LETTER

Urbanization alters the spatiotemporal dynamics of plant–pollinator networks in a tropical megacity

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Abstract

Urbanization is a major driver of biodiversity change but how it interacts with spatial and temporal gradients to influence the dynamics of plant–pollinator networks is poorly understood, especially in tropical urbanization hotspots. Here, we analysed the drivers of environmental, spatial and temporal turnover of plant–pollinator interactions (interaction β-diversity) along an urbanization gradient in Bengaluru, a South Indian megacity. The compositional turnover of plant–pollinator interactions differed more between seasons and with local urbanization intensity than with spatial distance, suggesting that seasonality and environmental filtering were more important than dispersal limitation for explaining plant–pollinator interaction β-diversity. Furthermore, urbanization amplified the seasonal dynamics of plant–pollinator interactions, with stronger temporal turnover in urban compared to rural sites, driven by greater turnover of native non-crop plant species (not managed by people). Our study demonstrates that environmental, spatial and temporal gradients interact to shape the dynamics of plant–pollinator networks and urbanization can strongly amplify these dynamics.

KEYWORDS
Bangalore, environmental filtering, India, interaction beta-diversity partitioning, interaction rewiring, seasonal dynamics, species turnover

INTRODUCTION

All species engage in interactions, and the complex ecological networks resulting from these interactions—such as those between plants and their pollinators—are key components of ecosystems (Barnes et al., 2018; Bascompte & Jordano, 2007; Harvey et al., 2017; Memtsas et al., 2022). While our knowledge on the structure of interaction networks has improved considerably in recent decades, we still know little about how dynamic these interactions are across environmental, spatial and temporal gradients. Indeed, although plant–pollinators

interactions are multilayered in nature, most studies focus on a single point in space and/or time, aggregating interactions across multiple spatial locations and times (Pilosof et al., 2017). This ignores the environmental, spatial and temporal variability of species interactions despite recent studies indicating their considerable dynamics (CaraDonna et al., 2017; Caradonna & Waser, 2020; Schwarz et al., 2020).

A potential reason for the comparatively little research on the variability of species interactions—that is interaction β-diversity—is that it is challenging to analyse and interpret, as it comprises four distinct ecological processes: species turnover of the lower trophic level (e.g. plants), species turnover of the higher trophic level (e.g. pollinators), simultaneous turnover of both trophic levels and interaction rewiring (i.e. turnover in interactions not due to species turnover) (Novotny, 2009; Poisot et al., 2012). Processes such as dispersal limitation, local environmental conditions or seasonality affect species turnover of plants and their pollinators (i.e. the first three components). Interaction rewiring is influenced by species abundances, phenology and behaviour (Burkle et al., 2022), and may also change with environmental conditions, spatial proximity or timing.

Urbanization is recognized as a growing threat to biodiversity (Li et al., 2022; Simkin et al., 2022), which strongly alters and often homogenizes biotic communities (Marcacci et al., 2021; Piano et al., 2020). Urban areas are modified ecosystems with unique environmental conditions. Cities typically harbour a greater diversity of flowering plants than rural landscapes due to the presence of non-native cultivated and introduced (e.g. ornamental and exotic) plant species (Lowenstein et al., 2019; Seitz et al., 2022). Urbanized landscapes also influence the composition of pollinator communities as they select for specific traits, such as dispersal ability, nesting behaviour or sociality (Liang et al., 2023; Marcacci, Grass, et al., 2022; Wenzel et al., 2020). Moreover, local environmental conditions in urban areas (e.g. urban warming) affect the phenology of both flowering plants and pollinators and may thereby buffer or amplify the effects of seasonality on β-diversity of plant–pollinator interactions (Fisogni et al., 2020, 2022). In conclusion, environmental, spatial, and temporal determinants strongly affect how plants and pollinators interact in urban areas. But their relative importance, as well as potential interactions such as changing temporal effects across environmental or spatial gradients, remain underexplored, thus preventing a good understanding of spatiotemporal dynamics of interaction networks. Given the current expansion of urban areas, especially in understudied tropical regions, studying how anthropogenic disturbances influence these dynamics is critical if we are to predict their impact on plant–pollinator interactions and their associated ecological functions and services.

Here, we studied the environmental, spatial and temporal drivers of plant–pollinator interaction β-diversity across three seasons in a tropical megacity, Bengaluru, India. We recorded plant–pollinator interactions throughout the year, covering the winter, summer and monsoon seasons, on 36 vegetable-producing farms spread along a continuous urbanization gradient from rural over peri-urban to urban areas. We analysed the individual and interactive effects of environmental, spatial and temporal gradients on interaction β-diversity. Furthermore, we partitioned interaction β-diversity in its four additive components to unravel the underlying drivers explaining variations in the composition of interaction networks. We expected urbanization, spatial distance, season and their interactive effects to structure the composition and dynamics of plant–pollinator interaction, mainly due to changes in plant communities. We found that plant–pollinator interactions differed more between seasons and with local urbanization intensity than with spatial distance, showing the importance of seasonality and environmental filtering for plant–pollinator interaction β-diversity. Plant–pollinator interaction β-diversity was mostly driven by the turnover of plant species and rewiring of interactions, highlighting the flexibility of urban bees in their choice of plant partners. Furthermore, urbanization amplified the seasonal dynamics of plant–pollinator interactions, with stronger temporal turnover in urban compared to rural areas because of greater turnover of non-crop native plant species. Our study underscores the importance of considering multiple gradients when studying the dynamics of plant–pollinator interactions and paves the way for future research leading to generalized principles in interaction networks community ecology and biogeography.

MATERIALS AND METHODS

Study area

This study was conducted in Bengaluru (formerly Bangalore), the capital city of the South Indian state Karnataka. Bengaluru is a megacity of 12.8 million inhabitants and is among the fastest-growing cities in the world (*UN World Urbanization Prospects*, United Nations 2018). It is embedded in an ancient agricultural landscape composed of small-scale farms interspersed with semi-natural habitats (e.g. hedges, woodlands, permanent fallows, marshes). Bengaluru's rapid urban development at its periphery increasingly encroaches (semi-) natural and agricultural land (Nagendra et al., 2012), making Bengaluru a prime example of the growing threats of urbanization to biodiversity in tropical regions (Li et al., 2022; Simkin et al., 2022).

Located on the Deccan Plateau at an elevation of 920 m a.s.l., Bengaluru experiences a moderate tropical climate with temperatures ranging between 12 and 38°C and annual precipitations at about 800 mm. There are three distinct seasons: a mild and mostly dry winter from October to January (post-monsoon season), a hot and dry summer from February to May (dry season) and the monsoon from June to September with extensive rainfalls.

Study design

We selected 36 conventional vegetable-producing small-holder farms of similar management intensities and cultivating similar vegetable crops (e.g. tomato, lablab, chilli, eggplant, cucumber) as study sites (mean size = 1.03 ha, SD = ±0.54 ha). These were spread along two transects (18 sites per transect) extending from urban Bengaluru towards rural villages, thus forming a rural–urban gradient north and south of the city centre. This study design allowed us to keep the focal habitat constant (i.e. vegetable farms) while varying the landscape context (i.e. urbanization intensity). We kept a minimum distance of 1 km between study sites to guarantee their independence. We quantified urbanization intensity as the amount of grey area (also called impervious area: that is, all sealed surfaces, such as roads, buildings, etc.), a typical proxy of the degree of urbanization (e.g. Geslin et al., 2016; Marcacci, Grass, et al., 2022; Piano et al., 2020). To identify grey areas, we used remote sensed data from 2020 with a 10 m spatial resolution acquired from cloud-free Sentinel-2 L2A imagery. A pixel-wise image classification was done using a deep learning model, that is a multilayer perceptron network (Marcacci et al., 2021). We then calculated the proportion of grey area in the study sites' surroundings within a 500 m radius, corresponding to the spatial scale at which most bee species experience the landscape in our study region (Marcacci, Grass, et al., 2022).

All farmers and owners granted us permission to work on their farm.

Plant–pollinator interactions sampling

We established a 100 m × 2 m transect in each of the 36 study sites. The transects were sub-divided into 10 sub-units of 10 m × 2 m each, with five sub-units located within cropping fields and five sub-units in semi-natural habitats at the fields' edges. The structure and types of semi-natural habitats (e.g. field margins, hedgerows) were similar across all study sites along the urbanization gradient. The location (but not the sampling effort) of the transect sub-units varied between the seasons to be more flexible with respect to the phenology of the cropped fields (e.g. when flowering fields became fallows in the following season), and the number of sub-units assigned to each crop was proportional to its relative area within the study site (Scherber et al., 2019; Westphal et al., 2008). We focused on bees as pollinators as they are the most dominant pollinator species in the region (Wenzel et al., 2022). Bees were sampled in all transects monthly for 1 year from February 2020 to January 2021. Because of the COVID-19 pandemic and the lockdown imposed by the Indian Government, fieldwork activities were suspended in April 2020, resulting in a total of 11 sampling rounds. However, this did not affect sampling completeness for this season (see section on sampling completeness below). All bees were sampled using sweep nets within 2 min (excluding handling time) in each of the 10 sub-units, thus leading to a total of 20 min per transect each month. The data of the 10 sub-units were then pooled and analyses were performed at the transect level (site). All transect-walks were conducted under good weather conditions (no rain, no heavy wind, minimum 18°C) between 9 a.m. and 3 p.m. and their order was carefully planned to avoid any temporal autocorrelation. We only considered as interactions when bees visited a flower and thereby potentially acted as pollinator, and we identified all visited flowering plant species to species level. Whenever possible, bees were identified in the field or were otherwise taken to the laboratory where a taxonomic expert (Tharini K.B.) identified the specimens. Taking advantage of the bee collection of the Agricultural Entomology Department of the University of Agricultural Sciences, GKVK, Bangalore, we could identify 66% of the recorded bee species. However, as the taxonomy of South Indian bees is still under development, especially for the Halictidae, 34% of specimens could only be identified to morphospecies level. All specimens are kept in the collections of the Agricultural Entomology department (University of Agricultural Sciences, GKVK, Bangalore, India).

Construction of plant–pollinator networks

We built plant–pollinator interaction networks from adjacency matrixes A_{ij} in which i refers to the visited plant species, j the bee species and ij their interaction frequency. We built one plant-interaction network for each of the 36 study sites and season ('monsoon', 'summer', 'winter'), resulting in a total of 108 interaction networks (36 per season). We used quantitative (weighted) networks because they are considered more robust and precise than binary networks (Blüthgen, 2010; Dormann & Strauss, 2014).

Sampling completeness

Prior to the statistical analyses, we estimated the sampling completeness across plant-interaction networks following Grass et al. (2018) to exclude any potential bias due to incomplete sampling. Specifically, for each network, we estimated the sampling completeness by dividing the observed by the expected interaction richness using the Chao1 estimator of asymptotic richness (Chao, 1987). Here, interaction richness corresponds to species richness and the visitation frequency to abundances. We calculated the sampling completeness for pooled data and for each season individually ($N = 36$). Additionally, we plotted accumulation curves of distinct pairwise interactions against the number of sampling rounds in each season, and the number of transect-walks performed across all rounds in each site.

β-diversity along environmental, spatial and temporal gradients

To investigate whether environmental conditions (% grey area as a proxy for urbanization intensity), spatial distance or seasonality had a stronger effect on plant–pollinator interaction β-diversity, we calculated pairwise interaction β-diversity (i.e. variations of plant–pollinator interactions between communities) using the Bray–Curtis dissimilarity index (quantitative networks including interaction frequencies). We additionally calculated the β-diversity of plant and bee communities to investigate whether changes in species composition influenced interaction β-diversity.

First, we calculated total pairwise plant, bee and interaction β-diversity across our 108 networks to include environmental and temporal variation. We visualized the turnover of plant and bee communities, and of their interactions along environmental (urbanization) and temporal (seasons) gradients using non-metric multidimensional scaling (NMDS) plots (*vegan* R-Package, Oksanen et al., 2017). We calculated the statistical significance of turnover using permutational analysis of variance (PERMANOVA). To confirm the robustness of our results, we repeated this analysis using multivariate GLMs with the *mvabund* R-package instead of PERMANOVA, which yielded qualitatively similar results (Wang et al., 2012).

Second, we calculated the pairwise plant, bee and interaction β-diversity pooling all seasons together and for each season individually (i.e. 36 networks pooled and per season) and regressed it against environmental and spatial distances using Mantel tests with 1000 permutations to assess whether β-diversity had stronger relationships with environmental or spatial gradients and whether the patterns differed between the seasons. Spatial distance was the distance in km (Euclidean) and environmental distance was measured as the Euclidean distance in urbanization intensity between pairs of sites. We additionally repeated this analysis using Procrustean superimposition (*vegan* R-package), which yielded qualitatively similar results (Peres-Neto & Jackson, 2001).

Similar to species β-diversity that is influenced by the number of species present in a community, interaction β-diversity is expected to be influenced by interaction richness and frequency (i.e. network size) due to random sampling from the regional species pool (Burkle et al., 2016). We therefore used a null model approach to calculate standardized effect sizes (z-scores) of plant, bee, and plant–pollinator interaction β-diversity that allow comparisons of communities with different species richness and networks of different sizes (Dormann et al., 2009). To this end, we used a null model approach used for β-diversity within a single trophic level following Ponisio et al. (2016) and Marcacci, Gremion, et al. (2022) and adapted it for interaction networks (see White et al., 2022). Specifically, we created 1000 randomly assembled communities (with plant–pollinator interactions instead of species for interaction networks), maintaining species/interaction richness and abundances/frequencies (column and row sums) and drawing species/interactions with probabilities proportional to their relative abundance/frequency from the observed community. Next, we calculated the expected plant, bee and interaction β-diversity for each randomly assembled community. Lastly, we calculated standardized effect sizes as follows: $\beta_{SES} = (\beta_{obs} - \mathrm{mean}(\beta_{null}))/\mathrm{sd}(\beta_{null})$. Positive values of standardized effect sizes indicate higher β-diversity than expected given species/interaction richness and abundances/frequencies (overdispersion, e.g. aggregation of species or plant–pollinator interactions due to different local environmental conditions or dispersal limitations which increased β-diversity), whereas negative values indicate underdispersion, for example homogenization of plant–pollinator interactions due to environmental filtering (Burkle et al., 2022). Z-scores beyond ±1.96 (corresponding to a 95% confidence interval) are considered significantly higher or lower than expected by chance under a null model. We then regressed standardized effect sizes of plant, bee and interaction β-diversity against environmental and spatial distances using the same procedure as above. We repeated the same procedure for all seasons pooled together and for each season individually.

Underlying drivers of interaction β-diversity

To unravel the underlying drivers of plant–pollinator interaction β-diversity, we partitioned the total (whole network) interaction β-diversity (β_{WN}) of each network into four additive components accounting for species turnover driven by the lower trophic level (i.e. plant species; β_{STl}), species turnover driven by the higher trophic level (i.e. bee species; β_{STh}), species turnover driven simultaneously by both bee and plant species (β_{STlh}) and interaction rewiring (β_{OS}) (Burkle et al., 2022; Fründ, 2021; Novotny, 2009). Interaction rewiring includes interaction β-diversity resulting from switches in interacting partners, while the species composition of both bees and plants remains unchanged. We calculated total interaction β-diversity and its four additive components for each season using the *betalinkr()* function (with method = 'commondenom' for common denominator, which allows the additive partitioning of interaction β-diversity) as implemented in R-package *bipartite* (Devoto et al., 2021; Dormann et al., 2008; Fründ, 2021). Given the current debate (see Fründ, 2021; Poisot, 2022), we also partitioned interaction β-diversity using the 'poisot' method, which yielded comparable results.

First, we calculated interaction β-diversity pooling all seasons together and within each individual season to assess the contribution of the four components to total environmental and spatial interaction β-diversity, and whether their contribution differed between the seasons. To this end, we calculated total interaction β-diversity and its four components from pairwise combinations of

plant–pollinator networks between sites pooled over the three seasons and within each of the three seasons, that is site1-season1 vs site2-season1, etc. Second, we calculated temporal interaction β-diversity across the seasons. We followed Arroyo-Correa et al. (2020) and calculated total interaction β-diversity and its components from pairwise combinations of plant–pollinator networks of each site across the three seasons, that is site1-season1 versus site1-season2, etc. We then calculated the relative contribution of each component to the total environmental/spatial (between sites, within seasons) and temporal (within sites, between seasons) interaction β-diversity. Finally, we regressed each component against environmental and spatial distances using Mantel tests as above.

Effects of urbanization intensity on temporal turnover

We used total interaction β-diversity and its four components calculated between seasons within each site to investigate how temporal patterns of interaction β-diversity change along the urbanization gradients. To this end, we tested how grey area (fixed effect, continuous variable) influenced total temporal β-diversity and its four components using linear mixed-effects models with the *lme4* R-package (Bates et al., 2015). «Season-pair» and «site-IDs» were set as random intercepts to account for the non-independence of pairwise comparisons (seasons were included in different pairs, see Arroyo-Correa et al., 2020) and the species composition of the site. To investigate whether the turnover of plant species was independent of planting by people (i.e. reflecting human preferences for ornamental and agricultural plants), we repeated the analyses considering only crops, non-crop native plants and exotic plants (ornamental and invasive plant species). We categorized each plant species following Inderjit et al. (2018). All models' assumptions were checked with diagnostic plots and statistical tests using

the DHARMa R-package (Hartig, 2022) and all analyses were conducted in R version 4.0.2 (R Core Team, 2021).

RESULTS

We recorded in total 26,407 plant–pollinator interaction events (6188 in monsoon; 1924 in summer; 18,295 in winter) from 389 unique plant–pollinator interactions (227 in monsoon; 177 in summer; 167 in winter) involving 63 plant species (45 in monsoon; 45 in summer; 35 in winter) and 38 bee species (26 in monsoon; 28 in summer; 19 in winter). On average, there were 10.8 ± 3.3 (mean ± SD) plant species interacting with 11.5 ± 3.3 pollinators in each study site across the three seasons. See Tables S1 and S2 for species lists.

The site-averaged sampling completeness of interactions was $92\% \pm 9\%$ (mean ± SD), $86\% \pm 14\%$ and $99\% \pm 1\%$ for monsoon, summer and winter, respectively, indicating sufficient sampling. Although the sampling completeness was a bit lower in summer, it was still higher than in most plant–pollinator studies (e.g. 55% in Chacoff et al., 2012; 56% in Devoto et al., 2012; $50\% \pm 10\%$ in Grass et al., 2018; see also accumulations curves in Figures S1 and S2).

Compositional turnover across temporal and spatial gradients

Although both grey area and season had a significant effect on the composition of plant (season: $R^2 = 0.28$, $F = 21.18$, *p*-value < 0.001; grey area: $R^2 = 0.04$, $F = 6.70$, *p*-value < 0.001) and bee (season: $R^2 = 0.49$, $F = 52.38$, *p*-value < 0.001; grey area: $R^2 = 0.03$, $F = 6.23$, *p*-value < 0.01) communities and their interactions (season: $R^2 = 0.24$, $F = 16.90$, *p*-value < 0.001; grey area: $R^2 = 0.03$, $F = 4.60$, *p*-value < 0.001), the NMDS plots showed greater compositional differences between the three seasons than along the urbanization gradient (Figure 1), indicating stronger
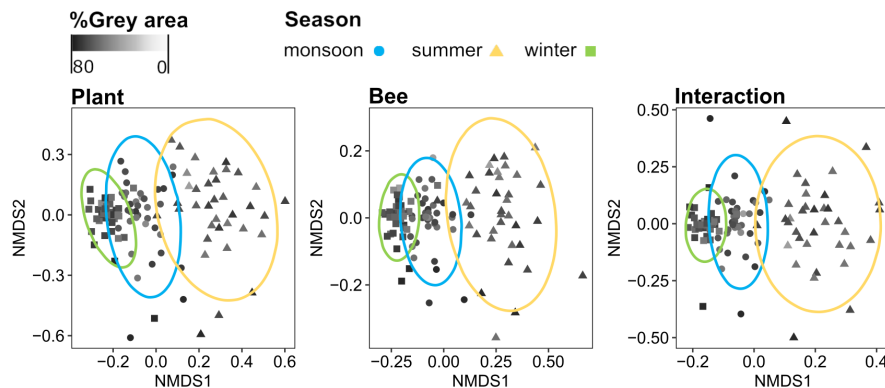
FIGURE 1   Non-metric multidimensional scaling (NMDS) plots showing changes in the composition of bees, plants and their interactions across the three seasons (circles = monsoon, triangles = summer, squares = winter) and the environmental gradient (grey area = proxy for urbanization intensity: The darker are the symbols, the more urbanized were the sites; note that grey area was log-transformed to increase the contrast of the plot).

temporal than environmental turnover (also shown by higher R^2 values for season).

β-diversity along environmental and spatial gradients

We found a positive correlation between environmental distance and observed plant, bee, and plant–pollinator interaction β-diversity for pooled seasons and each individual season (see Table 1). The same was true for standardized effect sizes, with plants and interaction networks that had low environmental distance being more similar (underdispersed) than randomly expected (Figure 2; Figures S3–S5). By contrast, there was no correlation with spatial distance

TABLE 1 Correlations (calculated via Mantel tests (R_m)) between plant, bee and interaction β-diversity (Bray–Curtis dissimilarity) and spatial and environmental distances for all seasons pooled together and each season individually. β_{Bray} = observed β-diversity; β_{SES} = standardized effect size (z-scores). Significant correlations are in bold font.

Response	Season	Spatial distance		Environmental distance	
		R_m	p-value	R_m	p-value
Plants					
β_{Bray}	Pooled	−0.059	0.817	0.59	**<0.001**
β_{Bray}	Summer	−0.003	0.522	0.285	**0.008**
β_{Bray}	Monsoon	−0.045	0.757	0.542	**<0.001**
β_{Bray}	Winter	−0.003	0.522	0.563	**<0.001**
β_{SES}	Pooled	−0.063	0.842	0.59	**<0.001**
β_{SES}	Summer	0.003	0.831	0.29	**0.007**
β_{SES}	Monsoon	−0.039	0.718	0.537	**<0.001**
β_{SES}	Winter	−0.061	0.831	0.556	**<0.001**
Bees					
β_{Bray}	Pooled	−0.069	0.896	0.499	**<0.001**
β_{Bray}	Summer	−0.049	0.731	0.216	**0.039**
β_{Bray}	Monsoon	−0.04	0.732	0.333	**0.008**
β_{Bray}	Winter	−0.048	0.768	0.492	**<0.001**
β_{SES}	pooled	−0.078	0.922	0.485	**0.002**
β_{SES}	Summer	−0.037	0.731	0.213	**0.033**
β_{SES}	Monsoon	−0.066	0.874	0.213	**0.047**
β_{SES}	Winter	−0.05	0.802	0.487	**0.002**
Interactions					
β_{Bray}	Pooled	−0.046	0.756	0.607	**<0.001**
β_{Bray}	Summer	−0.065	0.871	0.284	**0.007**
β_{Bray}	Monsoon	−0.051	0.796	0.551	**<0.001**
β_{Bray}	Winter	−0.037	0.69	0.57	**<0.001**
β_{SES}	Pooled	−0.052	0.795	0.604	**<0.001**
β_{SES}	Summer	−0.068	0.88	0.286	**0.005**
β_{SES}	Monsoon	−0.041	0.715	0.549	**<0.001**
β_{SES}	Winter	−0.041	0.723	0.562	**<0.001**

for any of the β-diversity indices tested. This indicates that variations in environmental conditions (i.e. urbanization intensity) had stronger effects on plant, bee and plant–pollinator interaction β-diversity than spatial distance.

Underlying drivers of interaction β-diversity

Total plant–pollinator interaction β-diversity between sites (environmental and spatial) was mostly driven by interaction rewiring (contribution to total β-diversity = 48%) followed by plant species turnover (44%), simultaneous turnover of plants and bees (6%) and bee species turnover (2%) (Figure 3). The same was true when considering each season individually (Figure S6). We found positive correlations between the turnover of plant species and the simultaneous turnover of both plant and bee species and environmental distance for each season (Table S3). Moreover, we found a positive correlation between interaction rewiring and environmental distance, but only in the winter season. In contrast, we only found a positive correlation between the simultaneous turnover of both plant and bee species and spatial distance in summer.

Results were qualitatively similar for total temporal interaction β-diversity, which was mostly driven by interaction rewiring (50%) followed by plant species turnover (32%), bee species turnover (10%) and simultaneous turnover of both plants and bees (8%). Total temporal interaction β-diversity (mean = 0.65) was higher than interaction β-diversity between sites (spatial and environmental; mean = 0.51), though we cannot test this difference as temporal and spatial/environmental interaction β-diversity are not directly comparable with this method.

## Effects of urbanization on temporal interaction β-diversity

Urbanization, measured as the amount of grey area surrounding study sites in a 500 m radius, had a positive significant effect on total temporal interaction β-diversity (estimate = 0.035, t = 3.084, p-value = 0.004) and the turnover of plant species (estimate = 0.019, t = 2.321, p-value = 0.026, Figure 4). This amplifying effect of urbanization increased total temporal interaction β-diversity by 45% and plant species turnover by 60% from low (0% grey area) to highly urbanized landscapes (80% grey area). This effect was driven by native non-crop plants (estimate = 0.015, t = 2.383, p-value = 0.025) and not by crop (−0.001, t = −0.703, p-value = 0.491) or exotic plants (estimate = −0.0001, t = −0.193, p-value = 0.848) (Figure 4).

DISCUSSION

Even though we can expect variations in the dynamics of plant–pollinator networks across environmental,
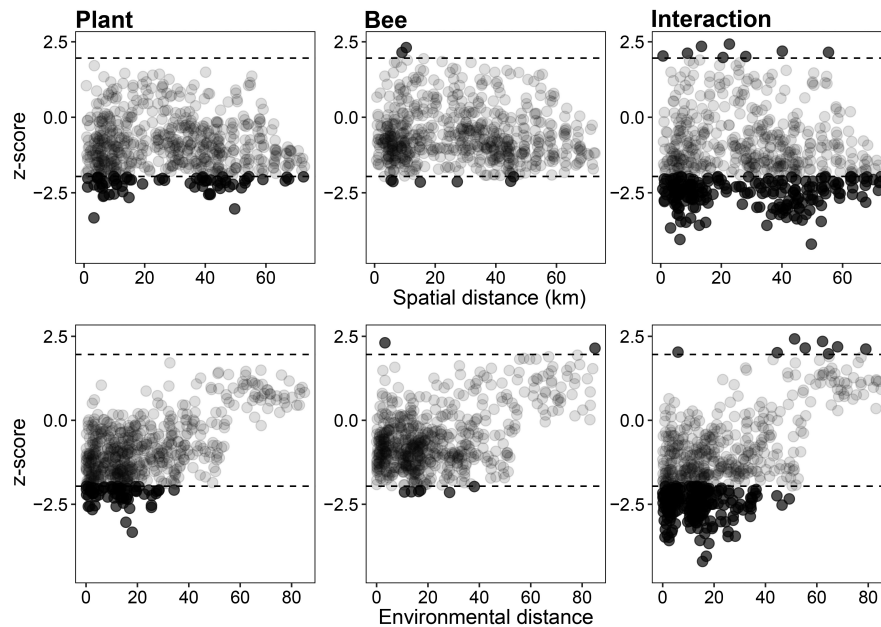
FIGURE 2 Relationship between standardized effect sizes (z-scores) of plant, bee and interaction β-diversity and spatial and environmental distances. Standardized effect sizes were calculated with null models of 1000 randomized communities. Spatial distance is the geographic distance in km between pairs of study site. Environmental distance is the Euclidean distance in grey area (proxy for urbanization intensity) between pairs of study sites. Values larger (overdispersed) or smaller (underdispersed) than 1.96 are considered to be significantly different from null expectation.
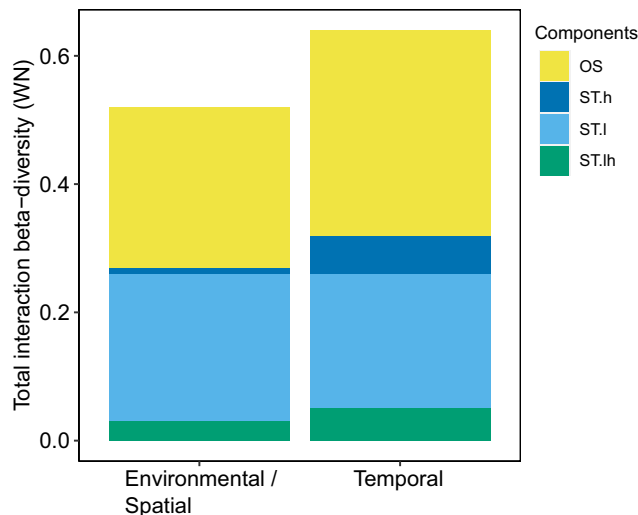
FIGURE 3 Contribution of the four components to total environmental/spatial and temporal interaction β-diversity (WN). Environmental/spatial β-diversity is calculated between study sites that vary in geographic distance and local environmental conditions (urbanization intensity). Temporal β-diversity is calculated within study sites across the three seasons. OS, interaction rewiring; ST.h, bee species turnover; ST.l, plant species turnover; ST.lh, simultaneous turnover of both bees and plants.

spatial and temporal scales, which of these gradients has the strongest influence on plant–pollinator interaction β-diversity is poorly known. Here, we found a higher plant–pollinator interaction turnover along the temporal than the environmental gradient. Indeed, although

urbanization also influenced the turnover of plant and bee communities, and their interactions, their composition differed more markedly between the three seasons than along the urbanization gradient (Figure 1). The composition of bee communities can greatly change with season (e.g. dry and rainy seasons; see Dzekashu et al., 2022; Samnegård et al., 2015), mediated by changes in floral resources availability and plant species composition (Fisogni et al., 2020). Although similar results have been reported in other studies conducted in different environments (e.g. Alpine meadows, agricultural areas; see Simanonok & Burkle, 2014; Tylianakis et al., 2005), the effects of urbanization on spatial and temporal turnover of plant–pollinator interactions are largely underexplored. Yet, in congruence with White et al. (2022), one of the few studies on the dynamics of plant–pollinator interactions in an urban setting, we found that anthropogenically induced environmental gradients, such as urbanization intensity, had stronger effects than spatial distance on plant–pollinator interaction β-diversity, and this applied for every season. Processes associated with urbanization, such as environmental filtering, may thus be more important than dispersal limitation for shaping the assembly and dynamics of plant–pollinator networks, at least for the spatial scale of our study. In line with White et al. (2022), part of the mechanism structuring the dynamics of plant–pollinator networks is environmental filtering of plant communities, and not bee communities, as only plant β-diversity was strongly associated with urbanization (Figure 2). This is further confirmed by the predominant contribution of plant species
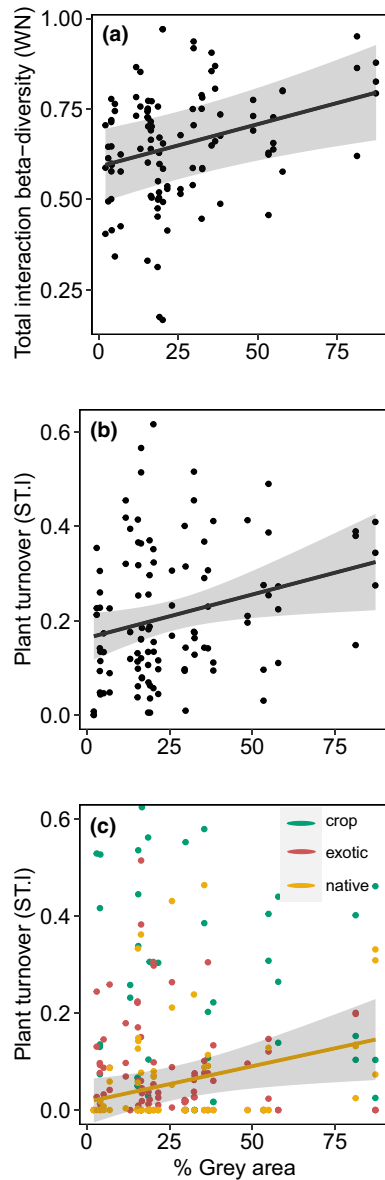
FIGURE 4 Effect of grey area (proxy for urbanization intensity) on total temporal interaction β-diversity (a), temporal turnover of all plant species (b) and temporal turnover of crops, non-crop native plants and exotic plants (c), between seasons within each site. Lines depict predicted means from linear mixed models, grey belts confidence intervals and dots the raw data.

with urbanization may alter the composition of plant–pollinator networks, such as loss or changes of nesting sites, availability of flowering resources, heat-island effects, preferences for ornamental plants or different farming practices (e.g. crop diversity or use of pesticides) between rural and urban farmers (Geppert et al., 2022; Prendergast et al., 2022; Wenzel et al., 2020).

Yet, these modifications are not only the results of filtering processes as urbanization can also influence the temporal dynamics of plant–pollinator networks. Indeed, we found that temporal interaction β-diversity was higher in urban areas because of the higher plant species turnover across seasons in urbanized landscapes (Figure 4). This finding is particularly relevant as it demonstrates that urbanization modulates the seasonal dynamics of plant–pollinator interactions, that is that interacting effects of temporal and environmental gradients drive the assembly of plant–pollinator interaction networks in urbanized landscapes (Fisogni et al., 2022). Urban green spaces are known to harbour a high diversity of flowering plants (including exotic plant species), often exceeding that of rural or natural areas, promoting plant species turnover in urban areas (Baldock et al., 2019; Lowenstein et al., 2019; see also Figure S7). In our study sites, farming activities are following the seasons with different crops grown throughout the year, which can further modify plant–pollinator interactions. Yet only the temporal turnover of native non-crop plant species increased with urbanization (Figure 4). This result is particularly important as it indicates that cities amplify the temporal turnover of plant species independently of whether they are planted or managed by people. This may imply that other mechanisms beyond direct plantings such as urban warming or specific local environmental conditions are responsible for this higher seasonal turnover of plant–pollinator networks in more urban areas. It has already been demonstrated that urbanization modifies the phenology of plants but not their pollinators, causing phenological mismatch, which could have important implications on the delivery of pollination services of native and cultivated plant species (Fisogni et al., 2020, 2022). The causes and mechanisms of this temporal alteration of plant–pollinator networks in urbanized landscapes as well as their consequences for the stability of mutualistic networks need to be further investigated, both in temperate and tropical regions. This is especially important given the rapid encroachment of cities on agricultural landscapes in the tropics.

While plant communities change faster in urbanized landscapes, the strong contribution of interaction rewiring to overall interaction β-diversity suggests that urban bees are highly flexible in making use of these temporally variable flower resources (Noreika et al., 2019). It has already been shown that a high diversity and turnover of plant species increases interaction rewiring (Dzekashu et al., 2023; Schwarz et al., 2020). This high flexibility of pollinators in their choice of plant partners may even

turnover to total interaction β-diversity, while bee species turnover was marginal (Figure 3). This emphasizes how urbanization can alter asymmetrically plant and bee communities, and the dynamics of their interactions (e.g. see Poisot et al., 2012). We further found that plant communities and plant–pollinator interactions that occur in landscapes of similar urbanization intensity were more similar than random expectations (Figure 2). This indicates processes of homogenization due to local environmental filtering within urbanization classes (e.g. networks within urban areas are more similar among them than those in rural areas, and vice versa; see White et al., 2022). Different environmental factors associated

be more important in urban areas, which favour generalist pollinators that can benefit from the high diversity of native and non-native flowering resources (Garbuzov et al., 2015; Geslin et al., 2013; Wenzel et al., 2020). The ability of bees to change plant partners may thus represent an advantage across the seasons. In temperate regions, past the peak flowering season of native plants, urban bees have been found to shift their plant partners and become increasingly reliant on non-native plant species, the latter allowing them to extend their flying period later in the year when native flowering resources are scarce (Staab et al., 2020). Likewise in the tropics, the high temporal flexibility of urban bee species may stabilize plant–pollinator interactions throughout the year (Stewart & Waitayachart, 2020). Therefore, to conserve plant–pollinator networks and associated ecosystem functions and services in urbanized landscapes, identifying key flowering resources that maintain and connect interaction networks across the seasons would provide critical information for the conservation of wild bees and their interactions (e.g. see Tew et al., 2022).

Study limitations and open questions

Although this study is one of the first to provide insights into the individual and interactive effects of urbanization and seasonality on plant–pollinator interaction β-diversity in a tropical megacity, it has some limitations. For example, we only sampled bees and no other groups of pollinators, resulting in lower richness in the upper trophic level. Asymmetric networks in the plant's direction are increasing the likelihood of plant species turnover, potentially masking other effects driven by urbanization. This is a general weakness of studies on interaction networks as we still lack a mechanistic understanding of the observed patterns beyond what is explained by the network structure. For example, we found that urbanization amplifies the temporal turnover of plant–pollinator interactions due to higher seasonal turnover of native non-crop plants in urban areas. Yet we cannot draw from our results which mechanisms link phenological and environmental filtering processes to the observed patterns and what are their consequences for the functioning of urban ecosystems. In this context, the field would benefit from a simulation study allowing to tease apart patterns arising purely from the structure of interaction networks ('statistical inevitability', see Dormann et al., 2009) and ecological processes. Another potential way forward is to integrate ecological details such as functional traits of the partners involved in key interactions. Indeed, as biodiversity response to urbanization is often trait-specific (Marcacci, Grass, et al., 2022), including species functional traits can help providing a mechanistic understanding linking the observed patterns to their underlying ecological causes and consequences on ecosystem functioning. Another limitation in urban ecology studies is that they often use one environmental indicator of urbanization (i.e. proportion of grey area in our study), neglecting many other stressors that are associated with urbanization such as modified abiotic conditions (e.g. temperature) or pollution (e.g. air, light, chemical) that can act as environmental filters and alter plant–pollinator networks (Geppert et al., 2022; Guenat & Dallimer, 2023). For instance, urban areas are known to be warmer than the surrounding environment (i.e. heat-island effect), which can have great implications on the phenology of plants and pollinators, potentially causing mismatch between the activity of two interacting partners or modifying important network properties (Fisogni et al., 2020). These open questions require urgent investigations to improve our understanding of the complex and multifaceted effects of urbanization on species interactions.

CONCLUSION

How environmental, spatial and temporal gradients interact to shape the dynamics of plant–pollinator interactions across rural–urban landscapes is poorly understood, especially in the tropics. Our study provides novel insights on how urbanization shapes the assembly of plant–pollinator interaction networks and their dynamics in an understudied part of the world. This is particularly important given that most ongoing and future urban expansion concerns tropical regions, which experience different environmental, climatic and social constraints than temperate cities. In addition, our results add to the recent literature demonstrating the large temporal turnover in species interactions, highlighting the importance to consider seasonality in plant–pollinator studies. As this study was conducted in Bangalore, one of the fastest-growing cities in the world that exemplifies key characteristics of urbanization in tropical regions, our finding may help to understand and predict the effects of urbanization on plant–pollinator networks in other megacities in India and elsewhere in the tropics. Yet, if we are to draw conclusions on how urbanization drives the dynamics of ecological interactions across biogeographical regions, more studies need to be conducted in tropical regions. Only in doing so we can attempt to establish generalized principles of community ecology and biogeography of interaction networks in urbanized landscapes, and our study is a first step in this direction.

AUTHOR CONTRIBUTIONS
Teja Tscharntke, Ingo Grass and Catrin Westphal conceived and designed the study with the help of Vasuki V. Belavadi and K. B. Tharini. Vikas S. Rao and Shabarish Kumar S. collected the biodiversity data. Nils Nölke

CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

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