study sites (vegetable-producing farms) indicated by red dots. Gray areas (sealed surfaces such as roads and buildings) are displayed in black and nongray areas in beige. Examples of cropping fields from two study farms growing (c) lablab and (d) tomatoes (© Arne Wenzel and Gabriel Marcacci).

the postmonsoon seasons (i.e., Rabi crops). A large proportion of farms are rainfed, partly preventing farming activities during the dry season (summer), with many fields lying fallow.

Study design

We selected 36 vegetable-producing smallholder farms as study sites spread along two transects (18 sites each)

extending from urban Bengaluru toward rural villages, thereby forming a rural–urban gradient north and south of the city (Figure 1). We kept a minimum distance of 1 km between sites to guarantee their independence. All selected farms were of similar size (mean = 1.03, SD = ± 0.54 ha) and had small cropping fields (0.12 ± 0.08 ha). They were all conventionally managed (e.g., using pesticides) and cultivated vegetables, such as lablab, red gram, tomato, egg-plant, cucumber, and chili. They also grew other crops, such as cereals (e.g., ragi or maize), spices (e.g., coriander,

sesame, jasmine), or fodder (e.g., elephant grass). In addition, several of them were also engaged in other farming activities, such as silk (e.g., growing mulberry) or dairy production.

Bee sampling

In each of the 36 sites, we sampled bees along 100×2 -m variable transect walks using sweep nets (Westphal et al., 2008). The transects were subdivided into 10 subunits of 10×2 m. Five subunits were located along seminatural habitats (e.g., field margins, hedges) and five within cropping fields. The number of subunits assigned to each crop or seminatural habitat type was proportional to its relative area within the study site (Scherber et al., 2019). To account for temporal variations in bee communities and cropping patterns, we sampled every site on a monthly basis. We chose variable over standardized transect walks in order to be more flexible with the phenology of cropping fields through the seasons, for example, a flowering field can remain fallow during the next sampling rounds. Nevertheless, the covered area (100×2 m) and the time spent (20 min) within each transect were always the same. We pooled bees sampled in the 10 subunits, and analyses were performed at the transect level. Bees were recorded within 2 min (excluding handling time) in each of the 10 subunits, leading to a total of 20 min per transect (per farm) each month. If possible, sampled species were directly identified in the field or were taken to the laboratory for further identification. A taxonomic expert (K. B. Tharini) confirmed the specimens' identification. Collected specimens are kept in the collections of the Agricultural Entomology department (University of Agricultural Sciences, GKVK, Bangalore, India). The taxonomy of South Indian bees is still under development, and several species could only be identified to the morphospecies level. Although *Apis cerana* Fabricius is managed in South India, bee keeping is uncommon in our study region, and a large proportion of its population is wild (e.g., nesting in termite mounds and hollow trees; see Jasmi et al., 2021). We thus kept this species in the analyses. Additionally, we recorded and identified plant species that were visited by bees. All transect walks were conducted between February 2020 and January 2021 under good weather conditions (no rain, no heavy wind, minimum 18°C) between 9 AM and 3 PM. The order of the visited sites was carefully planned to avoid temporal autocorrelation. Because of the COVID-19 pandemic and the lockdown imposed by the Indian government, fieldwork activities were suspended in April 2020, resulting in 11 sampling rounds in total. In addition, a few sites were not accessible

temporarily owing to local lockdown targeting certain neighborhoods: 18 sites in March 2020 and two sites in May 2020 (leading to $N = 376$). However, because these sites were not spatially aggregated (e.g., only urban sites), this did not cause bias in our analyses (see *Statistical analyses*).

Functional traits

To investigate how urbanization was driving different functional groups and functional composition of bee communities, we focused on four traits (nesting behavior, sociality, specialization, and body size) that are expected to be affected (filtered) by urbanization (Wenzel et al., 2020). To do so, we classified bee species into four nesting types (ground, cavity, parasitic [all kleptoparasite species], and others [e.g., open combs]) and two levels of sociality (social and solitary) based on the literature (Michener, 2007) and expert knowledge (K. B. Tharini). We measured the intertegular distance (ITD) as a proxy for body size (Cariveau et al., 2016; Kendall et al., 2019). These measures were taken on a minimum of one and a maximum of five female specimens per species. Because we did not observe males for several species, we restricted this measurement to female bees, which are the main pollinators. To estimate resource specialization, we followed Ponisio et al. (2016). Specifically, we first built a plants-by-bees matrix, with the number of visits per plant species as matrix values, before computing the standardized specialization d' for each bee species using the bipartite R package (Bluthgen et al., 2006; Dormann, 2011; Dormann et al., 2008). It measures the degree of interaction specialization and ranges from 0 for generalist species to 1 for specialist species. Kleptoparasites were excluded, as well as species that were recorded only once, because they would mistakenly receive the highest d' value of one (i.e., perfect specialist). See Appendix S1: Table S1 for each species' functional traits. We then calculated single-trait (i.e., community-weighted mean [CWM]) and multitrait (i.e., functional dispersion) diversities. The CWM measures the mean trait values weighted by species abundances and reflects which trait value is selected in a given environment. We calculated the CWM for continuous traits, that is, ITD and specialization. The functional dispersion (FDis) measures the mean functional distance of each species from a community to the centroid of all species of this community in a multidimensional functional traits space (Laliberté & Legendre, 2010). FDis is also abundance-weighted and was calculated based on three traits (nesting behavior, sociality, and ITD). We did not include specialization in the calculation of functional dispersion because we could

not calculate it for all species (i.e., kleptoparasites and rare species). Before doing these calculations, we built a species-by-species Gower distance matrix to estimate the functional distances between species, accounting for both categorical (i.e., sociality and nesting behavior) and continuous (i.e., ITD) variables (Gower, 1971). To do so, we used the `gawdis()` function in R, which has the advantage that it gives equal weight to each trait (de Bello et al., 2021). These functional diversity indices were then computed with the `FD` package in R (Laliberté et al., 2015).

Environmental predictors

At the local scale, we recorded the total flower cover (in square centimeters) within each transect. To do so, we measured the size (diameter) of the flower of the five dominant flowering plant species and counted, for each species, the number of opened flowers inside the transect surface (100×2 m), after having completed a transect walk. We further classified each plant species into “crop/cultivated,” “native,” and “exotic” and calculated their respective flower cover (see Inderjit et al., 2018 for exotic plant species). To record the local crop diversity, we mapped all cropping fields within a 100-m radius buffer around the farm centroid every month (Martin et al., 2020). The relative area covered by each crop species at the farm level was used to calculate crop diversity using the Shannon index (`vegan` R package; Oksanen et al., 2020). We also summed the total area covered by all crop species to estimate the cropping area in square meters.

At the landscape scale, we used remote sensed data to calculate the share of gray area in the surroundings of the study sites within various radii. Gray area is often used as a proxy to estimate the effects of urbanization on bees and other taxa (Geslin, Le Féon, et al., 2016; Marcacci et al., 2021; Piano et al., 2020). We produced a land-cover map with a 10-m spatial resolution from cloud-free Sentinel-2 L2A imagery that was acquired in December 2020. A pixel-wise image classification was performed using a deep learning model, a so-called multi-layer perceptron network. Six land-cover classes were distinguished: gray area, trees, grass and shrubs, water bodies, agricultural lands, and barren lands. For this study, we focused on two contrasting land-cover classes, that is, gray area (impervious and sealed surfaces, such as roads, buildings and constructions in general) and nongray area, including all other land-use classes. We calculated the proportional share of gray area (percentage land cover) at different landscape scales, that is, within

circular buffers with varying radii (100, 250, 500, 750, 1000, 1500, and 2000 m).

Statistical analyses

To assess the representativeness of our samples, we calculated sampling completeness using the Chao1 estimator of asymptotic richness (Chao, 1987).

To investigate the effects of local and landscape variables on bee communities, we used generalized linear mixed models (`glmmTMB` package; Brooks et al., 2020). Analyses were performed on data summarized by round across the entire year, that is, at the individual transect-walk level ($N = 376$). The response variables were species richness, total abundance, abundance of social bees, abundance of solitary bees, abundance of cavity-nesting bees, abundance of ground-nesting bees, ITD and specialization CWMs, and functional dispersion. To analyze the response of each of the four social bee species separately, we ran additional models with their respective abundance as response variables. Explanatory (fixed) variables were crop diversity (Shannon index), total flower cover within the transect (cm^2), flower cover of exotic plant species within transect (cm^2), cropping area (ha), share of gray area (%) within varying radii, and season (three levels: winter, summer, monsoon). Since flower cover had a few extreme values, we log-transformed this variables to ensure the normality of the residuals. All explanatory continuous variables were standardized (mean = 0, SD = 1) to improve the convergence of the models. We also checked for potential collinearity between all our environmental predictors with Pearson's correlation tests. Since the total flower cover and the flower cover of exotic plant species were correlated ($|r| > 0.7$), we kept total flower cover in the global model (i.e., model selection) and ran additional analyses only considering the flower cover of exotic plant species. Site IDs (i.e., to account for repetitive rounds of transect walks) were set as random effects (fixed slopes and random intercepts). To account for differences in sampling effort (because of COVID-19 in 20 out of 36 sites we have 10 instead of 11 sampling rounds, see the section *Bee sampling*), we included the $\log(\text{number of rounds per site})$ as an offset in the models, but this caused convergence problems and was removed. However, we repeated the analyses with a balanced subset of the sampling rounds (i.e., 10 sampling rounds), which did not change the results.

Because not all bees have the same foraging range (e.g., solitary vs. social species or large vs. small species; see Gathmann & Tscharrnke, 2002; Greenleaf et al., 2007; Steffan-Dewenter et al., 2002), we selected the best

landscape scale for every response variable prior to fitting the global models (Wilson & Jamieson, 2019). We selected the best landscape scale based on their AIC_c values. When several scales had ΔAIC_c values ≤ 2 , we retained the scale that had the largest effect size (Grass et al., 2018; see Appendix S1: Table S2).

We hence fitted the global models with all our environmental predictors (except flower cover of exotic plant species), including all possible two-way interactions between them. We first selected the best model structure and chose the most appropriate distribution for our response variables based on their diagnostic plots and their AIC_c values. Species richness and functional dispersion were normally distributed and fitted with a Gaussian error distribution. ITD and specialization CWM were first log-transformed to ensure the normality of residuals and then fitted with a Gaussian distribution, too. For abundance response variables, we selected either a Poisson error or a negative binomial distribution when overdispersion was detected. We also added a zero-inflation term when needed to account for an excess of zeros. We then followed a multimodel inference approach where models with the lowest AIC_c (within $\Delta AIC_c \leq 2$) score sorted by the dredge() function from the MuMIn package in R (Barton, 2018) were selected as the most informative models, that is, considered to have similar empirical support (Burnham & Anderson, 2002). Models that contained additional parameters compared with the better-ranked models but that had a higher AIC_c value were excluded as these additional parameters are likely to be uninformative (i.e., they cannot overcome the penalty of two AIC_c units for each additional parameter; see Arnold, 2010; Galipaud et al., 2017). We restricted the number of parameters in the model comparison procedure to a maximum of five variables. We calculated the sum of Akaike weights (Σw_i) of each predictor over the whole set of candidate models in which it appeared. This value informs on the relative (not the absolute) importance of the explanatory variables (Galipaud et al., 2017): The larger the value, the more important is the variable (max = 1 when the variable appears in all candidate models). We only reported Σw_i values for the predictors selected in the models with substantial empirical support within $\Delta AIC_c \leq 2$. We computed the appropriate (i.e., Nakagawa's R^2 for mixed models and zero-inflated R^2 for models with a zero inflation term) marginal (R_m^2) and conditional (R_c^2) R^2 with the performance package in R to assess the goodness of the models' fit (Lüdecke et al., 2021; Nakagawa et al., 2017). To further interpret the results (e.g., positive or negative effects of the most important variables), we averaged (conditional average) the models' coefficients (estimates, SE, z-value) over the sets of best-fitting models (within $\Delta AIC_c \leq 2$) with

the model.avg() function (MuMIn package in R; Barton, 2018).

We used the packages emmeans (Lenth et al., 2021) and effects in R (Fox et al., 2019) to obtain models' predictions, which were plotted with the ggplot2 package in R (Wickham et al., 2021). All plots were based on the best models' predictions, unless otherwise specified. All models' assumptions were checked and validated with the performance (Lüdecke et al., 2021) and DHARMA R packages (Hartig, 2021). All analyzes were conducted in R version 4.0.1 (R Core Team, 2020).

RESULTS

We recorded 26,627 bees belonging to three families (Apidae, Megachilidae, and Halictidae) that were identified to 40 species or morphospecies (Appendix S1: Table S1). This number of species is similar to that of other studies conducted in Asian tropical cities (e.g., Stewart et al., 2018; Tangtorwongsakul et al., 2018). The five most abundant species were *Apis florea* Fabricius (13 941), *Apis cerana* (5462), *Amegilla* (*Zonamegilla*) spp. (2097), *Apis dorsata* Fabricius (1725), and *Tetragonula* spp. (1431). Social bees (*A. florea*, *A. cerana*, *A. dorsata*, and *Tetragonula* spp.) were largely dominant and made up 84.7% of all sampled individuals. On average, we recorded 70.6 ± 64.7 (mean \pm SD) bees of 4.6 ± 2 species per individual transect-walk. Chao1 species estimation (Chao, 1987) indicated that we sampled 78.4% of the regional bee richness.

Effects of urbanization on species richness and overall abundance

Gray area positively influenced bee richness (model-averaged coefficients: estimate = 0.33, SE = 0.14, z = 2.44; Figure 2b) and had a relatively high importance ($\Sigma w_i = 0.78$; only one best-fitting model; see Table 1). The share of gray area within a 250-m radius provided the best model fit (lowest AIC_c ; Appendix S1: Table S2) and was considered the best landscape scale on which to examine the effects of urbanization on species richness. Conversely, overall bee abundance slightly decreased with urbanization (estimate = -0.04, SE = 0.05, z = 0.81; Figure 2e), with gray area being moderately important ($\Sigma w_i = 0.49$) and included in two out of the four best-fitting models (Table 1). The best landscape scale to which overall bee abundance responded was 1000 m, highlighting the fact that urbanization affected bee communities up to large spatial scales (Appendix S1: Table S2).

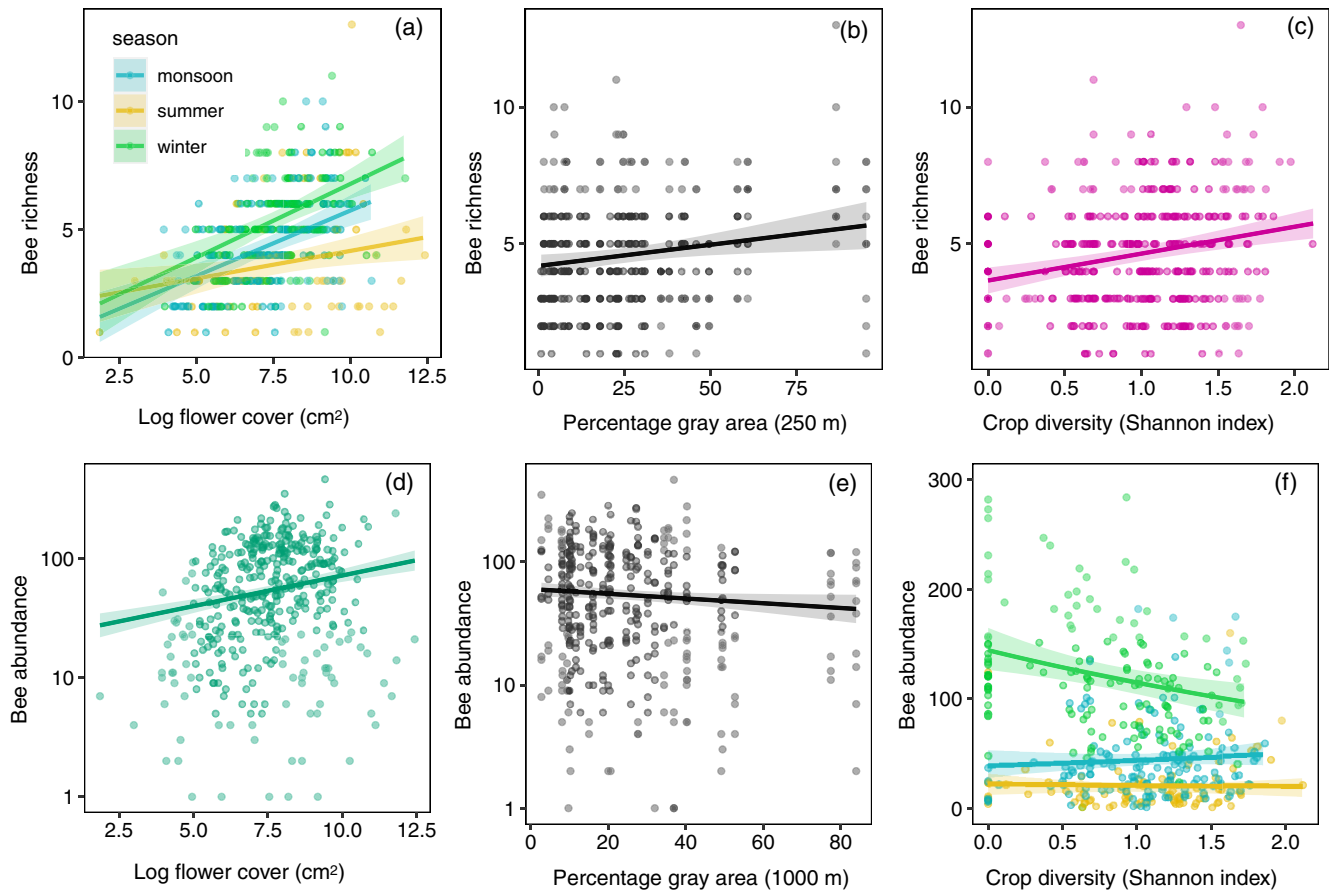


FIGURE 2 Species richness and overall abundance of bees. Effects of (a) flower cover (interactive effect with season), (b) gray area (%) within a radius of 250 m around the study farm, and (c) crop diversity on bee richness. Effects of (d) flower cover, (e) gray area (1000 m), and (f) crop diversity (interactive effect with season) on overall bee abundance. The lines depict the predicted mean values, the different colored belts the 95% confidence intervals, and the dots the raw data. The y-axes for panels (d) and (e) were log-transformed for graphical reasons.

Functional responses to urbanization

The abundance of solitary (estimate = 0.17, SE = 0.08, $z = 2.12$), cavity-nesting (estimate = 0.31, SE = 0.11, $z = 2.86$) and, surprisingly, ground-nesting (estimate = 0.10, SE = 0.08, $z = 1.27$) bees was positively affected by urbanization (Figure 3). For these three functional groups, gray area was found in all best-fitting models (except for ground-nesting bees, where it was included in four out of five best-fitting models; Table 1) and had a high importance ($\Sigma w_i = 0.95$; $\Sigma w_i = 0.90$; $\Sigma w_i = 0.77$, respectively). However, gray area had an unexpected negative influence on social bees' abundance (estimate = -0.17 , SE = 0.04, $z = 3.98$; Figure 3a) and was included in all models ($\Sigma w_i = 1.00$). Solitary and ground-nesting bees best responded to urbanization at 500 m and cavity-nesting bees at 750 m, whereas social bees were affected at larger spatial scales up to 2000 m (Appendix S1: Table S2). Among the four social bee species (which represented 85% of all bees in our study),

A. florea (estimate = -0.28 , SE = 0.06, $z = -4.05$) and *A. cerana* (estimate = -0.19 , SE = 0.05, $z = -3.63$) declined with urbanization, *A. dorsata* was not affected (estimate = 0.08, SE = 0.11, $z = 0.71$), and stingless bees (*Tetragonula* spp.) were positively affected (estimate = 0.25, SE = 0.16, $z = 1.57$; Appendix S1: Figure S7). *A. florea* was the most abundant of all bees and largely drove the observed decline of social bees and total bee abundance along the urbanization gradient.

Against our expectations, gray area also had positive effects on functional dispersion (estimate = 0.03, SE = 0.01, $z = 2.42$; Figure 3e) and interaction specialization of bees (d') (estimate = 0.05, SE = 0.02, $z = 2.47$; Figure 3c), it was included in all best-fitting models (Table 1) and had a high importance ($\Sigma w_i = 0.98$ and $\Sigma w_i = 1.00$, respectively). The best landscape scale for both these variables was 750 m (Appendix S1: Table S2). For ITD CWM (proxy for body size, best model fit at 2000 m; Appendix S1: Table S2), the model selection revealed an important interaction ($\Sigma w_i = 0.83$) between

TABLE 1 Best-fitting models (within $\Delta AIC_c \leq 2$) for all response variables. Marginal (R_m^2) and conditional (R_c^2) R^2 measure the goodness of the model fit.

Response variable	Model	df	AIC _c	ΔAIC _c	Akaike weight	Explanatory variables	R _c ²	R _m ²
Species richness	R1	11	1428.70	0.00	0.61	CD + G + FC:S	0.40	0.31
Abundance	A1	10	3488.19	0.00	0.22	CD:S + G + FC	0.72	0.67
	A2	11	3488.30	0.12	0.20	CD:S + FC:S	0.72	0.67
	A3	9	3489.43	1.24	0.11	CD:S + FC	0.72	0.66
	A4	10	3489.47	1.28	0.11	CD + G + FC:S	0.72	0.67
Abundance of social bees	S1	11	3367.48	0.00	0.30	CD:S + G + FC	0.70	0.67
	S2	9	3367.72	0.24	0.26	CD + G + FC + S	0.70	0.66
Abundance of solitary bees	Sy1	9	2354.51	0.00	0.18	G:S + FC:S	0.52	0.34
	Sy2	10	2354.58	0.07	0.17	CD + G + FC:S	0.55	0.39
	Sy3	10	2354.61	0.11	0.17	CD + G:S + FC	0.53	0.37
	Sy4	11	2355.10	0.59	0.13	G:S + FC:S	0.53	0.34
	Sy5	10	2356.43	1.93	0.07	G:S + G:FC	0.53	0.36
Abundance of cavity-nesting bees	C1	11	1494.25	0.00	0.53	CD + G + FC:S	0.34	0.19
Abundance of ground-nesting bees	G1	7	2112.11	0.00	0.22	G + FC + S	0.83	0.56
	G2	9	2112.44	0.33	0.19	G:S + FC	0.83	0.56
	G3	6	2112.81	0.71	0.15	FC + S	0.83	0.55
	G4	9	2113.47	1.36	0.11	G + FC:S	0.83	0.55
	G5	8	2113.95	1.84	0.08	G:FC + S	0.83	0.56
CWM ITD	ITD1	8	-252.94	0.00	0.31	CD:G + G:FC	0.14	0.10
	ITD2	6	-253.50	0.44	0.25	CD:G	0.13	0.08
CWM specialization	special1	7	-105.18	0.00	0.29	G + FC + S	0.23	0.14
	special2	8	-105.17	0.01	0.29	G:FC + S	0.24	0.15
	special3	9	-103.99	1.20	0.16	G:S + FC	0.24	0.15
	special4	10	-103.19	2.00	0.11	G:FC + G:S	0.24	0.15
Functional dispersion	FDis1	10	-597.24	0.00	0.29	CD + G:S + FC	0.30	0.18
	FDis2	8	-596.24	1.00	0.18	CD + G + FC + S	0.29	0.17
	FDis3	10	-595.34	1.91	0.11	CD + G + FC:S	0.29	0.17
	FDis4	9	-617.57	1.12	0.11	CD:G + FC + S	0.28	0.17

Abbreviations: CD, farm-level crop diversity (Shannon index); CWM, community-weighted mean; FC, log local flower cover (cm²); FD, functional dispersion; G, gray area (%); ITD, intertegular distance (proxy for body size); S, season (monsoon, summer, winter).

gray area and crop diversity (estimate = 0.2, SE = 0.01, z = 2.58), meaning that larger bees were found in farms with higher crop diversity, especially when the amount of gray area was high (Figure 3d).

Effects of crop diversity and flower cover on bee communities

As expected, crop diversity positively influenced bee richness (estimate = 0.49, SE = 0.11, z = 4.63; Figure 2c), the abundance of solitary (estimate = 0.08, SE = 0.05, z = 1.65; Appendix S1: Figure S2c) and cavity-nesting bees (estimate = 0.25, SE = 0.09, z = 2.86; Appendix S1: Figure S3c), and functional dispersion (estimate = 0.02, SE = 0.01,

z = 3.17; Appendix S1: Figure S6c). However, it had a negative effect on social bees' abundance (estimate = -0.06, SE = 0.07, z = 0.86; Appendix S1: Figure S1c). In fact, crop diversity was included in most of the best-fitting models and usually had a high importance (Tables 1 and 2). The model selection further revealed an interaction of moderate importance ($\Sigma w_i = 0.59$) between crop diversity and season for total bee abundance: Crop diversity had no effect on total bee abundance in the monsoon season and summer, whereas it had a negative effect in winter (Figure 2e).

As expected, flower cover had positive effects on total bee richness and total bee abundance (Appendix S1: Table S3; Figure 2), as well as on the abundance of all functional groups and functional dispersion (Appendix S1:

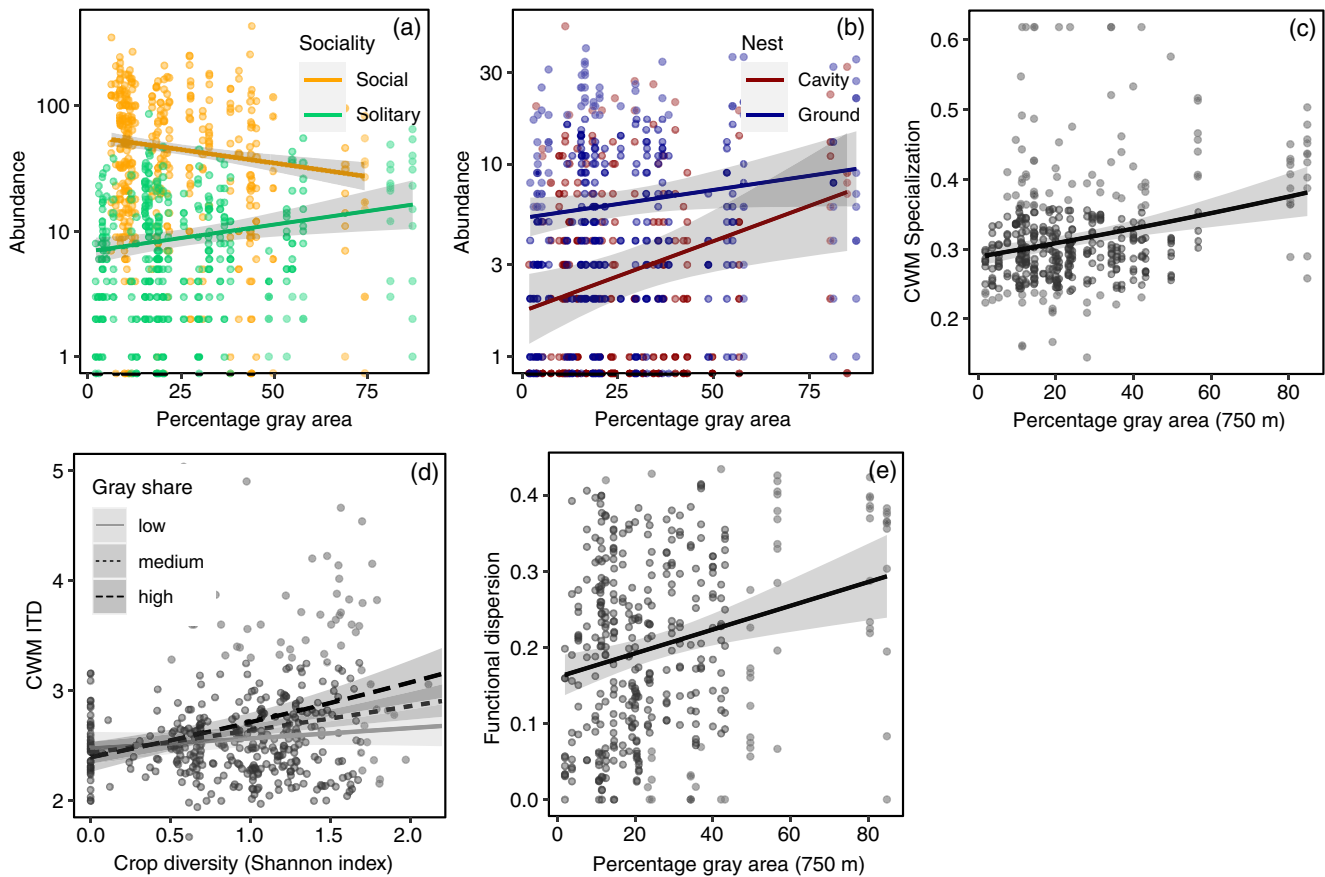


FIGURE 3 Functional responses to urbanization. Effects of (a) gray area on abundance of social (2000 m radius) and solitary (500 m) bees, (b) cavity-nesting (750 m) and ground-nesting (500 m) bees, (c) community-weighted mean (CWM) interaction specialization d' (0 = generalists, 1 = specialists), (d) intertegular distance (ITD) (proxy for body size) CWM (interactive effect with gray area), and (e) functional dispersion. The lines depict the predicted mean values, the gray belts the 95% confidence intervals, and the dots the raw data. For panels (a) and (b) the y-axes were log-transformed for graphical reasons. Note that for the abundance of social and solitary bees, ITD CWM and functional dispersion, the predictions were drawn from the second-best-fitting models (S2, Sy2, ITD2, and FDis2; see Table 1). Note that for social bee abundance, the line and gray belt stop before that of solitary bee abundance because we only plotted predicted values within the range of our recorded variables, that is, no social bees were recorded beyond 75% of gray area within a radius of 2000 m.

Table S3 and Figures S1–S6). It appeared in almost all best-fitting models and had a high importance for all response variables (Tables 1 and 2). The model selection revealed important interactions between season and flower cover for total bee richness ($\Sigma w_i = 0.81$; Figure 2a) and cavity-nesting bees' abundance ($\Sigma w_i = 0.67$; Appendix S1: Figure S3a): the positive effects of flower cover were more pronounced during the cropping seasons (i.e., winter, followed by monsoon) than during the dry season (i.e., summer).

However, the flower cover of exotic plant species had negative effects on cavity-nesting bees' abundance (estimate = -0.11 , SE = 0.08, $z = -1.38$), CWM of specialization of bees (estimate = -0.04 , SE = 0.01, $z = -3.12$; Figure 4a), and functional dispersion (estimate = -0.02 , SE = 0.01, $z = -2.74$; Figure 4b), suggesting that exotic plants promoted generalist species and reduced functional diversity.

Seasonal variations

Season was found in the best-fitting models for all response variables (except ITD CWM; Table 1) and always had the highest importance value of 1.00, that is, it was included in all candidate models. Bee richness, total bee abundance, and the abundance of all functional groups were higher in the cropping seasons (i.e., winter, followed by monsoon) than in the dry season (i.e., summer). The CWM of interaction specialization of bees was higher in summer, followed by monsoon and winter (Appendix S1: Figure S5), and functional dispersion was higher in the monsoon season, followed by summer and winter (Appendix S1: Figure S6). These seasonal differences may reflect fluctuations in the availability of floral resources related to climate (i.e., monsoon) and cropping patterns.

TABLE 2 Relative importance Σwi (sum of Akaike weights) of explanatory variables across all candidate models. Only variables and their two-way interactions that were included in the best-fitting models (within $\Delta AIC_c < 2$) are shown.

Response variable	CD	G	FC	FS	S	CD:S	CD:G	CD:FS	FC:S	G:S	CD:FC	G:FC
Species richness	1.00	0.78	1.00	...	1.00	0.81
Total abundance	0.94	0.49	1.00	...	1.00	0.59	0.45
Social bee abundance	1.00	1.00	1.00	...	1.00	0.3
Solitary bee abundance	0.5	0.95	1.00	...	1.00	0.42	0.55	...	0.11
Cavity-nesting bees abundance	0.89	0.9	1.00	...	1.00	0.67
Ground-nesting bees abundance	...	0.77	1.00	...	1.00	0.29	0.32	...	0.19
CWM ITD	1.00	0.96	0.59	0.83	0.37
CWM specialization	...	1.00	0.94	...	1.00	0.31	...	0.43
Functional dispersion	0.98	0.98	0.95	...	1.00	0.11	0.17	...	0.12	0.33	0.14	...

Abbreviations: CD, farm-level crop diversity (Shannon index); CWM, community-weighted mean; FC, log local flower cover (cm²); FD, functional dispersion; G, gray area (%); ITD, intertegular distance; S, seasons (monsoon, summer, winter).

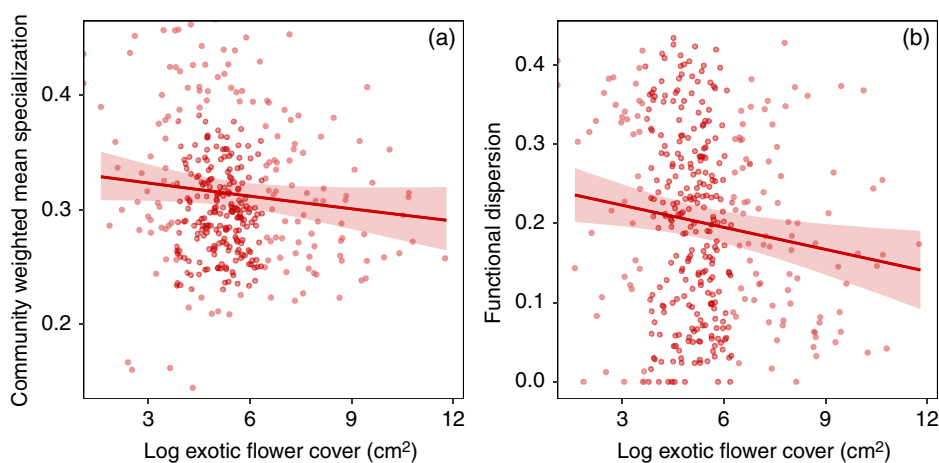


FIGURE 4 Effects of flower cover of exotic plants on (a) community-weighted mean (CWM) interaction specialization d' and (b) functional dispersion. The lines depict the predicted mean values, the belts the 95% confidence intervals, and the dots the raw data.

DISCUSSION

We studied the functional responses of farmland bees to urbanization across rural–urban agricultural landscapes in Bengaluru, a rapidly growing megacity in South India. We found that bees’ functional responses to urbanization were trait specific. Most functional groups (i.e., cavity nesters, ground nesters, solitary bees, larger bees, specialists) benefited from an increase in gray area at the landscape scale, whereas social bees (85% of all bees) exhibited a negative response, threatening crop pollination. Farm-level crop diversity enhanced the taxonomic and functional diversity of bee communities and the abundance of cavity-nesting, solitary, and larger bees. This enhancement was presumably due to increasing floral resource complementarity and diversity, especially in highly urbanized areas, where the distances between

foraging patches are expected to be higher. Increasing flower cover of both cultivated plants and native weeds promoted bees at the local scale and could, thus, help to maintain pollinator communities across the seasons, that is, native weeds filling food gaps during the noncropping season. However, the flower cover of exotic plants had strong negative effects on certain functional groups (e.g., cavity nesters), functional diversity (function dispersion), and interaction specialization.

Bees’ responses to urbanization were largely trait specific, as already demonstrated (Banaszak-Cibicka & Zmihorski, 2012; Buchholz & Egerer, 2020; Wenzel et al., 2020; Wilson & Jamieson, 2019), and not all functional groups were affected at the same landscape scale (Steffan-Dewenter et al., 2002; Wilson & Jamieson, 2019). Gray area had a positive effect on species richness, presumably driven by solitary cavity-nesting bees such as

Megachile spp. or *Xylocopa* spp., which benefited from buildings and constructions providing nesting habitats (Banaszak-Cibicka & Żmihorski, 2012; Cohen et al., 2022; Fortel et al., 2014; see Figures 2b and 3). Carpenter bees (*Xylocopa* spp.) were particularly abundant in urban areas and have already been identified as one of the main pollinators of lablab (*Lablab purpureus*), a very popular pulse crop in South India (Wenzel et al., 2022). These large bees, which have greater foraging range (Greenleaf et al., 2007), could travel longer distances between foraging patches scattered within the urban matrix (Crowther et al., 2014; Kremen et al., 2007). They can therefore benefit from urbanization provided enough floral resources are supplemented (Fortel et al., 2014). Indeed, Hamblin et al. (2018) demonstrated that abundant floral resources promoted large bees (more than small bees) in dense urban environments as they can fly longer distances in fragmented landscapes and concentrate in highly rewarding flowering patches, such as mass-flowering crops (e.g., lablab) (Beyer et al., 2021; Zaninotto et al., 2021).

Against our expectations, ground-nesting bees were slightly positively affected by an increase in gray area (Figure 3b), which contrasts with most studies assessing the effects of urbanization on ground nesters (e.g., Banaszak-Cibicka & Żmihorski, 2012; Hinnens et al., 2012). However, these studies usually come from temperate regions, where bare soil is often replaced by sealed surfaces and intensively managed lawns, offering less suitable habitats for ground nesters in urban areas. By contrast, cities from the Global South have proportionally less impervious surfaces, and small areas of bare soil are still widely available due to unsealed surfaces besides the roads and around buildings and constructions, mostly in less developed neighborhoods (Guenat et al., 2019; Wenzel et al., 2022).

Our results indicate that urban areas in Bengaluru offered sufficient nesting habitats (i.e., bare soil and cavities) for different functional groups. Furthermore, urban areas generally have high availability and diversity of floral resources in gardens and parks (e.g., including horticultural flowering plants; Banaszak-Cibicka et al., 2018; Geslin, Oddie, et al., 2016). This could increase niche space availability (e.g., types of flowering resources, phenological diversity of flowering plants; see Prendergast et al., 2022; Tew et al., 2022) and, contrary to our expectations, result in higher functional diversity in these landscapes (Figure 3e).

However, unlike most studies conducted in temperate cities, social bees were negatively affected by urbanization (Figure 3a; but see Wilson & Jamieson, 2019, who also found a decline of social bees with urbanization in three cities of the US state of Michigan). Social bees are usually considered to be “winners” of urbanization as they perform better in cities due to their greater behavioral

and ecological flexibility (Banaszak-Cibicka & Żmihorski, 2012; Bennett & Lovell, 2019). In our study area, we recorded four social bee species: the Indian honey bee (*A. cerana*), the red dwarf honey bee (*A. florea*), the giant honey bee (*A. dorsata*), and stingless bees (*Tetragonula* spp.). Among these four species, *A. florea* (and, to a lesser extent, *A. cerana*) strongly declined with increasing gray area (Appendix S1: Figure S7), thereby explaining the overall negative response of social bees. *A. florea* typically builds its open comb in small trees or bushy vegetation (e.g., hedges), which may be lacking in urban areas, where most of the remaining vegetation consist in large old trees or tree galleries (e.g., in parks or along streets) offering fewer nesting opportunities. Conversely, stingless bees (*Tetragonula* spp.) nest in human infrastructures (e.g., crevices in a wall) and, thus, benefited from urbanization (Appendix S1: Figure S7; see Rahman et al., 2015).

These four social species were largely dominant and made up for 85% of all bees recorded. Other studies conducted in Asian tropical cities (e.g., in Thailand) also reported a strong dominance of social bees in their study area (Stewart et al., 2018; Tangtorwongsakul et al., 2018: 90% and 93% respectively, with *A. florea* alone representing 80% of all individuals for the latter). Consequently, social bees drove the observed patterns regarding interaction specialization and total bee abundance in our study. Contrary to our predictions, social and polylectic bee species, which exploit many different floral resources (i.e., generalists), declined in urban areas while the proportion of specialized bee species in the communities (e.g., solitary bees that were promoted by urbanization) increased with gray area (Figure 3a). In addition, the decline of social bees with urbanization reduced overall bee abundance (Figure 2e). This result is particularly worrying since gray area affected social bees at large spatial scales (up to 2000 m). In the tropics, social bees, such as wild honey bees (*Apis* spp.) and stingless bees (*Tetragonula* spp.), form large colonies (compared to bumblebees, which are characterized by much smaller colonies in temperate regions) and are essential for crop pollination (Mukherjee et al., 2019). The rapid urban expansion of Bengaluru (e.g., built-up area increases of 176% between 1991 and 2018 in our north transect; Nautiyal et al., 2020) poses a major threat to crop pollination in urban agricultural systems because it is swallowing up the surrounding agricultural landscapes, with negative consequences on bee abundance. The promotion of beneficial seminatural habitats that provide nesting opportunities for social bee species (e.g., *A. florea*), such as structurally rich hedges around cropping fields, should be fostered to conserve pollinator communities and safeguard crop pollination in urban farms at the landscape scale (Beyer et al., 2020; Ganser et al., 2021; Klein et al., 2012).

Furthermore, it is critical to devise management practices that enhance pollinators also at the local scale. We found that farm-level crop diversity had positive effects on the taxonomic and functional diversity of bee communities (Figure 2c and Appendix S1: Figure S6c). Increasing crop diversity in urban farms, just as in rural agricultural landscapes, may, hence, offer more diverse floral resources within a foraging patch that are required by species-rich and diverse bee assemblages (Raderschall et al., 2021). It has already been shown that diversified farms diminished bees' reliance on the surrounding landscapes (Kennedy et al., 2013). In addition, higher crop diversity enhances complementarity in key floral resources, which can foster both rare and common wild bee species (Sutter et al., 2017) and prevent gaps in food resource across seasons (Mallinger et al., 2016; Martins et al., 2018). However, crop diversity can also reduce bee abundance when intensively managed crops are favored over crops that provide more food (e.g., pulse crops, vegetables, aromatic crops and spices; see Hass et al., 2018). In our study region, many farmers give up vegetable farming for cash crops that yield higher income, such as mulberry for silk production or turf grass dedicated to large estates' lawns (personal observations). These practices may threaten regional pollinator communities in the future.

Not only the diversity but also the abundance of floral resources is essential to support bee communities. Overall bee abundance increased locally with increasing flower cover (Figure 2d), emphasizing the importance of floral resources both within cropping fields and in surrounding seminatural habitats (e.g., field margins, hedges) in urban environments. This has already been demonstrated in urban green areas, such as parks and gardens, both in temperate and tropical cities (Pardee & Philpott, 2014; Stewart et al., 2018; Wilson & Jamieson, 2019). However, in the tropics, unlike temperate regions, bees remain active year round (Stewart & Waitayachart, 2020), although we recorded some extent of seasonal variability due to fluctuations in food resources related to climatic events (e.g., monsoon, dry season) and cropping patterns. Thus, a constant provision of food resources is necessary. During the cropping seasons, some species (e.g., *Megachile* spp., *Xylocopa* spp.) relied more on flowering crops, such as pulses (e.g., lablab or red gram; see Wenzel et al., 2022), than on natural vegetation. Nevertheless, natural weeds within and around cropping fields are essential to maintain bee communities throughout the year and to fill the food gap during the noncropping season (i.e., dry summer). Both native and nonnative flowering plants (e.g., ornamental plants and weeds) can promote pollinators in cities (Frankie et al., 2013; Larson et al., 2014; Lowenstein et al., 2019). In the context of urban agriculture, planting

or promoting attractive flowering plants around cropping fields (e.g., field margins, wildflower strips) may benefit both pollinator communities and crop yield, just as in rural agricultural landscapes (Albrecht et al., 2020; Beyer et al., 2020; Ganser et al., 2021).

Urban areas are known to harbor more exotic plants than natural habitats, which either have an ornamental use or were introduced and dispersed better in highly disturbed anthropogenic environments (Skultety & Matthews, 2017). Exotic plants can be highly attractive to urban pollinators (Garbuzov et al., 2015) and allow them to extend their flight period later in the year in temperate cities (Staab et al., 2020; Stelzer et al., 2010). However, they may have effects that are more negative in tropical cities where plant–pollinator networks are more stable through the year (Stewart & Waitayachart, 2020). In our study, we found that functional dispersion and interaction specialization (d') decreased with increasing exotic plant cover (Figure 4). This indicates that exotic plants favor mainly generalist bees, filtering out specialists and, thus, leading to a loss of functional diversity (Grass et al., 2013, 2014). Moreover, the two most common and dominant species among the exotic plants we recorded were *Lantana camara* and *Parthenium hysterophorus*, both listed in the top 100 of the worst invasive species of IUCN and are a serious threat to ecosystem integrity in India (Kohli et al., 2006; Usharani & Raju, 2018). *Lantana camara* was mostly visited by *Amegilla* spp. and *P. hysterophorus* by *A. florea*. As these two invasive plant species expand rapidly across rural–urban landscapes competing with native and cultivated plants, they represent a major threat to bees and pollinators by disrupting native plant–pollinator interactions (Ojija et al., 2019), also in crops.

CONCLUSION

Pollinators showed contrasting and inconsistent responses to urbanization across studies in temperate regions, and our work provides important and novel insights in an understudied part of the world. Consistent with temperate regions, bees' responses to urbanization were trait specific in our study, highlighting the importance of considering functional traits in urban ecology. However, in the tropics, urban areas seem to offer sufficient nesting opportunities for different functional groups (e.g., bare soil and cavities) and can promote taxonomic and functional diversity of bee communities. Nevertheless, we did not quantify other disturbances associated with urban areas (e.g., removal of seminatural vegetation) that may cause the decline of certain social bees (e.g., *A. florea*) and therewith could threaten crop pollination services.

Thus, to conserve diverse bee communities and enhance crop pollination services in urban agricultural systems, we recommend preserving seminatural vegetation (e.g., hedges) around cropping fields to provide nesting opportunities for aboveground nesters such as wild honey bees. In addition, farm-level crop diversification, such as the cultivation of beneficial crops, including pulses (e.g., lablab, red gram), vegetables (e.g., cucurbitaceous, tomatoes), and spices (e.g., coriander, jasmine), should be encouraged and cash crop monocultures (e.g., mulberry, turf grass) avoided. We further suggest maintaining native natural vegetation along field margins and hedges, especially during the noncropping season (i.e., dry season in summer) to support diverse pollinator communities throughout the year. However, actions need to be taken to systematically control and remove invasive plant species, which reduced interaction specialization and functional diversity, to conserve ecosystem integrity and safeguard crucial ecosystem services upon which smallholders depend.

In conclusion, our study suggests that urban agriculture in tropical regions can support functionally diverse bee communities across the entire year even in a rapidly growing megacity and, if managed in a sustainable manner, be used to develop win–win solutions for biodiversity conservation of pollinators and food security in and around cities.

ACKNOWLEDGMENTS

This study was performed within the Research Unit FOR2432: Social-Ecological Systems in the Indian Rural–Urban Interface: Functions, Scales, and Dynamics of Transition (<https://www.uni-kassel.de/fb11agrар/fachgebiete/-einrichtungen/opats/for2432-1>). We thank Stefan von Cramon-Taubadel, Andreas Bürkert, and Ellen Hoffmann for their coordination efforts and acknowledge the help from our Indian partners. We are grateful for the collaboration with the local farmers who allowed us to conduct this study on their farms, as well as K.T. Vijayakumar for his logistical support. We thank Arne Wenzel for his advice and Matthias Spangenberg for his help with the production of the land-cover maps and his advice for the study design. We are thankful that the Research Unit FOR2432 is funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation), Project 289781364. Catrin Westphal is grateful for funding by the DFG Projects 405945293 and 493487387. Finally, we are grateful to Claudio Gratton and the anonymous reviewers for their valuable suggestions that helped to improve the manuscript. Open Access funding enabled and organized by Projekt DEAL.


CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Marcacci et al., 2022) are available in Dryad at <https://doi.org/10.5061/dryad.sqv9s4n67>.

ORCID

Gabriel Marcacci  <https://orcid.org/0000-0002-2199-0141>

Ingo Grass  <https://orcid.org/0000-0001-7788-1940>

Teja Tscharnitke  <https://orcid.org/0000-0002-4482-3178>

Catrin Westphal  <https://orcid.org/0000-0002-2615-1339>

REFERENCES

- Aizen, M. A., S. Aguiar, J. C. Biesmeijer, L. A. Garibaldi, D. W. Inouye, C. Jung, D. J. Martins, et al. 2019. “Global Agricultural Productivity Is Threatened by Increasing Pollinator Dependence without a Parallel Increase in Crop Diversification.” *Global Change Biology* 25: 3516–27.
- Albrecht, M., D. Kleijn, N. M. Williams, M. Tschumi, B. R. Blaauw, R. Bommarco, A. J. Campbell, et al. 2020. “The Effectiveness of Flower Strips and Hedgerows on Pest Control, Pollination Services and Crop Yield: A Quantitative Synthesis.” *Ecology Letters* 23: 1488–98.
- Armanda, D. T., J. B. Guinée, and A. Tukker. 2019. “The Second Green Revolution: Innovative Urban Agriculture’s Contribution to Food Security and Sustainability – A Review.” *Global Food Security* 22: 13–24.
- Arnold, T. W. 2010. “Uninformative Parameters and Model Selection Using Akaike’s Information Criterion.” *Journal of Wildlife Management* 74: 1175–8.
- Baldock, K. C. R., M. A. Goddard, D. M. Hicks, W. E. Kunin, N. Mitschunas, L. M. Osgathorpe, S. G. Potts, et al. 2015. “Where Is the UK’s Pollinator Biodiversity? The Importance of Urban Areas for Flower-Visiting Insects.” *Proceedings of the Royal Society B: Biological Sciences* 282: 20142849.
- Banaszak-Cibicka, W., L. Twerd, M. Fliszkiwicz, K. Giejdasz, and A. Langowska. 2018. “City Parks vs. Natural Areas - Is it Possible to Preserve a Natural Level of Bee Richness and Abundance in a City Park?” *Urban Ecosystem* 21: 599–613.
- Banaszak-Cibicka, W., and M. Żmihorski. 2012. “Wild Bees along an Urban Gradient: Winners and Losers.” *Journal of Insect Conservation* 16: 331–43.
- Bartomeus, I., S. G. Potts, I. Steffan-Dewenter, B. E. Vaissière, M. Woyciechowski, K. M. Krewenka, T. Tscheulin, et al. 2014. “Contribution of Insect Pollinators to Crop Yield and Quality Varies with Agricultural Intensification.” *PeerJ* 2014: 1–20.
- Barton, K. 2018. *MuMIn: Multi-Model Inference*. <https://cran.r-project.org/web/packages/MuMIn/index.html>
- Bates, A. J., J. P. Sadler, A. J. Fairbrass, S. J. Falk, J. D. Hale, and T. J. Matthews. 2011. “Changing Bee and Hoverfly Pollinator Assemblages along an Urban-Rural Gradient.” *PLoS One* 6: e23459.
- de Bello, F., Z. Botta-Dukát, J. Lepš, and P. Fibich. 2021. “Towards a More Balanced Combination of Multiple Traits When Computing Functional Differences between Species.” *Methods in Ecology and Evolution* 12: 443–8.
- Bennett, A. B., and S. Lovell. 2019. “Landscape and Local Site Variables Differentially Influence Pollinators and Pollination Services in Urban Agricultural Sites.” *PLoS One* 14: 1–21.

- Beyer, N., D. Gabriel, F. Kirsch, K. Schulz-Kesting, J. Dauber, and C. Westphal. 2020. "Functional Groups of Wild Bees Respond Differently to Faba Bean *Vicia faba* L. Cultivation at Landscape Scale." *Journal of Applied Ecology* 57: 2499–508.
- Beyer, N., F. Kirsch, D. Gabriel, and C. Westphal. 2021. "Identity of Mass-Flowering Crops Moderates Functional Trait Composition of Pollinator Communities." *Landscape Ecology* 36: 2657–71.
- Birdshire, K. R., A. L. Carper, and C. E. Briles. 2020. "Bee Community Response to Local and Landscape Factors along an Urban-Rural Gradient." *Urban Ecosystem* 23: 689–702.
- Buchholz, S., and M. H. Egerer. 2020. "Functional Ecology of Wild Bees in Cities: Towards a Better Understanding of Trait-Urbanization Relationships." *Biodiversity and Conservation* 29: 2779–801.
- Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Inference: A Practical Information-Theoretic Approach*. 2nd Edition. New York: Springer-Verlag.
- Blüthgen, N., F. Menzel, and N. Blüthgen. 2006. "Measuring Specialization in Species Interaction Networks." *BMC Ecology* 6.
- Brooks, M., B. Bolker, K. Kristensen, M. Maechler, A. Magnusson, M. McGillicuddy, H. Skaug, et al. 2020. "glmmTMB; Generalized Linear Mixed Models Using Template Model Builder." <https://cran.r-project.org/web/packages/glmmTMB/index.html>
- Cabannes, Y., and M. Pasquini. 2008. "Cities Farming for the Future, Mid Term Review Report."
- Cariveau, D. P., G. K. Nayak, I. Bartomeus, J. Zientek, J. S. Ascher, J. Gibbs, and R. Winfree. 2016. "The Allometry of Bee Proboscis Length and its Uses in Ecology." *PLoS One* 11: 1–13.
- Cohen, H., M. Egerer, T. Summer-Solstice, and S. M. Philpott. 2022. "Local and Landscape Features Constrain the Trait and Taxonomic Diversity of Urban Bees." *Landscape Ecology* 37: 583–99.
- Crowther, L. P., P. L. Hein, and A. F. G. Bourke. 2014. "Habitat and Forage Associations of a Naturally Colonising Insect Pollinator, the Tree Bumblebee *Bombus hypnorum*." *PLoS One* 9: e107568.
- Chao, A. 1987. "Estimating the Population Size for Capture-recapture Data with Unequal Catchability." *Biometrics* 43(4): 783–91.
- De Zeeuw, H., R. Van Veenhuizen, and M. Dubbeling. 2011. "The Role of Urban Agriculture in Building Resilient Cities in Developing Countries." *Journal of Agricultural Science* 149: 153–63.
- Dormann, C., B. Gruber, and J. Fründ. 2008. "Introducing the Bipartite Package: Analysing Ecological Networks." *Interactions* 1: 2413793.
- Dormann, C. F. 2011. "How to Be a Specialist? Quantifying specialisation in pollination networks." *Network Biology* 1: 1–20.
- Faeth, S. H., C. Bang, and S. Saari. 2011. "Urban Biodiversity: Patterns and Mechanisms." *Annals of the New York Academy of Sciences* 1223: 69–81.
- Fortel, L., M. Henry, L. Guilbaud, A. L. Guirao, M. Kuhlmann, H. Mouret, O. Rollin, and B. E. Vaissière. 2014. "Decreasing Abundance, Increasing Diversity and Changing Structure of the Wild Bee Community (Hymenoptera: Anthophila) along an Urbanization Gradient." *PLoS One* 9: e104679.
- Fox, J., S. Weisberg, B. Price, M. Friendly, J. Hong, R. Andersen, D. Firth, and S. Taylor. 2019. "effects: Effect Displays for Linear, Generalized Linear, and Other Models." <https://cran.r-project.org/web/packages/effects/index.html>
- Frankie, G. W., S. B. Vinson, M. A. Rizzardi, T. L. Griswold, R. E. Coville, M. H. Grayum, L. E. S. Martinez, J. Foltz-Sweat, and J. C. Pawelek. 2013. "Relationships of Bees to Host Ornamental and Weedy Flowers in Urban Northwest Guanacaste Province, Costa Rica." *Journal of the Kansas Entomological Society* 86: 325–51.
- Galipaud, M., M. A. F. Gillingham, and F. X. Dechaume-Moncharmont. 2017. "A Farewell to the Sum of Akaike Weights: The Benefits of Alternative Metrics for Variable Importance Estimations in Model Selection." *Methods in Ecology and Evolution* 8: 1668–78.
- Ganser, D., M. Albrecht, and E. Knop. 2021. "Wildflower Strips Enhance Wild Bee Reproductive Success." *Journal of Applied Ecology* 58: 486–95.
- Garbuzov, M., E. E. W. Samuelson, and F. L. W. Ratnieks. 2015. "Survey of Insect Visitation of Ornamental Flowers in Southover Grange Garden, Lewes, UK." *Insect Science* 22: 700–5.
- Gathmann, A., and T. Tschardt. 2002. "Foraging Ranges of Solitary Bees." *Journal of Animal Ecology* 71: 757–64.
- Geslin, B., V. Le Féon, M. Folschweiller, F. Flacher, D. Carmignac, E. Motard, S. Perret, and I. Dajoz. 2016. "The Proportion of Impervious Surfaces at the Landscape Scale Structures Wild Bee Assemblages in a Densely Populated Region." *Ecology and Evolution* 6: 6599–615.
- Geslin, B., M. Oddie, M. Folschweiller, G. Legras, C. L. Seymour, F. J. F. van Veen, and E. Thébault. 2016. "Spatiotemporal Changes in Flying Insect Abundance and their Functional Diversity as a Function of Distance to Natural Habitats in a Mass Flowering Crop." *Agriculture, Ecosystems and Environment* 229: 21–9.
- Grass, I., P. Batáry, and T. Tschardt. 2021. "Combining Land-Sparing and Land-Sharing in European Landscapes." *Advances in Ecological Research* 64: 251–303.
- Grass, I., D. G. Berens, and N. Farwig. 2014. "Natural Habitat Loss and Exotic Plants Reduce the Functional Diversity of Flower Visitors in a Heterogeneous Subtropical Landscape." *Functional Ecology* 28: 1117–26.
- Grass, I., D. G. Berens, F. Peter, and N. Farwig. 2013. "Additive Effects of Exotic Plant Abundance and Land-Use Intensity on Plant-Pollinator Interactions." *Oecologia* 173: 913–23.
- Grass, I., B. Jauker, I. Steffan-Dewenter, T. Tschardt, and F. Jauker. 2018. "Past and Potential Future Effects of Habitat Fragmentation on Structure and Stability of Plant-Pollinator and Host-Parasitoid Networks." *Nature Ecology and Evolution* 2: 1408–17.
- Greenleaf, S. S., N. M. Williams, R. Winfree, and C. Kremen. 2007. "Bee Foraging Ranges and their Relationship to Body Size." *Oecologia* 153: 589–96.
- Grimm, N. B., S. H. Faeth, N. E. Golubiewski, C. L. Redman, J. Wu, X. Bai, and J. M. Briggs. 2008. "Global Change and the Ecology of Cities." *Science* 319: 756–60.
- Gu, B., X. Zhang, X. Bai, B. Fu, and D. Chen. 2019. "Four Steps to Food Security for Swelling Cities." *Nature* 566: 31–3.

- Guenat, S., W. E. Kunin, A. J. Dougill, and M. Dallimer. 2019. "Effects of Urbanisation and Management Practices on Pollinators in Tropical Africa." *Journal of Applied Ecology* 56: 214–24.
- Hamblin, A. L., E. Youngsteadt, and S. D. Frank. 2018. "Wild Bee Abundance Declines with Urban Warming, Regardless of Floral Density." *Urban Ecosystem* 21: 419–28.
- Hass, A. L., U. G. Kormann, T. Tschardtke, Y. Clough, A. B. Baillod, C. Sirami, L. Fahrig, et al. 2018. "Landscape Configurational Heterogeneity by Small-Scale Agriculture, Not Crop Diversity, Maintains Pollinators and Plant Reproduction in Western Europe." *Proceedings of the Royal Society B: Biological Sciences* 285: 20172242.
- Hartig, F. 2021. "DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models." <https://cran.r-project.org/web/packages/DHARMA/index.html>
- Hinners, S. J., C. A. Kearns, and C. A. Wessman. 2012. "Roles of Scale, Matrix, and Native Habitat in Supporting a Diverse Suburban Pollinator Assemblage." *Ecological Applications* 22: 1923–35.
- Hoehn, P., T. Tschardtke, J. M. Tylianakis, and I. Steffan-Dewenter. 2008. "Functional Group Diversity of Bee Pollinators Increases Crop Yield." *Proceedings of the Royal Society B: Biological Sciences* 275: 2283–91.
- Hülsmann, M., H. von Wehrden, A. M. Klein, and S. D. Leonhardt. 2015. "Plant Diversity and Composition Compensate for Negative Effects of Urbanization on Foraging Bumble Bees." *Apidologie* 46: 760–70.
- Inderjit, J. Pergl, M. van Kleunen, M. Hejda, C. R. Babu, S. Majumdar, P. Singh, et al. 2018. "Naturalized Alien Flora of the Indian States: Biogeographic Patterns, Taxonomic Structure and Drivers of Species Richness." *Biological Invasions* 20: 1625–38.
- Gower, J. C. 1971. "A General Coefficient of Similarity and some of its Properties." *Biometrics* 27: 857–71.
- Jasmi, D. P. Putra, Syarifuddin, H. Herwina, and M. N. Janra. 2021. "Breeding Efforts on Wild Honey Bee *Apis cerana* Fabr. Within Coconut Plantations in Padang Pariaman, West Sumatra." *IOP Conference Series: Earth and Environmental Science* 757: 012024.
- Kendall, L. K., R. Rader, V. Gagic, D. P. Cariveau, M. Albrecht, K. C. R. Baldock, B. M. Freitas, et al. 2019. "Pollinator Size and its Consequences: Robust Estimates of Body Size in Pollinating Insects." *Ecology and Evolution* 9: 1702–14.
- Kennedy, C. M., E. Lonsdorf, M. C. Neel, N. M. Williams, T. H. Ricketts, R. Winfree, R. Bommarco, et al. 2013. "A Global Quantitative Synthesis of Local and Landscape Effects on Wild Bee Pollinators in Agroecosystems." *Ecology Letters* 16: 584–99.
- Klatt, B. K., A. Holzschuh, C. Westphal, Y. Clough, I. Smit, E. Pawelzik, and T. Tschardtke. 2013. "Bee Pollination Improves Crop Quality, Shelf Life and Commercial Value." *Proceedings of the Royal Society B: Biological Sciences* 281: 20132440.
- Klein, A. M., C. Brittain, S. D. Hendrix, R. Thorp, N. Williams, and C. Kremen. 2012. "Wild Pollination Services to California Almond Rely on Semi-Natural Habitat." *Journal of Applied Ecology* 49: 723–32.
- Klein, A. M., B. E. Vaissière, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tschardtke. 2007. "Importance of Pollinators in Changing Landscapes for World Crops." *Proceedings of the Royal Society B: Biological Sciences* 274: 303–13.
- Kohli, R. K., D. R. Batish, H. P. Singh, and K. S. Dogra. 2006. "Status, Invasiveness and Environmental Threats of Three Tropical American Invasive Weeds (*Parthenium hysterophorus* L., *Ageratum conyzoides* L., *Lantana camara* L.) in India." *Biological Invasions* 8: 1501–10.
- Kremen, C., N. M. Williams, M. A. Aizen, B. Gemmill-Herren, G. LeBuhn, R. Minckley, L. Packer, et al. 2007. "Pollination and Other Ecosystem Services Produced by Mobile Organisms: A Conceptual Framework for the Effects of Land-Use Change." *Ecology Letters* 10: 299–314.
- Laliberté, E., P. Legendre, and B. Shipley. 2015. "FD: Measuring Functional Diversity from Multiple Traits, and Other Tools for Functional Ecology." R Package:Version 1.0-12. <https://cran.r-project.org/web/packages/FD/index.html>
- Lanner, J., S. Kratschmer, B. Petrović, F. Gaulhofer, H. Meimberg, and B. Pachinger. 2020. "City Dwelling Wild Bees: How Communal Gardens Promote Species Richness." *Urban Ecosystem* 23: 271–88.
- Laliberté, E., and P. Legendre. 2010. "A Distance-based Framework for Measuring Functional Diversity from Multiple Traits." *Ecology* 91(1): 299–305.
- Larson, J. L., A. J. Kesheimer, and D. A. Potter. 2014. "Pollinator Assemblages on Dandelions and White Clover in Urban and Suburban Lawns." *Journal of Insect Conservation* 18: 863–73.
- Lenth, R. V., P. Buerkner, M. Herve, J. Love, F. Miguez, H. Riebl, and H. Singmann. 2021. "emmeans: Estimated Marginal Means, aka Least-Squares Means." <https://cran.r-project.org/web/packages/emmeans/index.html>
- Lin, B. B., S. M. Philpott, and S. Jha. 2015. "The Future of Urban Agriculture and Biodiversity-Ecosystem Services: Challenges and Next Steps." *Basic and Applied Ecology* 16: 189–201.
- Lowenstein, D. M., K. C. Matteson, and E. S. Minor. 2019. "Evaluating the Dependence of Urban Pollinators on Ornamental, Non-native, and 'Weedy' Floral Resources." *Urban Ecosystem* 22: 293–302.
- Lüdecke, D., D. Makowski, M. S. Ben-Shachar, I. Patil, P. Waggoner, B. M. Wiernik, V. Arel-Bundock, and M. Jullum. 2021. "performance: Assessment of Regression Models Performance." <https://cran.r-project.org/web/packages/performance/index.html>
- Mallinger, R. E., J. Gibbs, and C. Gratton. 2016. "Diverse Landscapes Have a Higher Abundance and Species Richness of Spring Wild Bees by Providing Complementary Floral Resources Over Bees' Foraging Periods." *Landscape Ecology* 31: 1523–35.
- Marcacci, G., C. Westphal, A. Wenzel, V. Raj, N. Nölke, T. Tschardtke, and I. Grass. 2021. "Taxonomic and Functional Homogenization of Farmland Birds along an Urbanization Gradient in a Tropical Megacity." *Global Change Biology* 27(20): 4980–94.
- Marcacci, G., I. Grass, V. S. Rao, S. S. Kumar, K. B. Tharini, V. V. Belavadi, N. Nölke, T. Tschardtke and C. Westphal. 2022. "Functional Diversity of Farmland Bees across Rural–Urban Landscapes in a Tropical Megacity." Dryad, dataset. <https://doi.org/10.5061/dryad.sqv9s4n67>.
- Marín, L., M. E. Martínez-Sánchez, P. Sagot, D. Navarrete, and H. Morales. 2020. "Floral Visitors in Urban Gardens and

- Natural Areas: Diversity and Interaction Networks in a Neotropical Urban Landscape." *Basic and Applied Ecology* 43: 3–15.
- Martin, A. E., S. J. Collins, S. Crowe, J. Girard, I. Naujokaitis-Lewis, A. C. Smith, K. Lindsay, S. Mitchell, and L. Fahrig. 2020. "Effects of Farmland Heterogeneity on Biodiversity Are Similar To—Or Even Larger Than—The Effects of Farming Practices." *Agriculture, Ecosystems and Environment* 288: 106698.
- Martins, K. T., C. H. Albert, M. J. Lechowicz, and A. Gonzalez. 2018. "Complementary Crops and Landscape Features Sustain Wild Bee Communities." *Ecological Applications* 28: 1093–105.
- Martins, K. T., A. Gonzalez, and M. J. Lechowicz. 2015. "Pollination Services Are Mediated by Bee Functional Diversity and Landscape Context." *Agriculture, Ecosystems and Environment* 200: 12–20.
- Mukherjee, R., R. Deb, and S. M. Devy. 2019. "Diversity Matters: Effects of Density Compensation in Pollination Service during Rainfall Shift." *Ecology and Evolution* 9: 9701–11.
- Michener, C. D. 2007. *The Bees of the World*. Baltimore, MD and London: The Johns Hopkins University Press.
- Nautiyal, S., M. Goswami, R. Rao Nidamanuri, E. M. Hoffmann, and A. Buerket. 2020. "Structure and Composition of Field Margin Vegetation in the Rural-Urban Interface of Bengaluru, India: A Case Study on an Unexplored Dimension of Agroecosystems." *Environmental Monitoring and Assessment* 192: 520.
- Nakagawa, S., P. C. D. Johnson, and H. Schielzeth. 2017. "The Coefficient of Determination R^2 and Intra-class Correlation Coefficient from Generalized Linear Mixed-effects Models Revisited and Expanded." *Journal of the Royal Society Interface* 14(134): 20170213.
- Ojija, F., S. E. J. Arnold, and A. C. Treydte. 2019. "Impacts of Alien Invasive *Parthenium hysterophorus* on Flower Visitation by Insects to Co-Flowering Plants." *Arthropod-Plant Interactions* 13: 719–34.
- Oksanen, J., M. Blanchet, F. Guillaume Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, et al. 2020. "vegan: Community Ecology Package."
- Orsini, F., R. Kahane, R. Nono-Womdim, and G. Gianquinto. 2013. "Urban Agriculture in the Developing World: A Review." *Agronomy for Sustainable Development* 33: 695–720.
- Pardee, G. L., and S. M. Philpott. 2014. "Native Plants Are the Bee's Knees: Local and Landscape Predictors of Bee Richness and Abundance in Backyard Gardens." *Urban Ecosystem* 17: 641–59.
- Pereira, F. W., L. Carneiro, and R. B. Gonçalves. 2021. "More Losses than Gains in Ground-Nesting Bees over 60 Years of Urbanization." *Urban Ecosystem* 24: 233–42.
- Piano, E., C. Souffreau, T. Merckx, L. F. Baardsen, T. Backeljau, D. Bonte, K. I. Brans, et al. 2020. "Urbanization Drives Cross-Taxon Declines in Abundance and Diversity at Multiple Spatial Scales." *Global Change Biology* 26: 1196–211.
- Ponisio, L. C., L. K. M'Gonigle, and C. Kremen. 2016. "On-Farm Habitat Restoration Counters Biotic Homogenization in Intensively Managed Agriculture." *Global Change Biology* 22: 704–15.
- Potter, A., and G. LeBuhn. 2015. "Pollination Service to Urban Agriculture in San Francisco, CA." *Urban Ecosystem* 18: 885–93.
- Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. "Global Pollinator Declines: Trends, Impacts and Drivers." *Trends in Ecology and Evolution* 25: 345–53.
- Potts, S. G., V. Imperatriz-Fonseca, H. T. Ngo, M. A. Aizen, J. C. Biesmeijer, T. D. Breeze, L. V. Dicks, et al. 2016. "Safeguarding Pollinators and their Values to Human Well-Being." *Nature* 540: 220–9.
- Prendergast, K. S., K. W. Dixon, and P. W. Bateman. 2022. "A Global Review of Determinants of Native Bee Assemblages in Urbanised Landscapes." *Insect Conservation and Diversity* 15: 385–405.
- Raderschall, C. A., R. Bommarco, S. A. M. Lindström, and O. Lundin. 2021. "Landscape Crop Diversity and Semi-Natural Habitat Affect Crop Pollinators, Pollination Benefit and Yield." *Agriculture, Ecosystems and Environment* 306: 107189.
- Rahman, A., P. K. Das, P. Rajkumari, J. Saikia, and D. Sharmah. 2015. "Stingless Bees (Hymenoptera: Apidae: Meliponini): Diversity and Distribution in India." *International Journal of Science and Research* 4: 77–81.
- R Core Team. 2020. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Scherber, C., T. Beduschi, and T. Tschardtke. 2019. "Novel Approaches to Sampling Pollinators in Whole Landscapes: A Lesson for Landscape-Wide Biodiversity Monitoring." *Land-use Ecology* 34: 1057–67.
- Silva, J. L. S., M. T. P. de Oliveira, O. Cruz-Neto, M. Tabarelli, and A. V. Lopes. 2021. "Plant–Pollinator Interactions in Urban Ecosystems Worldwide: A Comprehensive Review Including Research Funding and Policy Actions." *Ambio* 50: 884–900.
- Sirami, C., N. Gross, A. B. Baillod, C. Bertrand, R. Carrié, A. Hass, L. Henckel, et al. 2019. "Increasing Crop Heterogeneity Enhances Multitrophic Diversity across Agricultural Regions." *Proceedings of the National Academy of Sciences of the United States of America* 116: 16442–7.
- Skultety, D., and J. W. Matthews. 2017. "Urbanization and Roads Drive Non-native Plant Invasion in the Chicago Metropolitan Region." *Biological Invasions* 19: 2553–66.
- Staab, M., M. H. Pereira-Peixoto, and A. M. Klein. 2020. "Exotic Garden Plants Partly Substitute for Native Plants as Resources for Pollinators When Native Plants Become Seasonally Scarce." *Oecologia* 194: 465–80.
- Steffan-Dewenter, I., U. Münzenberg, C. Bürger, C. Thies, and T. Tschardtke. 2002. "Scale-Dependent Effects of Landscape Context on Three Pollinator Guilds." *Ecology* 83: 1421–32.
- Steinhübel, L., and S. von Cramon-Taubadel. 2020. "Somewhere in between Towns, Markets, and Jobs – Opportunity Costs of Agricultural Intensification in the Rural-Urban Interface." *The Journal of Development Studies* 57: 669–94.
- Stelzer, R. J., L. Chittka, M. Carlton, and T. C. Ings. 2010. "Winter Active Bumblebees (*Bombus terrestris*) Achieve High Foraging Rates in Urban Britain." *PLoS One* 5: 1–7.
- Stewart, A. B., T. Sritongchuay, P. Teartitup, S. Kaewsomboon, and S. Bumrungsri. 2018. "Habitat and Landscape Factors Influence Pollinators in a Tropical Megacity, Bangkok, Thailand." *PeerJ* 2018: e5335.

- Stewart, A. B., and P. Waitayachart. 2020. "Year-Round Temporal Stability of a Tropical, Urban Plant-Pollinator Network." *PLoS One* 15: 1–12.
- Sutter, L., P. Jeanneret, A. M. Bartual, G. Bocci, and M. Albrecht. 2017. "Enhancing Plant Diversity in Agricultural Landscapes Promotes both Rare Bees and Dominant Crop-Pollinating Bees through Complementary Increase in Key Floral Resources." *Journal of Applied Ecology* 54: 1856–64.
- Tangtorwongsakul, P., N. Warrit, and G. A. Gale. 2018. "Effects of Landscape Cover and Local Habitat Characteristics on Visiting Bees in Tropical Orchards." *Agricultural and Forest Entomology* 20: 28–40.
- Tew, N. E., K. C. R. Baldock, I. P. Vaughan, S. Bird, and J. Memmott. 2022. "Turnover in Floral Composition Explains Species Diversity and Temporal Stability in the Nectar Supply of Urban Residential Gardens." *Journal of Applied Ecology* 59: 801–11.
- Thebo, A. L., P. Drechsel, and E. F. Lambin. 2014. "Global Assessment of Urban and Peri-Urban Agriculture: Irrigated and Rainfed Croplands." *Environmental Research Letters* 9: 114002.
- Theodorou, P., K. Albig, R. Radzevičiūtė, J. Settele, O. Schweiger, T. E. Murray, and R. J. Paxton. 2017. "The Structure of Flower Visitor Networks in Relation to Pollination across an Agricultural to Urban Gradient." *Functional Ecology* 31: 838–47.
- Theodorou, P., R. Radzevičiūtė, G. Lentendu, B. Kahnt, M. Husemann, C. Bleidorn, J. Settele, et al. 2020. "Urban Areas as Hotspots for Bees and Pollination but Not a Panacea for all Insects." *Nature Communications* 11: 1–13.
- United Nations. 2018. "World Population Prospects 2022." <https://population.un.org/wpp/>
- Usharani, B., and A. J. S. Raju. 2018. "Reproductive Ecology of the Globally Invasive Whitetop Weed, *Parthenium hysterophorus* (Asteraceae)." *Phytologia Balcanica* 24: 225–38.
- van Vliet, J., D. A. Eitelberg, and P. H. Verburg. 2017. "A Global Analysis of Land Take in Cropland Areas and Production Displacement from Urbanization." *Global Environmental Change* 43: 107–15.
- Wagner, D. L., E. M. Grames, M. L. Forister, M. R. Berenbaum, and D. Stopak. 2021. "Insect Decline in the Anthropocene: Death by a Thousand Cuts." *Proceedings of the National Academy of Sciences of the United States of America* 118: 1–10.
- Wenzel, A., I. Grass, V. V. Belavadi, and T. Tschardt. 2020. "How Urbanization Is Driving Pollinator Diversity and Pollination – A Systematic Review." *Biological Conservation* 241: 108321.
- Wenzel, A., I. Grass, N. Nölke, A. Pannure, and T. Tschardt. 2022. "Wild Bees Benefit from Low Urbanization Levels and Suffer from Pesticides in a Tropical Megacity." *Agriculture, Ecosystems & Environment* 336: 108019.
- Westphal, C., R. Bommarco, G. Carré, E. Lamborn, N. Morison, T. Petanidou, S. G. Potts, et al. 2008. "Measuring Bee Diversity in Different European Habitats and." *Ecological Monographs* 78: 653–71.
- Wilson, C. J., and M. A. Jamieson. 2019. "The Effects of Urbanization on Bee Communities Depends on Floral Resource Availability and Bee Functional Traits." *PLoS One* 14: 1–18.
- Wickham, H., W. Chang, L. Henry, T. L. Pedersen, K. Takahashi, C. Wilke, K. Woo, H. Yutani, and D. Dunnington. (2021). "ggplot2: Create Elegant Data Visualisations Using the Grammar of Graphics." <https://cran.r-project.org/web/packages/ggplot2/index.html>
- Zaninotto, V., A. Perrard, O. Babiar, A. Hansart, C. Hignard, and I. Dajoz. 2021. "Seasonal Variations of Pollinator Assemblages among Urban and Rural Habitats: A Comparative Approach Using a Standardized Plant Community." *Insects* 12: 1–18.
- Zeza, A., and L. Tasciotti. 2010. "Urban Agriculture, Poverty, and Food Security: Empirical Evidence from a Sample of Developing Countries." *Food Policy* 35: 265–73.

SUPPORTING INFORMATION

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

How to cite this article: Marcacci, Gabriel, Ingo Grass, Vikas S. Rao, Shabarish Kumar S, K. B. Tharini, Vasuki V. Belavadi, Nils Nölke, Teja Tschardt, and Catrin Westphal. 2022. "Functional Diversity of Farmland Bees across Rural–Urban Landscapes in a Tropical Megacity." *Ecological Applications* 32(8): e2699. <https://doi.org/10.1002/eap.2699>