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RESEARCH ARTICLE

Direct and indirect effects of urbanization, pesticides and wild insect pollinators on mango yield

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Abstract

1. Expanding cities increasingly encroach fertile farmlands, questioning the viability of maintaining agriculture within and around them. Yet, our knowledge on how urbanization influences pollinator communities and the provision of pollination services to crops is limited, especially for the urbanization hotspots of the Global South.
2. Mango *Mangifera indica* is one of the most important fruit crops in tropical countries. To analyse the dependency of mango on its main insect pollinators, and the direct and indirect effects of urbanization and insecticides on pollinator abundance and mango yield, we conducted a pollinator exclusion experiment and sampled flower visitors on 16 mango farms spread across rural–urban landscapes in Bengaluru, a South Indian megacity.
3. We found that allowing flowers access to ants and flying visitors (bees, hoverflies, nonsyrphid flies), dramatically increased mango yield by 350%, highlighting the importance of wild insects for mango pollination. We detected a trend between wild bee abundance and the final fruit set, with an increase of 20% when the number of bees increased from 25 to 125.
4. Urbanization did not directly affect pollinator abundance or mango yield. However, the amount of insecticide applications had strong negative effects on wild bee abundance at low and intermediate levels of urbanization, while it had no effect in highly urbanized areas, presumably because of higher availability of flowering resources. Moreover, the amount of insecticides decreased the weight of harvested mango fruits by almost 30%. This may indicate trade-offs between conventional pest control and enhanced crop yields through pollination by wild insects in rural areas.

5. *Synthesis and applications*: Our results indicate that mango production can be maintained at a profitable level in urbanized landscapes with insect pollinators more than tripling final yield. However, increasing use of insecticides, besides raising farmers' expenses, can have negative effects on wild insect pollinators and mango yield, especially in rural areas. To safeguard crucial pollination services, it is therefore critical to conserve and promote wild insect pollinators by minimizing the negative effects of insecticide applications in these areas.

KEYWORDS
Bangalore, ecosystem services, India, insecticides, management trade-offs, mango pollinator, urban agriculture

1 | INTRODUCTION

Urbanization, one of the most severe forms of land use intensification, alters biodiversity and the functioning of natural ecosystems (Marcacci et al., 2021; Simkin et al., 2022). At the same time, expanding cities increasingly compete with agricultural landscapes, threatening food security, especially in the Global South (Gu et al., 2019; van Vliet et al., 2017). Yet, urban agriculture is becoming increasingly popular with already millions of urban farmers producing an important share of global crops (Orsini et al., 2013; Zezza & Tasciotti, 2010). By contrast, the question whether agricultural activities can be maintained at a profitable level in urbanized landscapes has so far received little attention.

As one third of global crops depend on animals, mostly insects, for their pollination (Aizen et al., 2019; Klein et al., 2007), conserving insect pollinators is critical. Consequently, it is of great importance to foster the provisioning of pollination services to crops across rural–urban landscapes. However, pollinators are declining due to different factors ranging from land use change, intensification of agricultural practices (e.g. widespread use of pesticides), landscape homogenization, loss of flowering resources and nesting sites to pathogens and invasive plant species (Goulson et al., 2015; Potts et al., 2010), and many of these factors are associated with urbanization (Wagner et al., 2021). For example, urbanized landscapes are highly fragmented and pollinators have to travel long distances to find the floral resources they need, while natural habitats are converted into sealed surfaces (Burdine & McCluney, 2019; Marcacci et al., 2022; Wenzel et al., 2020).

Nevertheless, an increasing body of studies suggest that cities can host diverse and abundant pollinator communities, at least in comparison to modern intensive agricultural landscapes (Baldock et al., 2015; Wenzel et al., 2020). In particular, urban green spaces, such as gardens, allotments or parks, can provide enough food resources and nesting opportunities for pollinators (Baldock et al., 2019; Banaszak-Cibicka & Żmihorski, 2020). However, although our understanding of the effects of urbanization on pollinator communities has recently received a lot of research attention, less is known on how urbanization drives pollination outcomes of different crops. The few pollination studies conducted in urbanized landscapes reported mixed outcomes with results ranging from negative effects of urbanization on the provision of pollination services to crops (Pellissier et al., 2012), no effects (neutral) (Potter & Lebuhn, 2015; Theodorou et al., 2020; Wenzel et al., 2022) to positive effects (Eckerter et al., 2022). But tropical regions, which are hotspots of urbanization, remain largely understudied (Silva et al., 2021; Wenzel et al., 2020). Moreover, potential interactions between urbanization and agricultural management practices on crop yield have rarely been studied.

In this study, we focus on mango *Mangifera indica* L., one of the most important tropical fruit crops (FAO, 2022). India is the centre of origin for mangoes and is one of the largest producers worldwide (FAO, 2022). Mango flowers are visited by a diverse community of crawling (i.e. ants) and flying (i.e. bees, flies) insects and despite the fruit's global popularity, it still remains unclear which species groups are the most effective pollinators (Ramírez & Davenport, 2016). Several insect pests (e.g. leafhoppers, weevils, mealybugs, fruit flies) can damage mango flowers and fruits, causing yield loss (Peng & Christian, 2005). Consequently, mango trees are sprayed preemptively with copious amounts of pesticides, including neonicotinoid insecticides that are known to severely harm bee communities (Blacquière et al., 2012; Rundlöf et al., 2015). However, the effects of pesticide applications on the delivery of ecosystem services such as crop pollination are poorly known. Being a traditional and important fruit crop, mango cultivation is simultaneously prone to agricultural intensification and urbanization. Yet until now, no studies have investigated the combined effects of urbanization and insecticide use on pollinators and their pollination services to mango in an urban setting.

To fill this knowledge gap, we investigated the direct and indirect effects of urbanization and insecticide use on pollinator communities and pollination of mango across rural–urban landscapes in Bengaluru, a South Indian megacity. We conducted a pollinator exclusion experiment and sampled flower visitors in mango farms spread along an urbanization gradient to answer three main questions. (1) Are mango yields increasing with flower visitation? (2) Which species groups are the most important pollinators of mango? (3) How do urbanization and the amounts of insecticides used affect the abundance of insect pollinators and their pollination services?

2 | MATERIALS AND METHODS

2.1 | Study area

This study was conducted in Bengaluru (Bangalore), a South Indian megacity, capital of the state of Karnataka (Figure 1). Bengaluru has a population of 12.8 million inhabitants and is the second fastest growing city in India after New Delhi (UN World Urbanization Prospects, United Nations, 2018; https://esa.un.org/unpd/wup/). Bengaluru is located in an important mango-producing region. However, mango farms are increasingly encroached by expanding urban areas, resulting in a mosaic of farmlands and urbanized areas (Nagendra et al., 2012).

Bengaluru is situated on the Deccan Plateau at an elevation of 920 m a.s.l. with a moderate tropical climate with temperatures ranging between 12 and 38°C and an annual average precipitation of about 800 mm. Mango trees start flowering at the end of the post-monsoon season (winter) in January and are harvested between May and June (end of the dry season) just before the onset of the monsoon.

2.2 | Study design

We selected 16 mango farms (mean size = 3.35 ha ± 6.34 SD) spread along a transect extending from urban Bengaluru towards rural villages, thus representing a rural–urban gradient (Figure 1). We kept a minimum distance of 1000 m between two mango farms to ensure their independence. We quantified urbanization intensity as the amount of grey area (also called impervious or built-up area; i.e. all sealed surfaces, such as roads, buildings, etc.), a typical proxy of the degree of urbanization (e.g. Geslin et al., 2016; Wenzel et al., 2022). We extracted information on grey area by applying remote sensing techniques on a 10 m spatial resolution cloud-free satellite image (Sentinel-2 L2A) acquired in December 2020. 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 within a 2000 m radius around the centroid of each mango farm. A radius of 2000 m was found to be the best spatial scale to explain the abundance of pollinators in our study region (Marcacci et al., 2022).

Although all mango farms were conventionally managed, they were also selected along a gradient of insecticide use (range = 0–300 L of insecticides per tree, see Section 2.5). Because not all mango varieties have the same dependency on insect pollination (Huda et al., 2015; Ramírez & Davenport, 2016), we only selected farms cultivating the variety *Badami* (also called *Karnataka Alphonso*), which is the most widespread variety in our study region. Nevertheless, other varieties such as *Totapuri*, *Mallika or Neelam* were often also cultivated within the same farm. Fieldwork was conducted between December 2020 and June 2021. All mango farmers and owners granted us the permission to work on their farm.

2.3 | Pollinator exclusion experiment

In each farm, we selected eight mango trees (four at the edge of the farm, four in the middle to account for potential differences in pollinator abundance and the delivery of pollination services between the edge and the centre of the farm) with one inflorescence per treatment tree, on which we carried out the pollinator exclusion experiment with three treatments (i.e. three inflorescences per tree), following Carvalheiro et al. (2010). Specifically, we excluded (1) all flying (i.e. bees, flies, hoverflies) and crawling (i.e. ants) flower visitors by bagging the inflorescences with a fine mesh bag using a wire structure to avoid any contact between the mesh and the flowers, thus preventing any damage. Additionally, we placed a sticky trap at the base of each inflorescence to prevent the visit of any potential crawling flower visitors. We took special care to remove branches, twigs and leaves that could serve as bridges to access the inflorescence. As second treatment, we excluded (2) only crawling flower visitors by placing the sticky trap, but not the mesh bag, therefore allowing flying flower visitors to visit the inflorescence. Finally, as third treatment, (3) the inflorescence was left 'open' to make it accessible to both crawling and flying flower visitors. All inflorescences were checked twice every month to renew the sticky trap and make sure that the mesh bag was not damaging the flowers. We recorded the initial fruit set (number of developed but still immature fruits per inflorescence treatment) 3 months after the start of the flowering period, and the final fruit set (number of mature fruits) at the time of the harvest. We also weighed the harvested fruits and calculated the mean fruit weight per inflorescence. Since mango is a mass-flowering tree with each inflorescence comprising several hundreds of tiny flowers (males, females and hermaphrodites) that bloom over an extended period, we could not conduct a hand pollination treatment or measure the fruit set as the proportion of flower setting fruits.

2.4 | Flower visitor sampling

We sampled all flower visitors along two 50 × 2 × 2 m transect walks per farm. One transect was located at the edge and one at the centre of the farm. Since we did not find differences in pollinator abundance ($p > 0.1$), both transects were pooled for the analyses. All transect walks were conducted between 9:00 AM and 2:00 PM (preliminary surveys revealed that there were fewer insects after 2:00 PM) under good weather conditions (no rain, no cloud, low wind, 20–30°C). All insects visiting mango flowers (i.e. potential pollinators) within 20 min (per transect) were sampled with sweep nets (two survey rounds in each farm). Pollinators were identified in the field whenever possible or otherwise taken to the laboratory where a taxonomic expert (Tharini K. B. from Department of Agricultural Entomology of the University of Agricultural Sciences, GKVK, Bangalore) identified the specimens. Some specimens were only identified to the genus or family level and morphospecies were used for analyses. All collected specimens are kept in the Department of

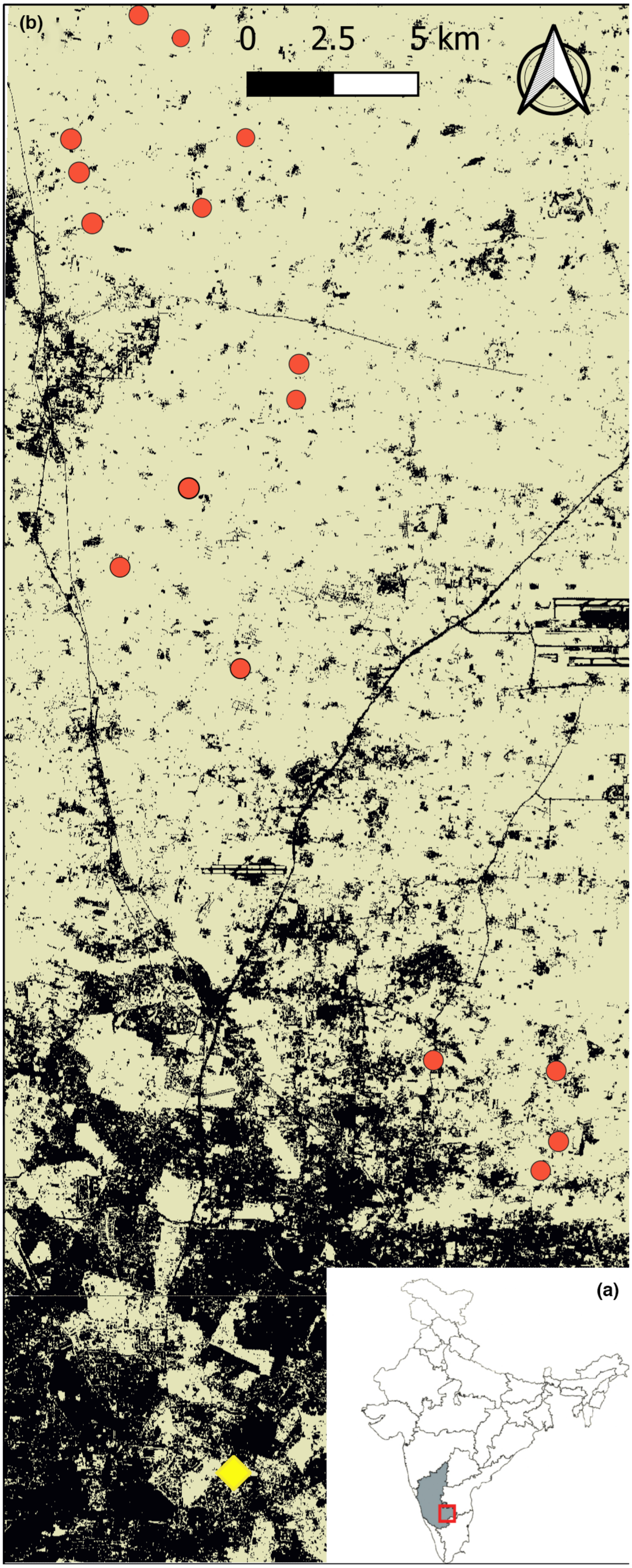

FIGURE 1 Map of India (a) with the state of Karnataka highlighted in grey and the study area with the red rectangle. Study area (b) with grey areas (sealed surfaced such as roads and buildings) in black and nongrey areas in beige. The red dots depict the 16 study sites (mango farms). The yellow diamond depicts the city centre.

Agricultural Entomology of the University of Agricultural Sciences, GKVK, Bangalore. To the best of our knowledge, there were no managed honeybees in our study farms, nor in the immediate surroundings and we assume to have only recorded wild bees. We also estimated the total number of open mango flowers within the transect. As mango is a mass-flowering tree, we counted the number of open flowers of three randomly selected inflorescences and multiplied their average by the total number of inflorescences recorded within the transect (Carvalheiro et al., 2010).

2.5 | Insecticides

We conducted targeted interviews to investigate the intensity of management practices in terms of pesticide use. For this analysis, we only considered insecticides, such as chlorpyrifos, clothianidin, cyhalothrin, fenpropathrin, imidacloprid and profenofos. All these insecticides are known to be harmful for pollinators (Blacquière et al., 2012). We asked the mango farmers for the amount (number of litres) of each insecticide they were spraying per mango tree for each application. Since all farmers were using the same insecticides, we summed up the total amount of insecticides sprayed in litre per tree as a proxy for insecticide use. Note that here the number of litres is estimated after dilution of the active substance (usually at a concentration of 1–1.5 mL/L water).

The presented work is based on a collaborative project of DFL (FOR2432: Social-Ecological Systems in the Indian Rural–Urban Interface: Functions, Scales, and Dynamics of Transition) with the University of Agricultural Sciences, Bangalore and Ashoka Trust for Research in Ecology and Environment, Bangalore. Fieldwork was conducted in private property with permission from of the land holders. All respondents gave their consent verbally before starting the interviews.

2.6 | Statistical analyses

We first tested the effect of the exclusion treatments on mango yield ($n = 128$). We ran generalized linear mixed-effects models (R-package GLMMTMB; Brooks et al., 2021) with initial fruit set (number of developed but still immature fruits per inflorescence treatment), final fruit set (number of mature fruits at harvest) and mean weight of mature fruits at harvest as response variable, the pollinator exclusion treatment as fixed effect and 'tree-ID' nested within 'site-ID' as random intercepts. We selected the best error distribution for each model based on model diagnostics and AICc values (Akaike information criterion corrected for small sample size). The initial fruit set was modelled with a Poisson error distribution and the weight with a Gaussian error distribution. There were very few inflorescences that produced more than one mature mango fruit, causing model convergence problems. We therefore modelled the final fruit set as a binomial response, which reflects the probability of an inflorescence to produce at least one mature mango fruit. We added the position of the tree (edge or centre) as covariate to account for potential edge effects. We further performed post-hoc Tukey tests for pairwise comparisons of predictions between each treatment with the EMMEANS R-packages (Lenth et al., 2021). We calculated marginal and conditional R^2 for mixed models with the PERFORMANCE R-package (Lüdecke et al., 2021).

Second, we averaged the initial fruit set and the fruit weight per farm (over the eight trees used in the exclusion experiment, only from open pollinator treatment) and calculated the probability of each inflorescence to produce at least one mature fruit (final fruit set). We also retained the maximum number of individuals of each group of flower visitors across the two sampling rounds as a conservative measure of flower visitor abundance. Next, we built structural equation models (SEMs) to investigate the direct and indirect effects of urbanization and insecticides use on mango flower visitors, and their subsequent effects on mango yield. We used a method called generalized multilevel path analysis, or piecewise SEM, which allows to test causal relationships with a relatively low sample size and to use a large variety of response distributions (Lefcheck, 2016; Shipley, 2009). We first built one hypothetical SEM for each 'yield variable', which were initial fruit set, final fruit set and weight. We combined four GLMs for each hypothetical SEM. In the first three GLMs, we tested the effects of urbanization (proportion of grey area within 2000 m) and insecticide use (number of litres per tree), as well as their interaction on the respective abundances of wild bees, hoverflies and nonsyrphid flies (group containing flies from various families), with one model per flower visitor group. We could not run models with ant abundance because their numbers were too low. We added the number of open mango flowers as covariate to correct for local variation in flowering resources. In the fourth GLM, we tested the subsequent effects of the abundance of each of the three flower visitor groups, as well as the direct effects of urbanization and insecticide use on mango yield (initial fruit set, final fruit set, weight). We added the age of the mango trees as covariate to control for potential variations in terms of yield between younger and older mango trees. As we expected correlations between wild bee, hoverfly and nonsyrphid fly abundances, we specified a correlated errors between these variables. Flower visitor abundances were modelled with a negative binomial distribution (MASS R-package; Venables & Ripley, 2002). The initial fruit set was modelled with a Gamma (log link) distribution, the final fruit set with a binomial distribution, and the weight with a Gaussian distribution. The best error distributions and model structure were selected prior to building the SEMs. Second, we used Shipley's d-separation test to detect missing paths and to assess the goodness-of-fit of the three hypothetical SEMs with Fisher's C statistics. We then manually added significant missing paths and stepwise deleted nonsignificant paths until AIC was no longer reduced. The diagnostics of each individual model within the final SEMs were verified with the DHARMA R-package (Hartig, 2021) and we used the variance inflation factor (VIF) to check for collinearity (CAR R-package; Fox & Weisberg, 2019). All variables had a VIF value <5. Finally, as the more urban farms were spatially clumped, we checked for spatial autocorrelation the residuals of all individual

GLMs using Moran's *I* tests (DHARMa R-package), and we did not detect any evidence of spatial autocorrelation (all $p > 0.05$). All statistical analyses were conducted in R version 4.0.2 (R Core Team, 2021).

3 | RESULTS

Overall, we recorded 3859 mango flower visitors belonging to 16 species or morphospecies. Species were represented by the following orders and families (number of individuals per family is given in brackets): Diptera: Syrphidae (638), other Diptera (including Muscidae, Calliphoridae and Bombyliidae) (883), Hymenoptera: Apidae (2323), Hymenoptera: Formicidae (15). The three most abundant species were (number of individuals in brackets) *Apis florea* Fabricius (1809), *Eristalinus* sp (539), *Chrysomya* sp1 (534). On average, we recorded 80.50 ± 39.9 (mean $\pm$ SD throughout) flower visitors and 4.3 ± 1.6 species per transect walk. See Table S1 in Supporting Information for the list of all species recorded.

3.1 | Pollinator exclusion experiment

The pollinator exclusion experiment revealed that both crawling (ants) and flying insect visitors (wild bees, hoverflies and nonsyrphid flies) significantly contributed to mango pollination, increasing pollination outcomes, that is, initial and final fruit sets and fruit weights (Table S2, Figure 2). When both crawling and flying visitors were excluded, almost no fruit were produced: initial fruit set (0.36 ± 0.8 fruit), final fruit set (0.2 ± 0.4 fruit) and their weight at harvest was lighter (281.12 ± 54.86 g). Allowing flying visitors to pollinate mango flowers significantly increased the initial fruit set (0.9 ± 1.1) and the final fruit set (0.5 ± 0.5) by 150% and the fruit weight by 11% (311.45 ± 48.04) compared to the pollination exclusion treatment. When both crawling and flying visitors could visit mango flowers, the initial fruit set further increased by 167% (2.4 ± 1.6), the final fruit set by 80% (0.9 ± 0.3) and the fruit weight by 8% (337.63 ± 48.04).

3.2 | Direct and indirect effects of urbanization, pesticide use and flower visitors on mango yield

All SEMs fitted the data well (initial fruit set: $C = 18.994$, $p = 0.522$; final fruit set: $C = 19.086$, $p = 0.387$; weight: $C = 20.629$, $p = 0.299$), and no important paths were missing (no independence claims remained significant; see Table S3 for best-fitting SEMs). The SEM analysis revealed a significant interaction effect of urbanization and insecticide on wild bee abundance: the amount of insecticide use had a strong negative effect on wild bee abundance only at low and intermediate levels of urbanization, while it had no effect in highly urbanized area (Figures 3 and 4). Moreover, the age of mango trees also had a negative effect on wild bee abundance, but it had a positive effect on the initial fruit set. Subsequently, wild bee abundance had a marginally significant positive effect on the final fruit set, with mango inflorescences having a 20% higher probability to produce

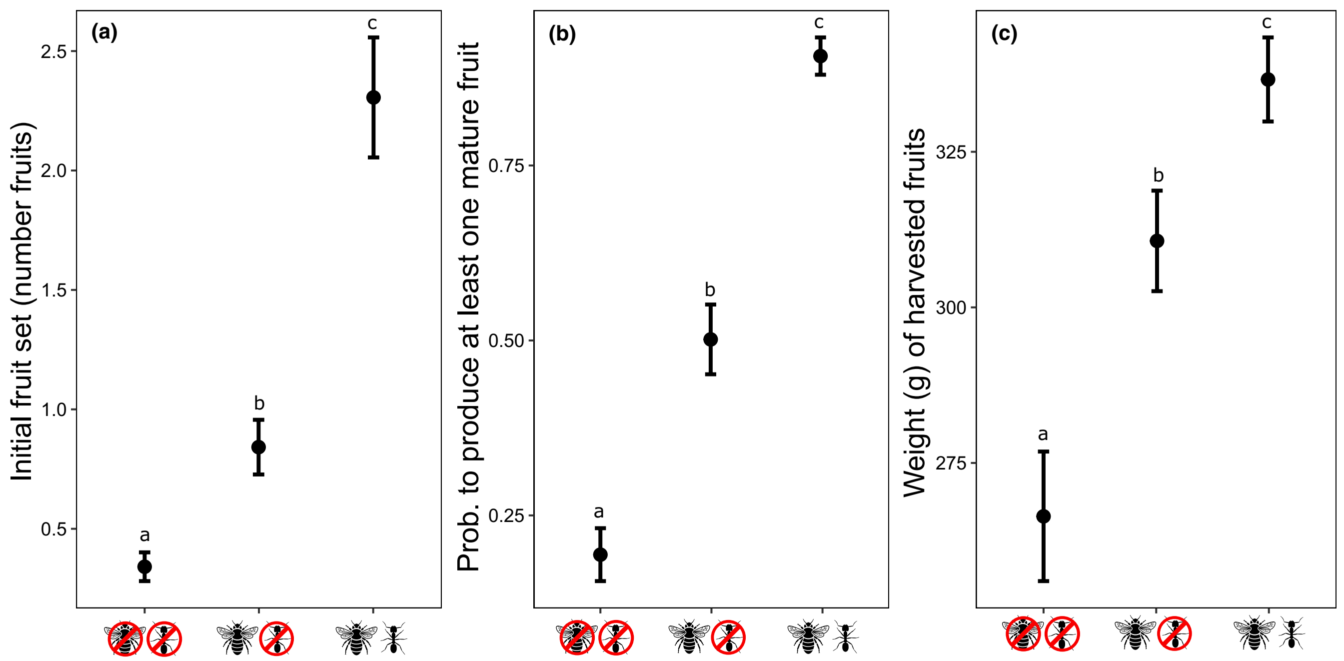

FIGURE 2 Effect of the pollinator exclusion treatment on (a) the initial fruit set (number of immature fruits 3 months after the start of the flowering period), (b) the final fruit set at harvest (probability that an inflorescence produces at least one mature fruit) and (c) the mean weight (g) of mature fruits at harvest. The pollinator exclusion treatments from left to right: both flying and crawling flower visitors were excluded, only crawling flower visitors were excluded, the inflorescence was accessible to both flying and crawling flower visitors. The dots depict the predicted means from generalized linear mixed-effects models and the error bars the 95% confidence intervals. Different letters represent significant differences between the treatments calculated via post-hoc Tuckey tests.

at least one mango fruit when the number of bees in the transect increased from 25 to 125. The amount of insecticide use had a direct negative effect on the mean fruit weight at harvest, which decreased by 29.7% from 0 to 300 litres of insecticide applied per tree (Figures 3 and 4). Regarding the other flower visitors, only the number of open mango flowers had a positive effect on hoverfly abundance, and we did not find any relationship with nonsyrphid fly abundance.

4 | DISCUSSION

4.1 | Wild insect pollinators increased mango yield

Wild bees (honeybees such as *A. florea* and stingless bees *Tetragonula* spp.), hoverflies (e.g. *Eristalinus* spp.), nonsyrphid flies (e.g. Muscidae, Calliphoridae) and ants were the main flower visitors and potential pollinators. Excluding flying visitors significantly reduced mango yield, which demonstrates that they are effective pollinators of mango, as already reported in other studies (e.g. Carvalheiro et al., 2010). The results of our study, conducted in the country of origin of mango, indicate that this also seems to be the case within an urban and peri-urban setting. The importance of both managed and wild bees for mango pollination is well established. For instance, managed honeybees are used in South Africa (Carvalheiro et al., 2010), and stingless bees in Australia (Anderson et al., 1982) to enhance pollination outcomes. But we did not record any managed bees (managed stingless bee colonies are not yet used by farmers in our study region), highlighting the dependency of mango on wild insects for its pollination. Flies (Diptera), and in particular hoverflies (Syrphidae) and blowflies (Calliphoridae) were already identified as important mango pollinators in other regions (e.g. Australia, Israel, India, see Anderson et al., 1982; Dag & Gazit, 2000; Kumar et al., 2021), and our study confirms their importance. In addition, we found that excluding ants (the only crawling flower visitor in our study) further reduced mango yields, highlighting that they too play a role in the pollination of mango. Carvalheiro et al. (2010) even attribute ants a predominant role for mango pollination. Although we observed ants in high numbers during some of our visits, surprisingly, very few ants were recorded during our transect walks. Nevertheless, we often found dead ants on the sticky traps from the pollinator exclusion experiment that prevented them from visiting the mango flowers. Perhaps, the social behaviours of the ants, temporal staggering of their activity with flying insects and their patchy distribution within the farm could have led to low encounters rates during the transect walks. Moreover, our exclusion experiment did not allow us to quantify the contribution of ants alone since we did not exclude flying visitors and allow ants to visit mango flowers. We contend that this is a limitation of our study and the role and contribution of ants to mango pollination need to be further investigated.

Although a diverse community of flower visitors visited mango flowers, we only found a positive, marginally significant effect of the abundance of wild bees on the final fruit set. This finding suggests that they are the most effective flying pollinators of mango in the context of Bengaluru. This result contrasts with other studies that found that flies were the most important insect group for mango pollination (see Rader et al., 2016), which highlights the importance to consider regional specificities as pollinator communities can greatly vary between geographic regions. Furthermore, Rajan and Reddy (2019) conducted a controlled pollination study in Bengaluru and found that blowflies (genus *Chrysomya*) were as efficient as *A. florea* for mango pollination and enhancing fruit set. However, as *A. florea* was the most abundant pollinator across rural–urban landscapes, they may play a predominant role for mango pollination in urban areas. However, results from the exclusion experiment suggest that ants also contribute significantly to mango yield. As we did not analyse the effects of ant abundance on mango yield because we did not encounter many ants in our transects, we cannot conclude which is the most important insect group for mango pollination.

4.2 | Direct and indirect effects of urbanization and insecticides on mango yield

Insecticide use had a strong negative effect on wild bee abundance and mean fruit weight at harvest (Figures 3 and 4). This result suggests that with increasing insecticide applications, mango flowers received less visits, impacting pollination effectiveness and, in turn, yield. The negative effect of insecticides on insect pollinators is well established (Blacquière et al., 2012; Goulson et al., 2015; Rundlöf et al., 2015), even in our study region (Steinhübel et al., 2022; Wenzel et al., 2022). However, these negative effects were only present at mid and low levels of urbanization (i.e. peri-urban and rural areas), and absent in highly urbanized areas. There could be several hypotheses explaining this finding. First, although it is expected that urbanization is associated with more intensive agricultural management, this is the contrary in our study area, notably due to high opportunity cost in urban areas through improved access to off-farm activities (Steinhübel & von Cramon-Taubadel, 2020). Second, many studies demonstrated positive effects of urbanization on bees and other flower-visiting insects (Baldock et al., 2019; Theodorou et al., 2020; Wenzel et al., 2020). Urban green spaces such as parks, gardens, allotments and vacant lots often have a higher availability and diversity of both native and exotic flowering plants (Banaszak-Cibicka & Żmihorski, 2020; Turo et al., 2021), sometimes even exceeding that of natural areas (Baldock et al., 2019). Consequently, flower-visiting insects can concentrate in urbanized areas, which may compensate for the negative effects of pesticides. It is also noteworthy that urbanization did not affect any of the pollination outcomes we tested. This result is in line with other studies from both temperate and tropical regions suggesting that urbanization does not necessarily induce pollination limitation and that it is possible to maintain agricultural activities at a profitable level (e.g. Eckerter et al., 2022; Potter & Lebuhn, 2015; Theodorou et al., 2020; Wenzel et al., 2022).

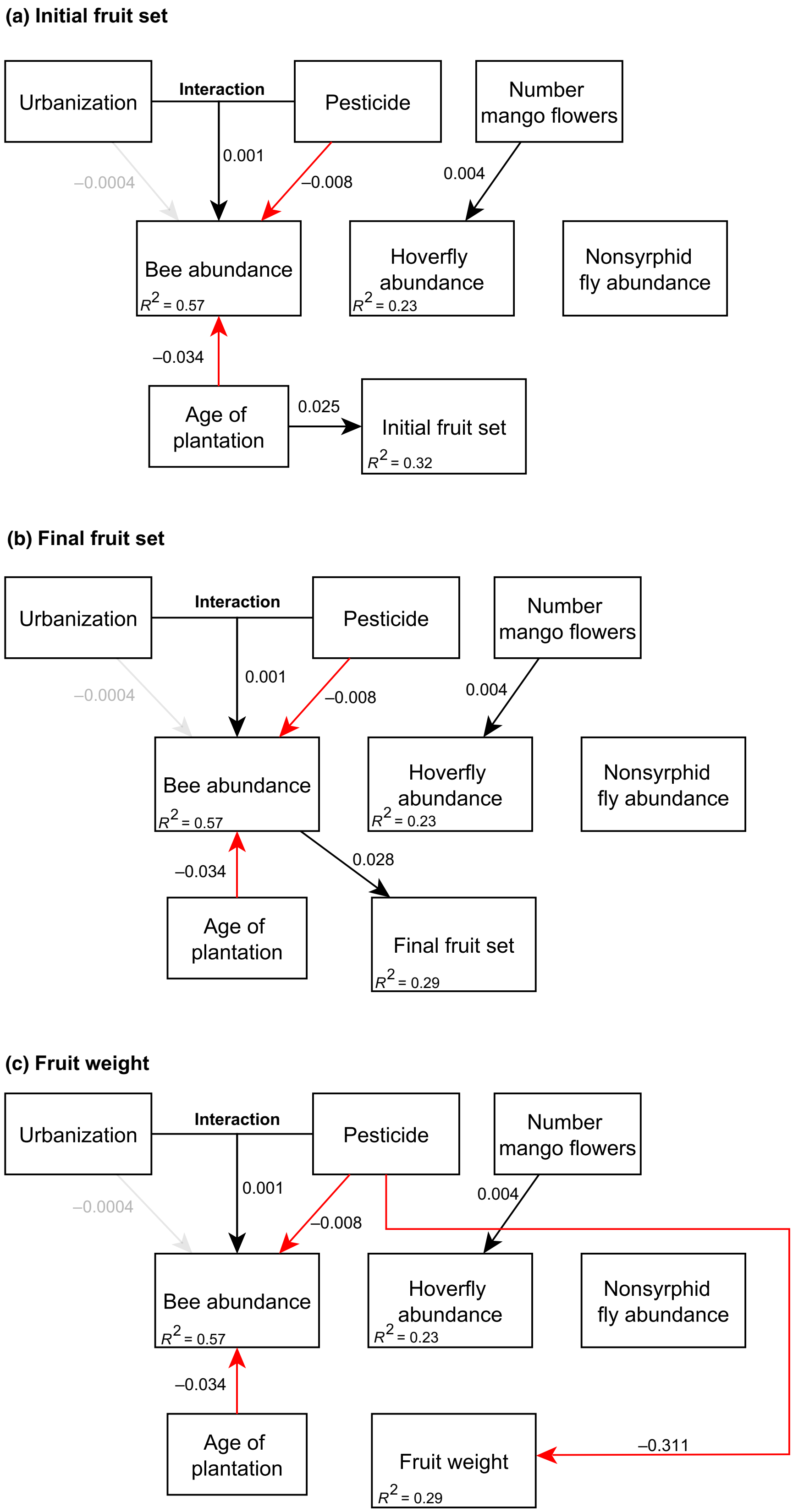

FIGURE 3 Results of the best piecewise structural equation models (SEMs) investigating the direct and indirect effects of urbanization, pesticides and pollinator abundance on initial fruit set (a), final fruit set (b), and fruit weight (c). Only statistically significant paths have been retained in the final SEMs, except for the lower order effect of urbanization on bee abundance (in light grey) resulting from the significant interaction between urbanization and pesticide. Standardized models' coefficients are displayed next to the arrows and R^2 of individual model in the box of response variables.

4.3 | Management recommendations

Our results suggest that above a certain level of applications, the harm caused by insecticides to pollinator communities may reduce mango yield and offset the positive effects of controlling insect pests, especially in rural areas. Pesticide overuse is a known problematic in India, also in mango cultivation, responsible for rising production cost (up to 35,000₹ = 424$ in our study

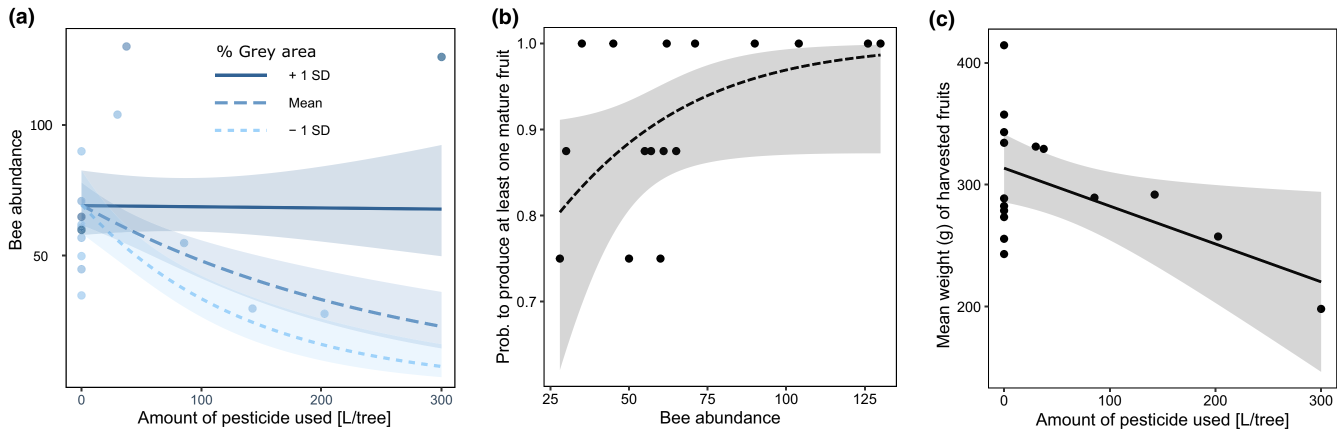

FIGURE 4 Interacting effect of pesticide and urbanization on bee abundance (a), marginally positive significant effect of bee abundance on final fruit set (b), and negative effect of pesticide on mean fruit weight (c). The lines depict the predicted mean values from generalized linear models, the coloured belts the 95% confidence intervals and the dots the raw data. These models were included in the structural equation models.

farms), environmental pollution and impacting farmers' health (Paruchuri et al., 2022; Selvarajah & Thiruchelvam, 2007). To avoid management trade-offs and to increase sustainability in mango production, there is a need to develop environmentally friendly methods for pest control, which do not negatively affect flower-visiting insect communities and associated pollination services (Knapp et al., 2022; Samnegård et al., 2019). In this context, new concepts such as Integrated Pest and Pollinator Management could be a promising strategy to maximize the synergies between pest control and crop pollination (Egan et al., 2020). For example, farmers could avoid spraying insecticides during the peak flowering period or to not use them preemptively to prevent harming pollinators. Alternatively, creating patches of native wild flowers within mango farms can compensate for the loss of natural habitats (e.g. driven by urbanization) and for the use of pesticides, promoting the abundance of flower visitors and their associated pollination services (Carvalheiro et al., 2012; Kleiman et al., 2021). Indeed, providing diverse floral resources may offset the negative effects of pesticides and sustain pollinator communities (Klaus et al., 2021; Knapp et al., 2022). Additionally, pollinators require diverse nesting habitats, which can be scarce in urbanized landscapes. For instance, Marcacci et al., (2022) found that *A. florea*, the main mango pollinator in our study, declined with urbanization because of the lack of suitable nesting sites such as hedges and bushy vegetation. We thus encourage the creation of patches of native wild flowering plants as well as the preservation of seminatural vegetation within mango farms to provide floral resources and nesting sites, which will eventually benefit pollinators and mango pollination. Furthermore, the orchard design could be improved by planting different varieties and facilitating pollinator movement, as recently shown for macadamia plantations (Anders et al., 2023). These sustainable practices and their multiple benefits should be better communicated to mango farmers (Paruchuri et al., 2022; Selvarajah & Thiruchelvam, 2007).

5 | CONCLUSIONS

Our study is one of the few that demonstrated interactive effects between urbanization and agricultural management on wild insect pollinators and yield of a tropical crop. More specifically, we highlighted the importance of wild insect pollinators for mango pollination across rural–urban landscapes. Moreover, urbanization did not affect pollination services for mango trees, suggesting that commercial mango production is viable within urbanized environments. However, high amounts of insecticides may pose a threat to wild bees and associated pollination services, which creates a management trade-off between pest control and pollination, especially in rural areas. Environmentally friendly management practices (e.g. integrated pest and pollinator management, reducing the amount of insecticides applied) and conservation measures (e.g. creating patches of native wild flowering plants to promote pollinators) need to be developed for sustainable mango production within and around cities.

AUTHOR CONTRIBUTIONS

Catrin Westphal, Soubadra Devy, Arne Wenzel, Vasuki V. Belavadi, Teja Tscharntke, Ingo Grass and Gabriel Marcacci conceived and designed the study; Vikas S. Rao, Shabarish Kumar S. and Nils Nölke collected and processed the data; Gabriel Marcacci conducted the analyses and wrote the manuscript and all authors revised and approved it.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.rbnzs7hhc (Marcacci et al., 2023).

ETHICS STATEMENT

This study did not require ethical approval.

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REFERENCES

Aizen, M. A., Aguiar, S., Biesmeijer, J. C., Garibaldi, L. A., Inouye, D. W., Jung, C., Martins, D. J., Medel, R., Morales, C. L., Ngo, H., Pauw, A., Paxton, R. J., Sáez, A., & Seymour, C. L. (2019). Global agricultural productivity is threatened by increasing pollinator dependence without a parallel increase in crop diversification. *Global Change Biology*, *25*(10), 3516–3527. https://doi.org/10.1111/gcb.14736

Anders, M., Grass, I., Linden, V. M. G., Taylor, P. J., & Westphal, C. (2023). Smart orchard design improves crop pollination. *Journal of Applied Ecology*, *60*, 624–637. https://doi.org/10.1111/1365-2664.14363

Anderson, D. L., Sedgley, M., Short, J. R., & Allwood, A. J. (1982). Insect pollination of mango in northern Australia. *Australian Journal of Agricultural Research*, *33*(3), 541. https://doi.org/10.1071/AR9820541

Baldock, K. C., Goddard, M. A., Hicks, D. M., Kunin, W. E., Mitschunas, N., Morse, H., Osgathorpe, L. M., Potts, S. G., Robertson, K. M., Scott, A. V., Staniczenko, P. P. A., Stone, G. N., Vaughan, I. P., & Memmott, J. (2019). A systems approach reveals urban pollinator hotspots and conservation opportunities. *Nature Ecology & Evolution*, *3*(3), 363–373. https://doi.org/10.1038/s41559-018-0769-y

Baldock, K. C., Goddard, M. A., Hicks, D. M., Kunin, W. E., Mitschunas, N., Osgathorpe, L. M., Potts, S. G., Robertson, K. M., Scott, A. V., Stone, G. N., Vaughan, I. P., & Memmott, J. (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*(1803), 20142849. https://doi.org/10.1098/rspb.2014.2849

Banaszak-Cibicka, W., & Żmihorski, M. (2020). Are cities hotspots for bees? Local and regional diversity patterns lead to different conclusions. *Urban Ecosystem*, *23*(4), 713–722. https://doi.org/10.1007/s11252-020-00972-w

Blacquière, T., Smagghe, G., van Gestel, C. A. M., & Mommaerts, V. (2012). Neonicotinoids in bees: A review on concentrations, side-effects and risk assessment. *Ecotoxicology*, *21*(4), 973–992. https://doi.org/10.1007/s10646-012-0863-x

Brooks, M., Bolker, B., Kristensen, K., Maechler, M., Magnusson, A., McGillycuddy, M., Skaug, H., Nielsen, A., Berg, C., van Bentham, K., Lüdecke, D., Lenth, R., O'Brien, J., Geyer, C. J., Jagan, M., & Wiernik, B. (2021). *glmmTMB: Generalized linear mixed models using template model builder*. https://CRAN.R-project.org/package=glmmTMB

Burdine, J. D., & McCluney, K. E. (2019). Interactive effects of urbanization and local habitat characteristics influence bee communities and flower visitation rates. *Oecologia*, *190*(4), 715–723. https://doi.org/10.1007/s00442-019-04416-x

Carvalheiro, L. G., Seymour, C. L., Nicolson, S. W., & Veldtman, R. (2012). Creating patches of native flowers facilitates crop pollination in large agricultural fields: Mango as a case study. *Journal of Applied Ecology*, *49*(6), 1373–1383. https://doi.org/10.1111/j.1365-2664.2012.02217.x

Carvalheiro, L. G., Seymour, C. L., Veldtman, R., & Nicolson, S. W. (2010). Pollination services decline with distance from natural habitat even in biodiversity-rich areas. *Journal of Applied Ecology*, *47*(4), 810–820. https://doi.org/10.1111/j.1365-2664.2010.01829.x

Dag, A., & Gazit, S. (2000). Mango pollinators in Israel. *Journal of Applied Horticulture*, *2*(1), 39–43.

Eckerter, P. W., Albrecht, M., Bertrand, C., Gobet, E., Herzog, F., Pfister, S. C., Tinner, W., & Entling, M. H. (2022). Effects of temporal floral resource availability and non-crop habitats on broad bean pollination. *Landscape Ecology*, *37*(6), 1573–1586. https://doi.org/10.1007/s10980-022-01448-2

Egan, A., Dicks, L. V., Hokkanen, H. M. T., & Stenberg, J. A. (2020). Delivering integrated pest and pollinator management (IPPM). *Trends in Plant Science*, *25*(6), 577–589. https://doi.org/10.1016/j.tplants.2020.01.006

FAO. (2022). Major tropical fruits: Market review preliminary results 2022. https://www.fao.org/3/cc3939en/cc3939en.pdf

Fox, J., & Weisberg, S. (2019). *An R companion to applied regression* (3rd ed.). Sage.

Geslin, B., Le Féon, V., Folschweiller, M., Flacher, F., Carmignac, D., Motard, E., Perret, S., & Dajoz, I. (2016). The proportion of impervious surfaces at the landscape scale structures wild bee assemblages in a densely populated region. *Ecology and Evolution*, *6*, 6599–6615.

Goulson, D., Nicholls, E., Botías, C., & Rotheray, E. L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*, *347*(6229), 1255957. https://doi.org/10.1126/science.1255957

Gu, B., Zhang, X., Bai, X., Fu, B., & Chen, D. (2019). Four steps to food security for swelling cities. *Nature*, *566*(7742), 31–33. https://doi.org/10.1038/d41586-019-00407-3

Hartig, F. (2021). *DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models*. https://CRAN.R-project.org/package=DHARMa

Huda, A. N., Salmah, M. R. C., Hassan, A. A., Hamdan, A., & Razak, M. N. A. (2015). Pollination Services of mango flower pollinators. *Journal of Insect Science*, *15*, 113. https://doi.org/10.1093/jisesa/iev090

Klaus, F., Tscharntke, T., Bischoff, G., & Grass, I. (2021). Floral resource diversification promotes solitary bees and may offset insecticide effects—Evidence from a semi-field experiment. *Ecology Letters*, *24*(4), 668–675. https://doi.org/10.1111/ele.13683

Kleiman, B. M., Koptur, S., & Jayachandran, K. (2021). Weeds enhance pollinator diversity and fruit yield in mango. *Insects*, *12*(12), 1–18. https://doi.org/10.3390/insects12121114

Klein, A. M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1608), 303–313. https://doi.org/10.1098/rspb.2006.3721

Knapp, J. L., Bates, A., Jonsson, O., Klatt, B., Kraus, T., Sahlin, U., Svensson, G. P., & Rundlöf, M. (2022). Pollinators, pests and yield - Multiple trade-offs from insecticide use in a mass-flowering crop. *Journal of Appliec Ecology*, *59*, 2419–2429.

Kumar, A., Bhuj, B. D., & Singh, C. P. (2021). Fruit drops in mango: A review. *Annals of the Romanian Society for Cell Biology*, *25*(6), 925–946.

Lefcheck, J. (2016). piecewiseSEM: Piecewise structural equation modeling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*(5), 573–579. https://doi.org/10.1111/2041-210X.12512

Lenth, R., Buerkner, P., Herve, M., Jung, M., Love, J., Miguez, F., Riebl, H., & Singmann, H. (2021). *Emmeans: Estimated marginal means, aka least-squares means*. https://CRAN.R-project.org/package=emmeans

Lüdecke, D., Makowski, D., Ben-Shachar, M. S., Patil, I., Waggoner, P., Wiernik, B. M., Arel-Bundock, V., & Jullum, M. (2021). *performance: Assessment of regression models performance*. https://CRAN.R-project.org/package=performance

Marcacci, G., Devy, S., Wenzel, A., Rao, V. S., Shabarish Kumar, S., Nölke, N., Belavadi, V. V., Tscharntke, T., Grass, I., & Westphal, C. (2023). Data from: Direct and indirect effects of urbanization, pesticides, and wild insect pollinators on mango yield. *Dryad Data Repository*. https://doi.org/10.5061/dryad.rbnzs7hhc

Marcacci, G., Grass, I., Rao, V. S., Kumar, S. S., Tharini, K. B., Belavadi, V. V., Nölke, N., Tscharntke, T., & Westphal, C. (2022). Functional diversity of farmland bees across rural-urban landscapes in a tropical megacity. *Ecological Applications*, *32*, e2699. https://doi.org/10.1002/eap.2699

Marcacci, G., Westphal, C., Wenzel, A., Raj, V., Nölke, N., Tscharntke, T., & Grass, I. (2021). Taxonomic and functional homogenization of farmland birds along an urbanization gradient in a tropical megacity. *Global Change Biology*, *27*(20), 4980–4994. https://doi.org/10.1111/gcb.15755

Nagendra, H., Nagendran, S., Paul, S., & Pareeth, S. (2012). Graying, greening and fragmentation in the rapidly expanding Indian city of Bangalore. *Landscape and Urban Planning*, *105*(4), 400–406. https://doi.org/10.1016/j.landurbplan.2012.01.014

Orsini, F., Kahane, R., Nono-Womdim, R., & Gianquinto, G. (2013). Urban agriculture in the developing world: A review. *Agronomy for Sustainable Development*, *33*(4), 695–720. https://doi.org/10.1007/s13593-013-0143-z

Paruchuri, P. K., Suganthi, A., Bhuvaneswari, K., Kavitha, C., & Geetha, P. (2022). Trend of pesticide use for mango cultivation in Tamil Nadu. *Biological Forum—An International Journal*, *14*(3), 159–166.

Pellissier, V., Muratet, A., Verfaillie, F., & Machon, N. (2012). Pollination success of *Lotus corniculatus* (L.) in an urban context. *Acta Oecologica*, *39*, 94–100. https://doi.org/10.1016/j.actao.2012.01.008

Peng, R. K., & Christian, K. (2005). Integrated pest management in mango orchards in the Northern Territory Australia, using the weaver ant, *Oecophylla smaragdina* (Hymenoptera: Formicidae) as a key element. *International Journal of Pest Management*, *51*(2), 149–155. https://doi.org/10.1080/09670870500131749

Potter, A., & Lebuhn, G. (2015). Pollination service to urban agriculture in San Francisco, CA. *Urban Ecosystems*, *18*(3), 885–893. https://doi.org/10.1007/s11252-015-0435-y

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology & Evolution*, *25*(6), 345–353. https://doi.org/10.1016/j.tree.2010.01.007

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Rader, R., Bartomeus, I., Garibaldi, L. A., Garratt, M. P. D., Howlett, B. G., Winfree, R., Cunningham, S. A., Mayfield, M. M., Arthur, A. D., Andersson, G. K. S., Bommarco, R., Brittain, C., Carvalheiro, L. G., Chacoff, N. P., Entling, M. H., Foully, B., Freitas, B. M., Gemmill-Herren, B., Ghazoul, J., … Woyciechowski, M. (2016). Non-bee insects are important contributors to global crop pollination. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(1), 146–151. https://doi.org/10.1073/pnas.1517092112

Rajan, V. V., & Reddy, P. V. R. (2019). A dead heat in pollination race: A comparative evaluation of the efficiency of a fly (*Chrysomya megacephala*) and a bee (*Apis florea*) in mango pollination. *Journal of Entomology and Zoology Studies*, *7*(1), 1087–1091.

Ramírez, F., & Davenport, T. L. (2016). Mango (*Mangifera indica* L.) pollination: A review. *Scientia Horticulturae*, *203*, 158–168. https://doi.org/10.1016/j.scienta.2016.03.011

Rundlöf, M., Andersson, G. K. S., Bommarco, R., Fries, I., Hederström, V., Herbertsson, L., Jonsson, O., Klatt, B. K., Pedersen, T. R., Yourstone, J., & Smith, H. G. (2015). Seed coating with a neonicotinoid insecticide negatively affects wild bees. *Nature*, *521*, 77–80. https://doi.org/10.1038/nature14420

Samnegård, U., Alins, G., Boreux, V., Bosch, J., García, D., Happe, A. K., Klein, A.-M., Miñarro, M., Mody, K., Porcel, M., Rodrigo, A., Roquer-Beni, L., Tasin, M., & Hambäck, P. A. (2019). Management trade-offs on ecosystem services in apple orchards across Europe: Direct and indirect effects of organic production. *Journal of Applied Ecology*, *56*(4), 802–811. https://doi.org/10.1111/1365-2664.13292

Selvarajah, A., & Thiruchelvam, S. (2007). Factors affecting pesticide use by farmers in Vavuniya District. *Tropical Agricultural Research*, *19*, 380–388.

Shipley, B. (2009). Confirmatory path analysis in a generalized multilevel context. *Ecology*, *90*(2), 363–368.

Silva, J. L. S., de Oliveira, M. T. P., Cruz-Neto, O., Tabarelli, M., & Lopes, A. V. (2021). Plant–pollinator interactions in urban ecosystems worldwide: A comprehensive review including research funding and policy actions. *Ambio*, *50*(4), 884–900. https://doi.org/10.1007/s13280-020-01410-z

Simkin, R. D., Seto, K. C., Mcdonald, R. I., & Jetz, W. (2022). Biodiversity impacts and conservation implications of urban land expansion projected to 2050. *Proceedings of the National Academy of Sciences of the United States of America*, *119*(12), e2117297119. https://doi.org/10.1073/pnas.2117297119

Steinhübel, L., & von Cramon-Taubadel, S. (2020). Somewhere in between towns, markets and jobs—Agricultural intensification in the rural-urban interface. *The Journal of Development Studies*, *57*(4), 669–694. https://doi.org/10.1080/00220388.2020.1806244

Steinhübel, L., Wenzel, A., Hulamani, P., von Cramon-Taubadel, S., & Mason, N. M. (2022). Effects of local farm management on wild bees through temporal and spatial spillovers: Evidence from Southern India. *Landscape Ecology*, *37*, 2635–2649. https://doi.org/10.1007/s10980-022-01507-8

Theodorou, P., Radzevičiūtė, R., Lentendu, G., Kahnt, B., Husemann, M., Bleidorn, C., Settele, J., Schweiger, O., Grosse, I., Wubet, T., Murray, T. E., & Paxton, R. J. (2020). Urban areas as hotspots for bees and pollination but not a panacea for all insects. *Nature Communications*, *11*(1), 1–13. https://doi.org/10.1038/s41467-020-14496-6

Turo, K. J., Spring, M. L. R., Sivakoff, F. S., de la Flor, Y. A. D., Yvan, A., & Gardiner, M. M. (2021). Conservation in post-industrial cities: How does vacant land management and landscape configuration influence urban bees? *Journal of Applied Ecology*, *58*(1), 58–69. https://doi.org/10.1111/1365-2664.13773

van Vliet, J., Eitelberg, D. A., & Verburg, P. H. (2017). A global analysis of land take in cropland areas and production displacement from urbanization. *Global Environmental Change*, *43*, 107–115. https://doi.org/10.1016/j.gloenvcha.2017.02.001

Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S* (4th ed.). Springer.

Wagner, D. L., Grames, E. M., Forister, M. L., Berenbaum, M. R., & Stopak, D. (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*(2), 1–10. https://doi.org/10.1073/PNAS.2023989118

Wenzel, A., Grass, I., Belavadi, V. V., & Tscharntke, T. (2020). How urbanization is driving pollinator diversity and pollination—A systematic review. *Biological Conservation*, *241*(October), 108321. https://doi.org/10.1016/j.biocon.2019.108321

Wenzel, A., Grass, I., Nölke, N., Pannure, A., & Tscharntke, T. (2022). Wild bees benefit from low urbanization levels and suffer from pesticides in a tropical megacity. *Agriculture, Ecosystems & Environment*, *336*, 108019. https://doi.org/10.1016/j.agee.2022.108019

Zezza, A., & Tasciotti, L. (2010). Urban agriculture, poverty, and food security: Empirical evidence from a sample of developing countries. *Food Policy*, *35*(4), 265–273. https://doi.org/10.1016/j.foodpol.2010.04.007

SUPPORTING INFORMATION

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

Table S1. List of all mango flower visitors we recorded with their abundances.

Table S2. Coefficients of pollinator exclusion experiment models. Numbers indicate direction and magnitude of coefficient estimates, with the standard errors in brackets. Numbers in bold indicate $p < 0.05$.

Table S3. Coefficients of the best fitting structural equation models for the initial fruit set, final fruit set and weight.

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