


Effects of urbanisation and management practices on pollinators in tropical Africa

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Funding information

Economic and Social Research Council; School of the Earth and Environment, University of Leeds; Natural Environment Research Council

Handling Editor: J. Scott MacIvor

Abstract

1. Urban expansion is an increasing threat to biodiversity, especially in tropical Africa where biodiversity hot spots are being encroached upon by fast-growing cities. Threatened species include bees and other pollinators, which deliver important ecosystem services but are sensitive to land use changes.
2. We investigated the impact of urbanisation and vegetation management practices on pollinator abundance, bee diversity, and bee functional traits. We sampled 126 locations in a stratified random design across an urbanisation gradient in two medium-sized cities in the West African Forests biodiversity hot spot, encompassing three management practices (farmed sites; amenity lands, i.e. green spaces managed for aesthetics; informal green spaces), and tested their effect with generalised linear models.
3. Urbanisation did not affect bee abundances or diversity but had a negative impact on both wasp and beetle abundances. There was also a management-mediated impact of urbanisation on bee abundances, which decreased with urbanisation on farmed sites but not amenity land or informal green spaces. Management practices alone influenced bee abundances with farms harbouring fewer bees, and amenity lands fewer beetles.
4. Bee genera occurrence and dominance patterns were influenced by both urbanisation and management, with some otherwise common genera rare in urban areas.
5. Most functional traits were influenced by management, with fewer polylectic bees, cavity-nesting bees and long-tongued bees in farmed sites. Amenity lands hosted smaller bees and fewer savanna specialists. Some traits were influenced by urbanisation, with more long-tongued bees and cavity-nesting bees found in urban areas.
6. *Synthesis and applications.* Pollinator responses to urbanisation are complex. In our research, we demonstrate how bee, lepidopteran, and non-fruit fly abundances have been maintained across an urbanisation gradient in tropical Africa, but not wasp and beetle abundances. Moreover, bee community composition and the distribution of traits shifted markedly. How green spaces were managed was also critical. We found that farmed sites hosted the lowest bee abundances and

amenity lands the fewest beetles. Retaining informal green spaces and amenity lands in African cities, including protecting nesting sites for stingless bees, and limiting pesticide application would be important for conserving bees and the pollination service they provide to both crops and native vegetation.

KEY WORDS

bees, conservation, functional traits, Ghana, Guinean Forests of West Africa, pollinators, urban agriculture, urban green spaces

1 | INTRODUCTION

Urbanisation as a land-use change has the greatest impact on biodiversity (McDonald, Kareiva, & Formana, 2008). Urban expansion, however, is not geographically homogenous, taking place mainly in developing countries (United Nations, 2015), where it frequently encroaches upon biodiversity hot spots (Seto, Güneralp, & Hutyra, 2012). Urban areas also include green spaces and their potential for biodiversity conservation is increasingly studied (Nilon et al., 2017). The majority of studies are based in the Global North, meaning that we know little about the biodiversity conservation potential of African cities (e.g. Magle, Hunt, Vernon, & Crooks, 2012). However, urban expansion in Africa differs from that of the Global North by being faster (Seto et al., 2012), happening mainly in smaller towns (DESA, 2015) and not always being associated with economic growth (Turok & McGranahan, 2013).

One group potentially threatened by urbanisation are insect pollinators (Jones & Leather, 2013), which are of particular concern given their importance for food security. The food system is highly reliant on their services, as 35% of crops require animal pollination (Klein et al., 2007), needing both high abundances and diversity for optimal productivity (Garibaldi et al., 2014). With concerns growing about the loss of pollinators in surrounding rural landscapes (Potts et al., 2010), some urban areas, which can have a high floral diversity due to decorative planting and a proliferation of small vegetation patches, might provide useful habitat within an otherwise inhospitable urban matrix (Harrison & Winfree, 2015). However, if urban areas are to contribute to pollinator conservation, or serve as spillover habitat for pollinator loss in rural agricultural landscapes (Pereira-Peixoto, Pufal, Martins, & Klein, 2014), quantifying the role of different urban vegetation management practices is essential (cf. for rural landscapes Ricketts et al., 2008). The potential for urban environments to contribute to pollinator conservation has gained prominence in recent years (Hall et al., 2017) and a positive effect of urbanisation on both abundances and diversity has been observed (e.g. Baldock et al., 2015). Such effects are often trait-related, with a negative effect of urbanisation on floral specialists and ground-nesting bees but a positive one for cavity-nesting bees (Fortel et al., 2014; Hernandez, Frankie, & Thorp, 2009), and are context-dependant. Despite this, few studies have been carried out in sub-Saharan Africa (Hernandez et al., 2009), which is part of the general paucity of research both on urban biodiversity (Magle et al., 2012)

and pollinator conservation (Rodger, Balkwill, & Gemmill, 2004) in the region. Those studies that have been carried out point towards a larger diversity of pollinators and steeper declines in pollinator visitor rates from natural to disturbed agricultural landscapes in tropical compared to temperate zones (Ricketts et al., 2008; Rodger et al., 2004). In a region which is extremely vulnerable to pollination deficit (Gallai, Salles, Settele, & Vaissiere, 2009), there is an urgent need to better understand the impact of urbanisation and management practices on the conservation of bees and pollination.

One of the many challenges in African cities is ensuring food security, something that urban agriculture can contribute to by supplementing food and incomes for an often substantial proportion of the human population (Zezza & Tasciotti, 2010). Additionally, urban agriculture can contribute to female empowerment, help reduce waste and the environmental impact of food transport, and improve urban air quality and biodiversity (Orsini, Kahane, Nono-Womdim, & Gianquinto, 2013). Crops cultivated in urban farms include staples such as maize or cassava, but also high-value vegetable and fruit crops often reliant on pollination for high yields (Ayerakwa, 2017; Klein et al., 2007). Consequently, a better understanding of the urban pollinator status in Africa is crucial for maximising the multiple benefits of urban agriculture.

Here, we redress this imbalance by investigating the effect of urbanisation and management practices on pollinator abundances, bee diversity, community structure, and functional traits in medium-sized tropical African cities. By sampling bees, wasps, lepidopterans, beetles, and flies to assess their abundances along an urbanisation gradient and different vegetation and management practices, we quantify the potential for pollinator conservation in cities and determine the type of green space management practices best suited for urban pollinator conservation.

2 | MATERIALS AND METHODS

2.1 | Study sites and sampling design

The cities of Sunyani (7°20'05"N, 2°19'40"W) and Techiman (7°34'53"N, 1°56'09"W), Brong Ahafo, Ghana (Supporting Information Figure S1a) are located at the fringe of the *Forests of West Guinea* biodiversity hot spot, increasingly threatened by urban expansion, despite having already lost 90% of its primary vegetation

(Seto et al., 2012). The flora of the hot spot includes approximately 9,000 vascular plant species and at least 482 are on the IUCN Red List (Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000). Data on pollination systems are lacking in the hot spot, as the little pollination research carried out in West Africa focuses on cash crops (Rodger et al., 2004). Sunyani and Techiman are medium-sized fast-growing cities, with a recent annual population growth rate of 4.8% (Ghana Statistical Services, 2013). They are embedded in an agricultural landscape with little semi-natural areas nearby. The only protected areas in the region are far from urban centres (IUCN/PACO, 2010).

We sampled 126 green spaces which encompassed three management practices and were distributed across an urbanisation gradient based on the proportion of built infrastructure (Supporting Information Figure S2). Land-cover data were extracted from Sentinel 2 aerial pictures from December 2015 (Copernicus Sentinel data 2015) within ArcMap 10.4.1 following a two-step image classification technique combining Jenks Natural Breaks classification with hierarchical clustering (Anchang, Ananga, & Pu, 2016). This map was used to extract the proportion of built infrastructure (buildings, surfaces such as roads, car parks, or any area covered with impervious structures) in a 250 × 250 m grid. Forty-two areas were randomly selected along the urbanisation gradient, ensuring an equal representation of rural (control), urban and peri-urban landscapes and a minimum distance of 1 km between each (Supporting Information Figure S1b,c). Rural area selection was confined to a 10 km radius around the city and limited to areas accessible from paved roads and dirt paths. The pre-identified areas were walked to select three green spaces of a minimum of 50 m², one each of (a) amenity land, a green space managed for aesthetic purposes, typically lawns, trimmed hedges, or cleared vegetation; (b) farmed sites, a green space managed for agricultural production, including mixed-crop gardens and farms; and (c) informal green spaces, a vegetated area receiving minimal to no management, such as fallows or abandoned sites.

Pollinators were sampled between August and November 2016, covering the shorter of the two annual rainy seasons. While little is known about the best period for sampling bees in West Africa, other tropical studies found higher abundances in the rainy season (Coulbaly, Pauly, Konaté, Linsenmair, & Stein, 2016) or similar abundances but different species composition, with smaller species and more ground-nesting bees found in the rainy season (Samnegard, Hamback, Eardley, Nemomissa, & Hylander, 2015). Pan traps were used, a method recommended for its lack of collector bias and its effectiveness in urban environments (Devigne & De Biseau, 2014). Five pan traps, each consisting of three 300 mL bowls painted in UV fluorescent yellow, white and blue (Sparvar Leuchtfarbe, Spray-Color GmbH), were set out on one occasion during the sampling period, with a maximum of five green spaces sampled simultaneously. They were set-up at the level of the ground-layer vegetation (varying from 0 to 0.5 m), separated by 5 m. These were two-thirds filled with water and a drop of unscented detergent and left active for 24 hr to account for the full diurnal activity of pollinators. Samples were stored in 70% alcohol

before being pinned for identification. All insects were identified to order in the field. Bees and wasps were pinned and differentiated with microscopy, based on Goulet and Huber (1993). Bees were subsequently identified with microscopy to sub-genera level following Eardley, Kuhlmann, and Pauly (2010) and then to morpho-species as per training received at Oxford University Museum of Natural History.

Bee functional diversity was assessed through a selection of traits relevant for pollinators, namely habitat, pollen specialisation, nesting behaviour, body size (inter-tegula distance measured on all specimens with a caliper), tongue length, and sociality (Supporting Information Table S1; Normandin, Vereecken, Buddle, & Fournier, 2017). Functional traits were categorised at sub-genera level based on the literature (Supporting Information Tables S2).

Sample sites were described by their habitat structure and floral resources, flowering plant diversity (Gini-Shannon's index), and species richness. Habitat structure was defined as a visual estimation of the proportion of six habitat features in a 200 m radius around the sampling site, namely unmanaged ground vegetation, regularly mown or grazed vegetation, shrub layer vegetation, tree layer vegetation, bare ground and concrete. We estimated the floral resources in a 1 m circle around the pan trap by (a) counting the flowering plant species richness, (b) estimating each species' flower head surface and (c) counting flower head abundance. In farmed sites, the presence of the different crop types was also noted.

2.2 | Data analysis

2.2.1 | Sample site characterisation

All analysis were carried out with R v.3.4.3 (R Core Team, 2017). To characterise the pollinator habitat, we analysed differences between the three management practices in terms of the estimated floral resources, flowering plant species richness and diversity (Gini-Shannon's index), and the six components of habitat structure (Supporting Information Table S3). None were normally distributed, so we used nonparametric Kruskal-Wallis tests. Given the focus on three specific green space categories, findings are representative of the immediate surrounding of green spaces, but not of the wider make-up of the cities as it excludes large areas of built infrastructure.

2.2.2 | Abundance and diversity

We ran generalised linear mixed-effect models to test the effect of management and the proportion of built infrastructure (extracted from land-cover maps) in a 600 m radius (the foraging range of most solitary bees; Gathmann & Tscharncke, 2002) around each sampling site on bee, wasp, lepidopteran, beetle and fly (excluding fruit flies) abundances and bee diversity per site ($N = 126$). Due to small catches, bee diversity was calculated only when abundances

were ≥ 2 with the Gini–Simpson index weighted by the inverse of its variance, as this diversity estimator is unbiased with respect to catch size (Lande, 1996).

After excluding correlated explanatory variables (variance influence factor < 3) (Zuur, Ieno, & Elphick, 2010), models included 13 variables describing weather and habitat (Supporting Information Table S4), the interaction between management practices and urbanisation, and a random grouping variable representing the nesting of the three management practices clustered in the sampling design. We used negative binomial error distributions to compensate for the over-dispersion observed for all abundances, except bee abundance for which we used Poisson distribution (Burnham & Anderson, 2002) and a Gaussian distribution for diversity. As bee and lepidopteran abundances had a high number of zeroes, we used zero-inflated models (Zuur, 2009), from the R statistical package GLMMTMB (Magnusson et al., 2017). Models were run with all possible combinations of variables and compared according to AIC_c , selecting those with $\Delta AIC_c \leq 2$ and averaging them using Akaike weights (Burnham & Anderson, 2002), using the R statistical package MuMIN, v.1.40.4 (Barton, 2018).

2.2.3 | Indicator species

Indicators are defined as taxa whose presence and abundance can reflect the state of the environment, highlight the impact of environmental changes, or predict the distribution of other taxa (DeCaceres & Legendre, 2009). They are determined by assessing the association between species abundances and grouped sites, through their specificity (probability that, if the species is found on a site, the site belongs to a wider group of sites) and their fidelity (probability of finding the species if the site belongs to the group) (DeCaceres & Legendre, 2009). To examine whether some bee genera are indicators, we carried out indicator species analysis with sites grouped by management type and urbanisation, with the R indicpecies package, v.1.7.6 (DeCaceres & Legendre, 2009). As categorical grouping variables are a prerequisite, sites were defined as urban or rural based on the proportion of built infrastructure in 600 m surrounding the sampling site (rural $< 15\%$ $<$ urban).

2.2.4 | Functional traits

To assess the effect of urbanisation and management practices on functional traits, we fitted generalised mixed-effect linear model of each trait independently against the same set of explanatory variables as for the abundance and diversity analysis (Supporting Information Table S4). We used a Gaussian distribution for the log-transformed ITD and binomial distributions for all other traits. We used the same model selection and averaging method as for the abundance and diversity analysis. As some traits could be inter-correlated, we quantified this with Spearman rank correlations to understand if similar relationships with urbanisation and management practices were linked to association between traits.

3 | RESULTS

3.1 | Sample site characterisation

Amenity land was characterised by (a) lower coverage of ground layer vegetation ($\chi^2 = 71.71$, $p < 0.001$, Figure 1a, Supporting Information Table S3), (b) higher cover of mown vegetation ($\chi^2 = 49.367$, $p < 0.001$, Figure 1b) and concrete ($\chi^2 = 13.791$, $p = 0.001$, Figure 1c), (c) lower flowering plant diversity ($\chi^2 = 16.7$, $p < 0.001$, Figure 1d), and (d) lower species richness ($\chi^2 = 26.086$, $p < 0.001$, Figure 1e) compared to other management practices. Farmed sites had a lower coverage of ground layer vegetation and flowering plant species richness than informal green spaces but more than amenity lands. They were characterised by a higher coverage of shrub layer vegetation ($\chi^2 = 40.095$, $p < 0.001$, Figure 1f) and bare ground cover ($\chi^2 = 21.938$, $p < 0.001$, Figure 1g) compared to the other management practices. In farmed sites, we identified 30 crops with variable reliance on animal pollination, most of which were found in both urban and rural landscapes (Supporting Information Table S5). Informal green spaces had the highest cover of ground layer vegetation cover and the highest flowering plant species richness. None of the management practices differed in their floral resources ($\chi^2 = 0.171$, $p = 0.918$) or tree cover ($\chi^2 = 2.797$, $p = 0.247$). Only the proportion of concrete increased along the urbanisation gradient ($\rho = -0.32$, $p < 0.001$, Figure 1h).

3.2 | Abundances and diversity

We caught 51,028 insects consisting of 167 bees (Supporting Information Figure S3), 323 wasps of the Vespidae, Scoliidae, Pompilidae, Ampulicidae and Tynnidae families, 222 lepidoptera, 1,090 beetles, and 49,226 flies. 93.7% (46,123) of the flies were Drosophilidae, likely attracted by other decaying insects and therefore not relevant for pollination. We do not consider them further. The remainder were species of the Calliphoridae, Diopsidae, Tephritidae, Asilidae, Culicidae, and Muscidae. Bees belonged to 18 genera and 76 morpho-species (Supporting Information Table S6).

Overall bee abundances were not affected by urbanisation but varied according to management. Abundances were lowest in farmed sites ($\beta = -1.511$, $SE = 0.729$, $p = 0.040$, Figure 2a, Supporting Information Table S7). However, the interaction between management and urbanisation was significant: bee abundances in amenity land and informal green spaces did not change with urbanisation, but they decreased in farmed sites ($\beta = 0.019$, $SE = 0.008$, $p = 0.025$, Figure 2b). Bee abundance was negatively influenced by rainfall ($\beta = -0.031$, $SE = 0.013$, $p = 0.016$) and positively influenced by cloud cover ($\beta = 1.005$, $SE = 0.470$, $p = 0.034$).

Bee genera and morpho-species diversity were not affected by management or urbanisation. No variables influenced morpho-species diversity. Genera diversity increased with the proportion of tree layer vegetation ($\beta = 0.296$, $SE = 0.145$, $p = 0.047$).

Wasp abundances did not change with management but decreased with urbanisation, although the data were highly variable ($\beta = 0.005$, $SE = 0.002$, $p = 0.032$, Figure 3a). Abundances increased

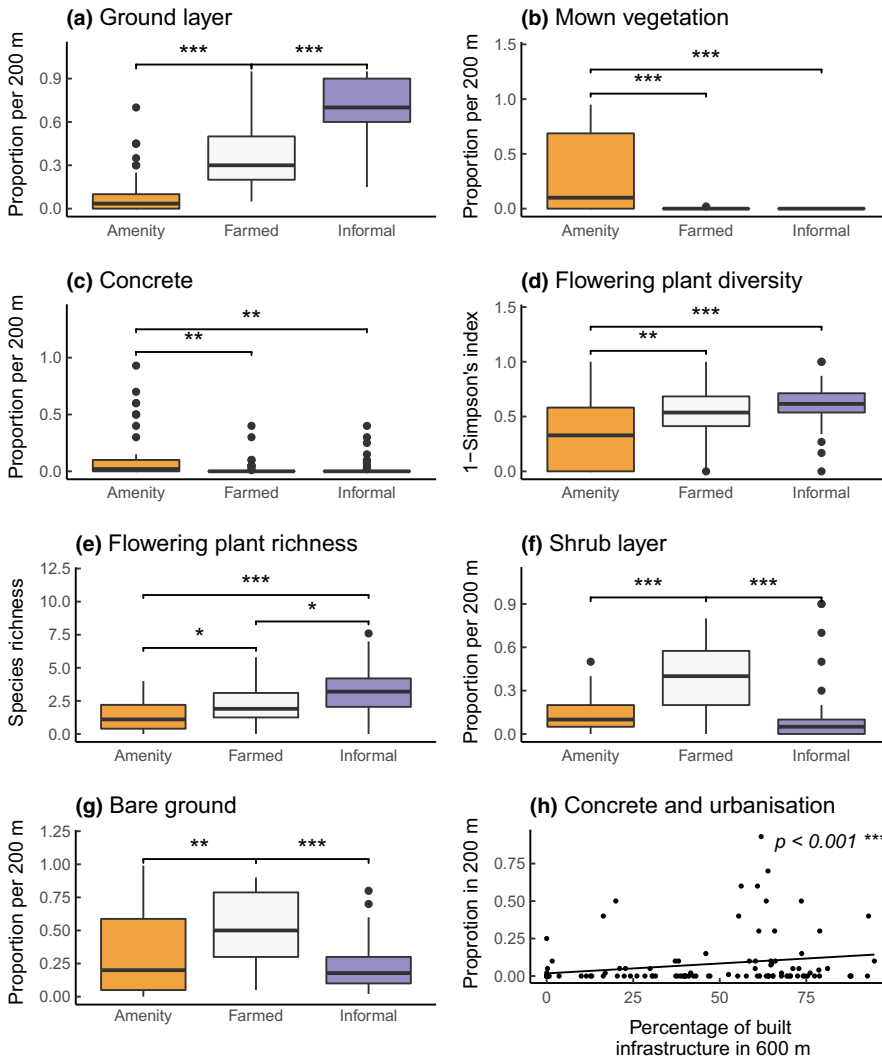


FIGURE 1 (a–f) Significant relationships between vegetation structure/flowering diversity measures and management practices for: (a) ground vegetation, (b) mown vegetation, (c) concrete, (d) flowering plant diversity, (e) flowering plants species richness, (f) shrubs, (g) bare ground, and (h) concrete by urbanisation. Boxes show median and interquartile ranges, with the whiskers extending to 1.5 of the interquartile range. Significance levels are indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

with cloud cover ($\beta = 1.382$, $SE = 0.302$, $p < 0.001$) and floral resources ($\beta = 0.001$, $SE = 0.000$, $p = 0.015$), but decreased with rainfall ($\beta = -0.015$, $SE = 0.007$, $p = 0.038$). Lepidoptera abundances were not affected by management or urbanisation, but increased with temperature ($\beta = 0.833$, $SE = 0.261$, $p = 0.002$).

Beetle abundances were significantly lower in amenity land than in farmed sites ($\beta = 1.936$, $SE = 0.392$, $p < 0.001$, Figure 3b) or informal green spaces ($\beta = 2.101$, $SE = 0.391$, $p < 0.001$), and

were negatively affected by urbanisation ($\beta = 0.019$, $SE = 0.004$, $p < 0.001$). This decline was greater in amenity lands than in farmed sites ($\beta = -0.012$, $SE = 0.005$, $p = 0.013$). Abundance was negatively related to rainfall ($\beta = -0.023$, $SE = 0.007$, $p = 0.013$), but increased with the proportion of mown vegetation ($\beta = 0.826$, $SE = 0.356$, $p = 0.022$).

Non-fruit fly abundances were not affected by management or urbanisation. They were sensitive to weather conditions, with a negative

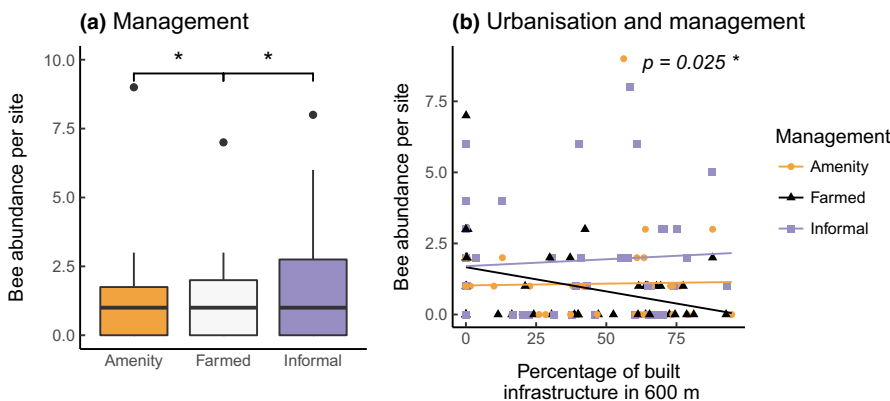


FIGURE 2 Relationship between bee abundances and (a) management practices and (b) urbanisation (built infrastructure) and its interaction with management practices. Boxes show median and interquartile ranges, with the whiskers extending to 1.5 of the interquartile range; each dot represents a sampling site ($N = 126$)

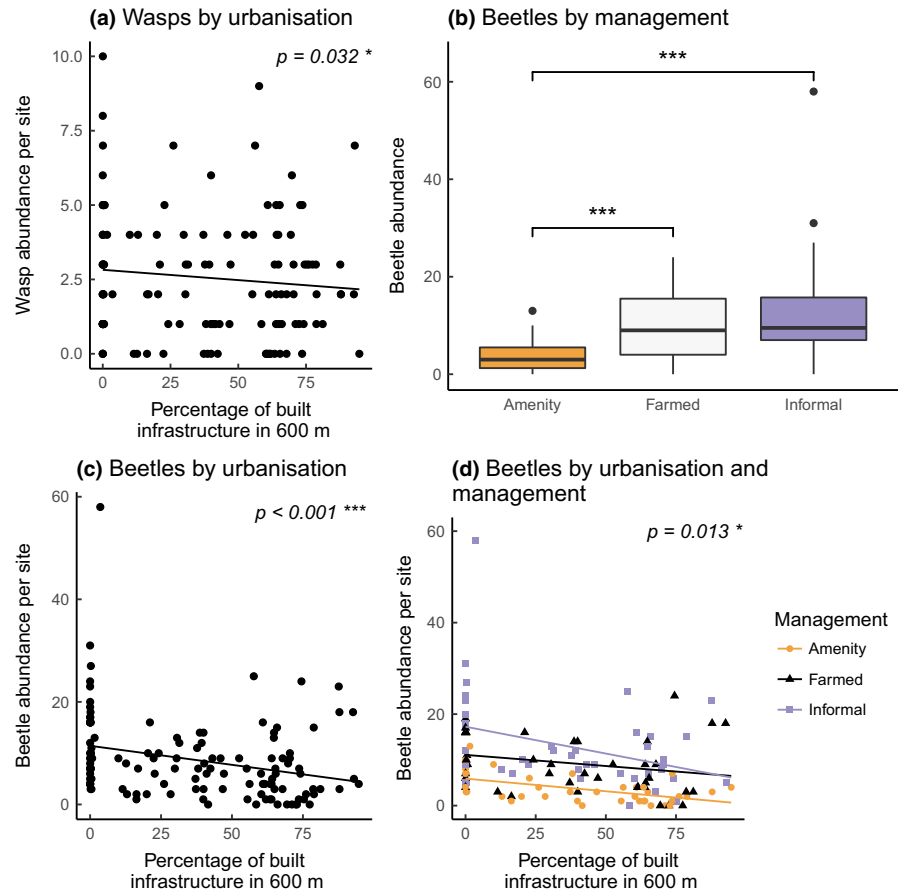


FIGURE 3 Influence of management and urbanisation on non-bee pollinator groups: (a) Wasp abundances by urbanisation; beetle abundances by (b) management, (c) urbanisation, and (d) the interaction between management and urbanisation. Boxes show median and interquartile ranges, with the whiskers extending to 1.5 of the interquartile range; each dot represents a sampling site ($N = 126$)

relationship with temperature ($\beta = -0.078$, $SE = 0.021$, $p < 0.001$) and rainfall ($\beta = -0.024$, $SE = 0.006$, $p < 0.001$) and a positive relationship with cloud cover ($\beta = 0.616$, $SE = 0.217$, $p = 0.005$). Additionally, more were found in Techiman ($\beta = 0.368$, $SE = 0.117$, $p = 0.002$).

3.3 | Indicator species

Overall fidelity scores were relatively low due to the small catch sizes, but three genera were indicators of management practices due to their high specificity. *Meliponula* sp. were indicators of amenity lands (specificity = 77.3%, fidelity = 23.9%, $stat = 0.429$, $p = 0.009$, Figure 4a, Supporting Information Table S8), *Seladonia* sp. of informal green spaces (specificity = 83.3%, fidelity = 31.5%, $stat = 0.315$, $p = 0.05$), and *Braunsapis* sp. of farmed sites and informal green spaces (i.e. “non-amenity land,” specificity = 88.2%, fidelity = 25%, $stat = 0.47$, $p = 0.021$). No genus was an indicator of urban areas but *Braunsapis* sp. was an indicator of rural areas (specificity = 90.3%, fidelity = 47.6%, $stat = 0.656$, $p = 0.001$, Figure 4b).

3.4 | Functional traits

The average inter-tegument distance for bees was 1.496 mm ($N = 167$, $SE = 0.051$). Most bees (64%) were habitat generalists, while the habitat specialists were split between savanna (41.6%) and woodland (58.3%) (Supporting Information Table S9). Long-tongued

bees constituted 52.7% of the community, ground nesters 56.2%, pollen specialists 35.9%, and social or semi-social 76%. Many functional traits were correlated, with especially strong correlations between pollen specialisation, tongue length, and nest location (Supporting Information Table S10).

Both social and solitary bees were evenly spread across the urbanisation gradient and management practices, and their presence was not affected by the other variables (Supporting Information Table S11). Similarly, the proportion of habitat generalists was constant across the urbanisation gradient and management practices, though within the habitat specialists, there was a lower proportion of savanna specialists in amenity lands than in informal green spaces ($\beta = -1.605$, $SE = 0.762$, $p = 0.041$) or farmed sites ($\beta = -2.629$, $SE = 0.877$, $p = 0.004$, Figure 5a). Body size differed between management practices and so did feeding and nesting habits; bees in amenity lands had smaller bodies than those in informal green spaces ($\beta = 0.340$, $SE = 0.080$, $p < 0.001$) or farmed sites ($\beta = 0.299$, $SE = 0.064$, $p < 0.001$, Figure 5b). Farmed sites hosted lower proportion of long-tongued bees ($\beta = -1.539$, $SE = 0.705$, $p = 0.031$, Figure 5c) and polylectic bees ($\beta = -1.807$, $SE = 0.675$, $p = 0.009$, Figure 5d). Cavity-nesting bees were more common in amenity lands than in farmed sites ($\beta = -1.539$, $SE = 0.705$, $p = 0.031$, Figure 5e). The proportion of long-tongued bees ($\beta = 0.340$, $SE = 0.080$, $p < 0.001$, Figure 6a) and cavity-nesters ($\beta = 0.025$, $SE = 0.009$, $p = 0.008$, Figure 6b) decreased with urbanisation.

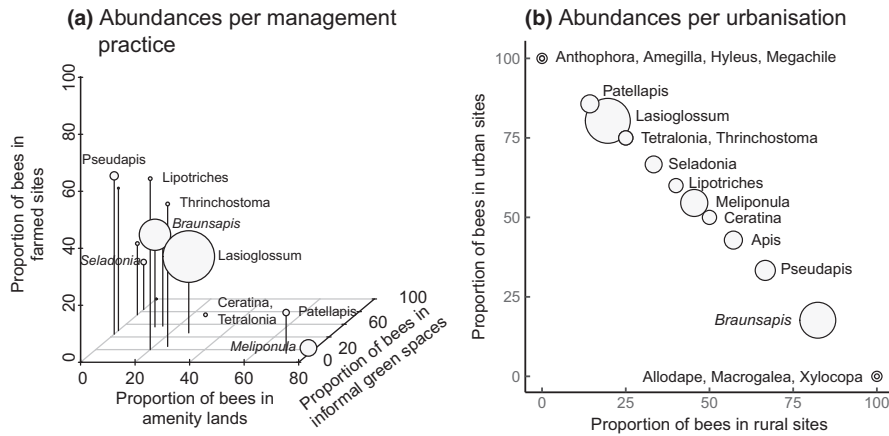


FIGURE 4 Relative abundance of the different bee genera, with indicator genera in italics. (a) Proportion of individuals sampled per genus in each management practice. Dot size is proportional to the number of individuals. For instance, *Seladonia* sp. had a low abundance but was found mainly in informal green spaces while *Meliponula* sp., more abundant, was collected primarily in amenity lands ($N = 42$ per practice). (b) Proportion of individuals sampled per genus in relation to urbanisation. Dot size is proportional to the number of individuals ($N = 84$ for urban sites and $N = 42$ for rural sites)

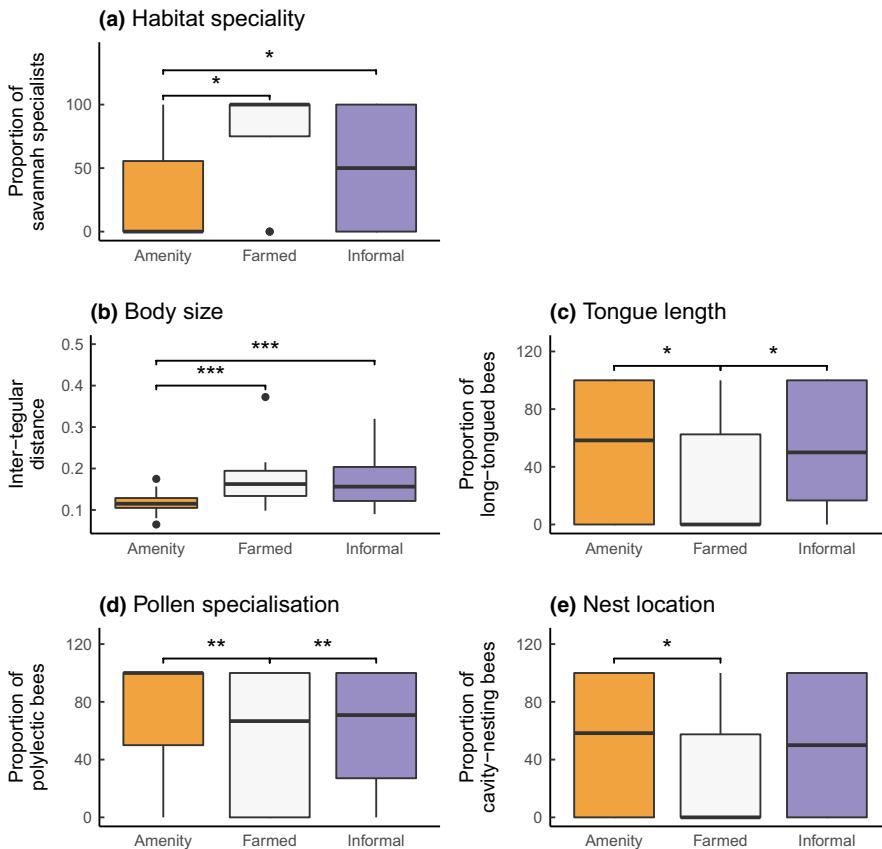


FIGURE 5 Functional traits significantly influenced by management practices. (a) Habitat speciality ($N = 42$), (b) body size, (c) tongue length, (d) pollen specialisation, (e) nest location. Boxes show median and interquartile ranges, with the whiskers extending to 1.5 of the interquartile range. Significance levels are indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

4 | DISCUSSION

In tropical Africa, vegetation management affected bee abundances and functional traits, with fewer bees in farmed sites. Although there was no direct effect of urbanisation on abundances, an interaction between management and urbanisation meant that the more urban a farmed site was, the fewer bees it hosted. Similarly, abundances of other pollinators such as wasps and beetles decreased

as the landscape became more urban. Urbanisation influenced bee community composition and their functional traits, favouring short-tongued bees and ground-nesting bees.

4.1 | Urbanisation

Although urban green spaces in temperate regions are a potential refuge for pollinators (Hall et al., 2017), evidence remains mixed

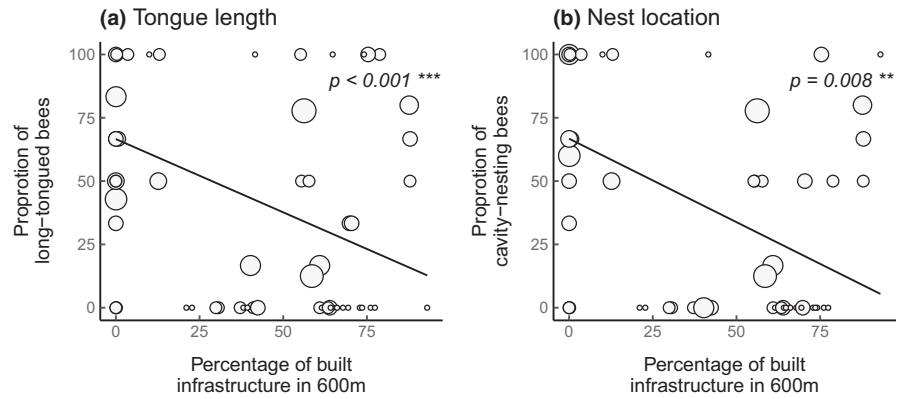


FIGURE 6 Functional traits significantly influenced by urbanisation. (a) Tongue length and (b) nest location. Dots are proportional of catch sizes ($N = 76$)

(Baldock et al., 2015; Ramírez-Restrepo & MacGregor-Fors, 2017). In a rarely studied tropical African context, we found no direct effect of urbanisation on overall abundance of bees, lepidoptera, or non-fruit flies. Increased urban cover did, however, negatively impact wasp and beetle abundances.

Some functional traits were affected by urbanisation; fewer long-tongued bees and cavity-nesting bees were found in urban than in rural areas. This change in nesting habits contrasts with the one observed in temperate regions, where ground-nesters are less present in cities, a decrease thought to be due to the increased cover of impervious surfaces offering little access to ground nesting sites (Cane, Minckley, Kervin, Roulston, & Williams, 2006). In contrast, African cities often have less coverage by impervious surfaces than cities of the Global North (Lall, Henderson, & Venables, 2017), therefore offering a greater extent of open ground for bees to nest in. Similarly, we found a low overall coverage of concrete, supporting the proposition that ground-nesting bees are affected by increased impervious surface cover and highlighting the need to retain bare ground in urban areas.

Despite the urban landscape likely being more fragmented than rural landscapes, the abundance of bees was maintained in our study sites, perhaps due to the variety of different-sized green spaces providing usable habitat in an otherwise inhospitable urban matrix (Harrison & Winfree, 2015). However, bee communities differed between urban and rural sites. For instance, *Braunsapis* sp. was virtually absent in urban areas despite being the most abundant genus in rural areas and a common genus in tropical Africa (Eardley et al., 2010). The only other urban pollination study on the continent focused on a specific bee, *Rediviva peringueyi*, and found it to be absent from urban sites (Pauw, 2007). Conversely, other genera such as *Lasioglossum* bees were common in urban samples, but rare or absent in rural environments. Our results highlight the fact that changes in resource availability and environmental conditions brought about by urbanisation induce a modification in bee community composition which would require further investigation.

The cities are surrounded by agricultural landscapes, within a biodiversity hot spot and without nearby protected areas (IUCN/PACO, 2010). The similarity in bee abundances across the urbanisation gradient might therefore reflect a generally depleted regional species pool, something that is likely the norm rather than the exception in urbanisation studies. The negative effect of rural farmed landscapes on

bee abundances in comparison to semi-natural rural areas has already been documented (Combey & Kwabong, 2016; Coulibaly et al., 2016). Further research on pollinator distribution in different West African rural landscapes could improve the understanding of the impact of urban landscapes on pollinator abundances and community composition. Nevertheless, our study demonstrates that urban areas can play a role in maintaining bee abundances and diversity in some ways equivalent to those in surrounding rural landscapes, despite changes in community structures. However, maintaining abundant and diverse bee populations in the long term, despite high development pressures and consequent disappearance of African urban green spaces (Mensah, 2014), might prove challenging. Insects are not recognised by policy makers as worthwhile of conservation (Ministry of Environment and Science, 2002), even though they provide important ecosystem functions. Proactive planning is crucial to maintain urban green spaces and ecosystem services while cities are expanding, rather than attempting to retrofit green spaces once cities have densified.

4.2 | Management

By highlighting the effect of management on bee abundances, our results raise concerns regarding the retention of insect pollination within an urbanising Afro-tropical landscape. Indeed, regardless of the level of urbanisation, farmed sites hosted lower bee abundances than any other management practices. Findings from other parts of Africa show a similar decrease in bee abundances in agricultural areas, regardless of their management or the heterogeneity of the landscape (e.g. Kehinde & Samways, 2011). Moreover, pollen generalist bees are known to be more resilient to land-use and climate change than specialists (IPBES, 2016), yet we found a higher proportion of specialists in farms, potentially decreasing the long-term resilience of their pollination.

Amenity lands also differed from other management practices by hosting bees of smaller sizes, a lower proportion of ground-nesting bees and savanna specialists. This was due to the association with stingless bees (*Meliponula* spp.), which are small-sized, cavity-nesting woodland specialists, and show the importance of providing nesting sites. Indeed, amenity lands had highly disturbed soils, with higher proportion of concrete and mown vegetation than the other management practices, and so provide little opportunities for

ground-nesters. Additionally, as body size is often linked with dispersal ability (Gathmann & Tscharntke, 2002), promoting only amenity lands as a source of dispersion for urban farms will not be optimal.

Other pollinators groups were not as affected by management practices. Only beetle abundances were lower in amenity lands, a pattern similar to trends observed elsewhere in Africa, where beetles are highly sensitive to habitat disturbances (Clark & Samways, 1997). Those results highlight the importance of structurally diverse habitat and low-intensity management practices for maintaining pollinator diversity and bee abundances. Conserving such informal green spaces while they are often perceived as derelict and vacant (Ruelle, Halleux, & Teller, 2013), will require concerted efforts from urban planners.

4.3 | Urban farming

An interaction between urbanisation and management also influenced bee abundances, with abundance staying stable with urbanisation in informal green spaces and amenity lands but decreasing with urbanisation in farmed sites. Parallely, other pollinator groups such as beetles and flies decreased with urbanisation (although not all beetles and flies were necessarily pollinators). This highlights the importance of using context-specific information when promoting urban farming practices. Bee studies in European cities suggest that bee abundances and species richness did not vary according to whether the site was farmed or cultivated for flowers (Foster, Bennett, & Sparks, 2017). One explanation given as to why urban green spaces have more bees than rural areas is that agricultural pesticides with negative impacts on pollinators (Goulson, Nicholls, Botías, & Rotheray, 2015), are less prevalent. However, the opposite might be true in tropical Africa, as their cost and accessibility is a barrier to pesticides' widespread use in rural farms (Williamson, Ball, & Pretty, 2008). Urban farmers are typically better off (Sahn & Stifel, 2003) and have access to a wider range of agricultural products (Linard, Gilbert, Snow, Noor, & Tatem, 2012) despite farming smaller plots (Asomani-Boateng, 2002). Chemical pesticides are also used by municipalities to reduce mosquito abundances to control vector borne diseases (S. Mensah, personal communication, 2016) and could affect pollinator populations. While the local Environmental Protection Agency is aware of the environmental impact of such chemicals (Atta-Agyem, 2016), pollinators are not considered when decisions on chemical use are made, reflecting the lack of insect conservation initiatives within national policy (Ministry of Environment and Science, 2002). Given that urban farms tend to focus on high value insect-pollinated crops, reduced or more targeted municipal pesticide use could benefit both insect conservation and food productivity.

4.4 | Other ecosystem (dis)services

We identified non-bee pollinators to order level, yet this taxonomic resolution does not allow for the identification of the diversity of ecosystem functions they could provide and can hide some potential pests or biocontrol agents. For instance, wasps and flies included members of families some of which are natural predators of crop pests (Goulet & Huber, 1993). However, wasp abundance decreased with urbanisation,

meaning that the pest control service they provide to urban agriculture is likely to be below its full potential. Flies also included some families with negative impacts on human health and agriculture, such as crop pests, bee predators, or human and livestock disease vectors (Picker, Griffiths, & Weaving, 2002). Indeed, an increase in malaria-carrying mosquitoes is often raised as a concern in irrigated urban agriculture (Afrane et al., 2004), highlighting both the importance of understanding locally relevant trade-offs if green spaces are to be managed for insect conservation and ecosystem service provision and the need for further research on the comparison of ecosystem service and disservice providers in tropical urban landscapes.

Honey production is also an important service provided by bees, and often more valued by urban residents than pollination (Eardley, Gikungu, & Schwarz, 2009). Although the honey bee (*Apis mellifera*) is usually the main producer, there is a growing market for stingless bee honey in Africa (Kwapong, Aidoo, Combey, & Karikari, 2010). We found that stingless bees are present in high abundances within amenity lands, and they are already known to have different patterns of adaptation to disturbances than other bee genera (Combey & Kwapong, 2016). Moreover, traditional beekeeping contributes to bee conservation by reducing destructive honey hunting practices (Dietemann, Pirk, & Crewe, 2009). The association between stingless bees and amenity lands could provide an opportunity to include hives in some green spaces and offer an additional ecosystem service in locations that are not optimal for many bee species.

5 | CONCLUSIONS

Pollinator responses to urbanisation and management practices were diverse, with lepidoptera not being affected at all, wasps being affected mainly by urbanisation and beetles by both. Bees were affected by management practices, but their responses were not homogeneous and varied across taxa. This demonstrates the importance of considering each pollinator group separately for maintaining their ecosystem services in urbanising landscapes.

Although urban farms had lower bee abundances compared to rural areas, both amenity land and informal green spaces kept stable abundances along the urbanisation gradient. This illustrates that urban areas, by retaining similar bee abundances to rural landscapes despite their inhospitable matrix, can contribute to bee conservation in tropical Africa. Urban bee conservation might not directly contribute to decreasing food insecurity through improved urban agriculture, but can benefit regional biodiversity and help maintain crop pollination in the surrounding rural landscape.

In sum, urban pollinator conservation is possible, but requires a radical change in direction by urban planners to ensure a mix of informal and formal green spaces in tropical African cities as they expand.

ACKNOWLEDGEMENTS

We thank the local residents for welcoming us to their farms and gardens, Dr. P. Antwi-Agyei (KNUST) and Dr. M. Derkyi (UENR) for

facilitation on the field and the EORIC, UNER for the meteorological data. The research was funded by NERC through the SPHERES DTP, Leeds University's Sustainable Agriculture Bursary Fund and ESRC CCCEP.

AUTHORS' CONTRIBUTIONS

S.G., M.D., W.E.K. and A.J.D. conceived the ideas and designed the methodology; S.G. collected the data; S.G. analysed the data; all the authors contributed to the writing of the manuscript and gave final approval for publication.

DATA ACCESSIBILITY

Data available via the NERC Environmental Information Centre, Centre for Ecology and Hydrology <https://doi.org/10.5285/2e245944-ee5b-4612-b866-cafa3a129270> (Guenat, Kunin, Dougill, & Dallimer, 2018).

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How to cite this article: Guenat S, Kunin WE, Dougill AJ, Dallimer M. Effects of urbanisation and management practices on pollinators in tropical Africa. *J Appl Ecol*. 2019;56:214–224. <https://doi.org/10.1111/1365-2664.13270>