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RESEARCH ARTICLE

Citizen science reveals socio-economic influences on solitary bee abundance across multiple scales in a Global South city

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Abstract
Context Urban ecosystems exhibit complex biodiversity patterns influenced by both socio-economic and ecological factors. While the role of ecological factors is widely recognised, the relationships between socio-economic and ecological factors, particularly across various spatial scales and considering both landscape composition and configuration, remains underexplored. This limits our understanding of urban environments as interconnected socio-ecological systems.
Objectives We examine the influence of socio-economic and ecological landscape factors on solitary bee abundance, aiming to elucidate the complex socio-ecological dynamics shaping urban biodiversity across multiple scales.
Methods Data on solitary bee abundance were gathered through a citizen science campaign, supported by 347 participants from Johannesburg, South Africa. We explored the correlations and interactions between solitary bee abundance, socio-economic status (i.e. annual household income) and landscape composition and configuration (i.e. urban green cover and NDVI, and urban vegetation patch density and cohesion), assessing these relationships at 300 m, 2000 m, and 5000 m scales.
Results Annual household income was significantly positively correlated with solitary bee abundance across all spatial scales examined, likely due to increased investment in gardens with diverse floral resources in affluent areas. In contrast, our ecological factors, including both landscape composition and configuration metrics, exhibited negligible effects on solitary bee abundance across all spatial scales.
Conclusions The strong positive relationship between annual household income and bee abundance across scales highlights potential disparities in access to biodiversity and ecosystem services within Johannesburg. Our results indicate the presence of environmental injustice in this African city and reflect the need for integrating socio-economic factors into landscape ecology. Policies on urban greening that consider both socio-economic and ecological factors are essential for equitable, sustainable urban ecosystems.

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Introduction

Exploring the interplay between socio-economic and ecological landscape factors is key to understanding urban biodiversity, crucial for the sustainable development of cities (Grimm et al. 2000; Pickett et al. 2017) and the just and equitable provision of ecosystem services (UN-SDG Goal 11, 2023). Socio-economic status is a complex but often overlooked driver of urban biodiversity and can enhance, moderate, or even supersede the effects of ecological landscape factors (Hope et al. 2003; Kuras et al. 2020; Schell et al. 2020).Wealth, ethnicity and culture can shape the distribution and abundance of species, creating distinct socio-economic gradients of access to biodiversity in urban areas (Chamberlain et al. 2019; Venter et al. 2020; Han et al. 2023; Reynolds and Howes 2023). This is exemplified globally by the luxury effect, which demonstrates a strong positive correlation between wealth and biodiversity in urban landscapes (Leong et al. 2018; Chamberlain et al. 2020).

In contrast, the impacts of ecological landscape factors on urban biodiversity have been extensively studied and documented (Aronson et al. 2014; Beninde et al. 2015; Lee et al. 2021; Lewthwaite et al. 2024). Landscape composition and configuration, including measures of patch size and connectivity, are recognised as key drivers of urban biodiversity (Kang et al. 2015; Beninde et al. 2015; Turrini and Knop 2015; Howes and Reynolds 2021; Vega and Küffer 2021). For instance, the amount of urban green space can have a strong positive effect on species richness and functional diversity (Schütz and Schulze 2015; Beninde et al. 2015). In addition, increased connectivity, such as green corridors or rivers, can also improve urban biodiversity by enabling dispersal and colonisation (Suri et al. 2017; Vega and Küffer 2021). Although the positive effects of improved urban green infrastructure on biodiversity are well documented, the way in which these effects compare to, or interact with, socio-economic influences remain relatively under-explored (Chamberlain et al. 2020), especially in the Global South (but see Howes and Reynolds 2021; Reynolds and Howes 2023).

Understanding the scale-dependent impacts of socio-economic and ecological landscape factors is critical for effective urban biodiversity management. Biodiversity patterns and their underlying drivers are often studied at a single scale, even though research has consistently shown that the drivers of biodiversity vary across scales (Egerer et al. 2017; Ballare et al. 2019; Swan et al. 2021; Uchida et al. 2021). Socio-economic and ecological landscape factors can either influence urban biodiversity at distinct spatial scales or have significant synergistic effects at the same spatial scale (Baldock et al. 2020; Uchida et al. 2021). For example, socio-economic status at a larger landscape or regional scale could dictate the quality, amount, and connectivity of urban green space (Venter et al. 2020). Thus, socio-economic status could be the primary driver of biodiversity at these scales, potentially superseding any effects of ecological landscape factors (e.g. Han et al. 2023). Conversely, ecological processes may have a more significant impact on biodiversity at a local scale, where greater biodiversity is already supported in large and productive patches (Beninde et al. 2015). Finally, socio-economic status could have synergistic relationships across scales, influencing both the composition and configuration of urban green infrastructure (Uchida et al. 2021), and requires scale- and context-specific management interventions.

In urban areas, patterns of biodiversity are ultimately shaped by complex and interacting socio-ecological dynamics arising at various spatial scales. A comprehensive understanding of biodiversity in urban landscapes thus necessitates exploring the relationships between socio-economic status and ecological landscape factors at multiple spatial scales (Baldock et al. 2020; Uchida et al. 2021). Importantly, cities in the developing world typically have stronger socio-economic gradients due to higher wealth disparities and historical contingencies of urban development, providing a valuable backdrop to examine the socio-ecological drivers of urban biodiversity (Shackleton et al. 2021; Reynolds et al. 2021).

We investigate how socio-economic and ecological landscape factors influence cavity-nesting solitary bee abundance across multiple spatial scales in Johannesburg, South Africa. These pollinators play a crucial role in supporting urban ecosystem services through their contribution to the pollination of ornamental plants and food crops (Danforth et al. 2013; Ballare et al. 2019). Solitary bees constitute almost 90% of all bee diversity globally, with cavity nesting solitary bees accounting for ~ 30% of this diversity (Danforth et al. 2013). South Africa supports nearly 1300 species of solitary bee (Gess and Gess 2014), but very little is known about solitary bees in African urban contexts (Wenzel et al. 2020). In cities, "bee hotels" (artificial nests with multiple holes or tubes) are becoming commonly used to provide nesting habitat for cavity nesting solitary bee species and are useful for attracting pollinators to the urban environment (Fortel et al. 2016). These artificial nests provide a simple and effective method for assessing solitary bee abundance.

South Africa displays one of the highest income inequalities globally, largely an artefact of its Apartheid legacy (Herbert and Murray 2015; World bank 2023). Here we leverage this strong gradient to investigate how socio-economic status correlates with solitary bee abundance at different spatial scales, and whether these correlations enhance, moderate, or supersede the effects of ecological landscape factors. We used a model selection approach to determine whether socio-economic or ecological landscape factors most influenced solitary bee abundance at three spatial scales relevant to solitary bee population dynamics, neighbourhood (300 m), landscape (2 km), and regional (5 km) (Steffan-Dewenter et al. 2002; Moreira et al. 2015; Zurbuchen et al. 2010; Egerer et al. 2017). We hypothesised that solitary bee abundance could either be related to socio-economic status (i.e. annual household income) (e.g. Baldock et al. 2019), ecological factors, characterised by landscape composition (i.e. urban vegetation cover and productivity) or configuration metrics (i.e. urban vegetation patch density and cohesion) (e.g. Hennig and Ghazoul 2011, 2012; Geslin et al. 2013; Wenzel et al. 2020; González-Césped et al. 2021; Graffigna et al. 2024), or by an interaction of both (e.g. Chamberlain et al. 2019; Baldock et al. 2020) (Table 1).

Methods

Study system

This study was undertaken in the City of Johannesburg Metropolitan Municipality (hereafter Johannesburg) in South Africa. Johannesburg is the largest and most populated city in South Africa, hosting ~ 10% of the total South African population (approx. 6.3 million inhabitants) and is the economic hub of the country (StatsSA 2021). The city's socio-economic and urban development status has been shaped by its history of racial segregation, which has resulted in stark and persistent inequality in income and living conditions across the landscape (Herbert and Murray 2015). Although Johannesburg can be considered developed in comparison to the rest of South Africa as 91% of residents have access to electricity and 96% have access to running water. However, approximately a quarter of its inhabitants still live in poverty relative to the upper poverty line of ~ $80 per month (StatsSA 2021). In contrast the city also supports areas of significant wealth, with residents reporting over $1 million in assets (Afrasia 2019). This stark socio-economic contrast within Johannesburg, characterised by both extreme poverty and substantial wealth, presents a unique urban landscape for studying the intricate relationships between socio-economic status and ecological landscape factors and their influence on access to urban biodiversity.

Ecologically, the city is shaped by its unique position on the Highveld grassland plateau, its mild climate (mean daily temperature of 18–20 °C during the austral summer) and good annual rainfall (~ 750 mm per annum mostly during the summer months). The city supports a range of habitats, and is a mix of open grassy habitats, naturally vegetated rocky ridges and afforested areas (Mucina and Rutherford 2006; Symes et al. 2017). Johannesburg is well known for its "leafy green suburbs", which feature extensive parks and gardens, and are characterised by high tree cover (largely exotic species e.g., *Jacaranda mimosifolia*, *Plantanus acerifolia*, and *Eucalyptus* spp.) (Symes et al. 2017).

The Jozi Bee Hotel Project

The abundance of cavity nesting solitary bees served as our biodiversity indicator in this study. To collect these data, we launched a citizen science project (the Jozi Bee Hotel Project), which engaged ~ 350 residents from across the diverse socio-economic and ecological gradient of Johannesburg. Jozi Bee Hotel Project participants were provided with a free and standardised bee hotel and asked to host and monitor the hotel, submitting weekly occupancy data of

Table 1 Hypothesised relationships between bee abundance, and socio-economic and ecological landscape factors across our three scales of interest. The hypotheses are formulated to explore the potential influences of annual household income, landscape composition, and landscape configurations (both linear and interactive effects) on solitary bee abundance. Note * denotes an interaction between the variables. Model number and model structure are linked to our model selection procedure

Model number	Hypothesis	Model structure
1 (Null)	If solitary bee communities are not structured by any measured landscape factors, then bee abundance will not be correlated with any predictor variables	Abundance ~ 1
2	If solitary bee communities are structured by socio-economic status, then bee abundance will to be correlated with annual household income (AHI)	Abundance ~ AHI
3	If solitary bee communities are structured by the composition of landscape resources in the form of urban vegetation quantity and quality, then bee abundance will to be correlated urban vegetation cover (Urban veg cover) and its productivity (NDVI)	Abundance ~ Urban veg cover + NDVI
4	If solitary bee communities are driven by the configuration of landscape resources in the form of urban vegetation connectivity and fragmentation, then bee abundance will to be correlated with urban vegetation cohesion (Urban veg cohesion) and urban vegetation patch density (Urban veg PD)	Abundance ~ Urban veg PD + Urban veg cohesion
5	If solitary bee communities are structured by an interaction between socio-economic status and landscape composition, then bee abundance will be correlated with the interaction between annual household income (AHI) and urban vegetation cover (Urban veg cover) and/or NDVI	Abundance ~ Urban veg cover *AHI + NDVI * AHI
6	If solitary bee communities are structured by an interaction between socio-economic status and landscape configuration, then bee abundance will be correlated with the interaction between annual household income (AHI) and urban vegetation cohesion (Urban veg cohesion) and/or urban vegetation patch density (Urban veg PD)	Abundance ~ Urban veg PD*AHI + Urban veg cohesion*AHI

cavity nesting solitary bees over the three-month study period (September–December 2021). The provision of bee hotels to urban residents was a valuable approach for assessing differences in solitary bee abundance relative to the socio-ecological gradients of the city, especially because nest availability is important in shaping bee communities in urban environments (Fortel et al. 2016).

Citizen science campaign

In the recruitment phase of the Jozi Bee Hotel Project, a multifaceted approach was employed to engage participants from across Johannesburg. We leveraged social media platforms (Facebook, Instagram and WhatsApp), email lists, community interest groups, public talks and developed a dedicated website to encourage project registration (www.jozibeehotelproject.com). We purchased a total of 400 bee hotels, all manufactured by a local South African business (Tutus Loco) for consistency (Fig. 1).

Official registration for the project was open from July to August 2021. Participation was entirely voluntary and not renumerated, and Jozi Bee Hotel Project participants were able to keep the complimentary bee hotels. Participants were invited to collect their freely provided bee hotels during designated information sessions, which were held in various public parks over several weekends, however, we also arranged delivery of hotels to several participants that could not attend the weekend events. We provided participants with an information pamphlet of where best to place the hotels (i.e. at least 1 m above the ground, in a shady and

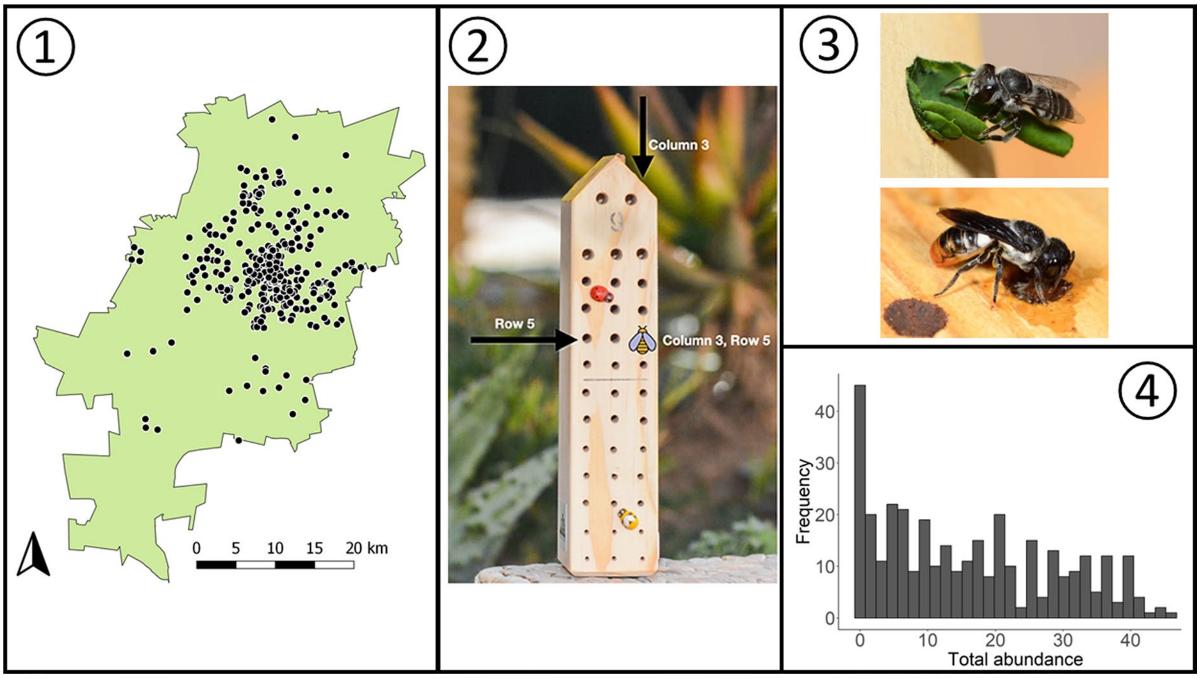

Fig. 1 Jozi Bee Hotel Study Design. (1) Map illustrating the geographic location of the 347 standardised bee hotels provided to participants in the Jozi Bee Hotel Project. (2) The monitoring process involved participants submitting weekly photographs of their bee hotel via a Google form. The photographs of the bee hotel enabled the identification and counting of sealed nesting holes (out of a total of 38 available holes per hotel) in a column by row format. (3) Examples of solitary bees (leaf cutter and mud bees) sealing nests with various materials, providing a clear indication of bee activity. (4) A bar chart depicting the frequency distribution of bee nesting activity observed across all bee hotels during the study period is shown

dry environment and near to vegetation if possible) to help standardise data collection. Bee hotels, however, are highly versatile and can be placed in various urban settings, including private gardens, verandas, external walls, balconies, windowsills, or rooftops, regardless of the amount of vegetation present. This flexibility ensured that anyone could participate in the citizen science project, whether they have a spacious garden or just a small urban space, allowing for data collection across diverse urban environments. The docile nature of solitary bees was another essential component of the success of our citizen science campaign as urban residents with small children and pets could easily be convinced to host a bee hotel as the perceived risk was negligible. Through our inclusive efforts we achieved good representation across the socio-ecological gradient of Johannesburg and although we had more participants in middle- to higher-income suburban areas, we were still able to engage a good representation of participants from the low-income and highly urban areas, with representation for example in Soweto, Hillbrow and Braamfontein (Appendix S1). However, participation from extreme low-income areas in Johannesburg, particularly informal settlements, was limited due to practical constraints. The project's reliance on cellular data for data submission inadvertently excluded potential participants who lacked consistent access to this resource. Additionally, safety concerns stemming from political unrest in July 2021, especially in Alexandria, one of Johannesburg's largest informal settlements, prevented researcher engagement with these communities. These factors have resulted in an under-representation of the city's most economically disadvantaged areas in our study. Despite this limitation, our socio-economic gradient still spans more than an order of magnitude (Appendix S1).

Data collection and processing

Data collection commenced on the 1st of September 2021 (spring day in the Southern Hemisphere), when all participants simultaneously "opened" their bee hotels. The data collection methodology for the Jozi Bee Hotel Project was designed for simplicity and efficiency, ensuring ease of participation and consistency in data submission. Each participant was required to submit a weekly cell phone photograph of the front of their bee hotel through a Google form. Participants could also email or WhatsApp the photograph to the project administrators facilitating submissions from participants that had limited access to data or experienced difficulties with the Google form. To enable accurate tracking and data association, all bee hotels were distinctly marked with a unique number. This identifier was linked to the GPS location of each hotel within Johannesburg, allowing precise (but anonymised) geographical mapping of the data. In total, 387 bee hotels were distributed to participants, and 347 participants submitted reliable and regular data (Fig. 1). Data submission occurred on a weekly basis from 1st of September to the 1st of December 2021.

Data processing was conducted weekly to maintain an up-to-date record of the project's progress, provide feedback to the citizen scientists, and maintain engagement with the project (Shilubane et al. 2024). To ensure timely and regular data submission, participants received weekly email reminders, prompting them to upload their photographs. The responsibility of processing incoming data was assigned to a dedicated individual (BK), who meticulously collated and reviewed the photographic evidence and counted and classified the nesting bees over the three-month period. Each hotel had 38 available holes of differing sizes (6–2 mm in range) (Fig. 1). The photographs clearly show which holes were sealed, reliably indicating bee activity (Fig. 1). Female bees lay eggs within the hotels and seal each completed nest, allowing us to allocate them to one of four functional groups based on the sealing material: *Allodapula sp*. (using their abdomen), Resin/Membrane, Mud, and Leaf Cutter (using saliva, mud, or vegetative material, respectively) (Gess and Gess 2014).This classification was important for accurate data processing, though later analyses combined these groups due to statistical considerations (see Sect. 2.3.1). In cases where it was not possible to allocate bees to a functional group based on the clarity of photographs the bee was classed as "other". Observations in this category were removed from further analysis as we could not be certain that these were in fact bees, and not other invertebrates.

Analysis overview

Our analytical approach consisted of three separate analyses. First, we used generalised linear models within a model selection framework to evaluate six competing hypotheses for drivers of solitary bee abundance at three spatial scales, namely 300 m, 2000 m, and 5000 m (Table 1). The motivation for choice of scales was as follows: 300 m was chosen as a measure of fine-scale effects given that this most likely provides a reasonable measure of solitary bee foraging ranges (Steffan-Dewenter et al. 2002; Zurbuchen et al. 2010; Egerer et al. 2017). The 2000 m scale allowed us to explore structuring effects at an intermediate landscape scale considering longer distance dispersal capacities of solitary bees (Steffan-Dewenter et al. 2002; Moreira et al. 2015; Egerer et al. 2017). Finally, the 5000 m scale was selected to explore the drivers of bee abundance at the broadest scale, expecting that at this scale the landscape would influence population dynamics and persistence (Moreira et al. 2015). The explanatory variables used in this set of models included: Median annual household income (AHI), normalised difference vegetation index (NDVI) of urban vegetation, and percentage cover, patch density, and cohesion index of urban vegetation cover (Table 2). Second, we used generalised linear models to test an additional set of models, which included an extra set of ecological variables focussed on more natural landscape elements (i.e., tree cover, and configuration and composition metrics of natural vegetation and wetlands (Appendix S5). The underlying hypothesis is that while urban vegetation composition and configuration plays a role, natural landscape features and availability of nesting sites in the form of trees might also significantly impact bee abundance in the urban environment (e.g. MacIvor et al. 2014; Wenzel et al. 2020). Third, we analysed how the density and distance to plant nurseries (also known as garden centres), varied with annual household income at three different scales (Appendix S6). This analysis served as a proxy for assessing the

Table 2 Details of the explanatory variables used in our primary bee abundance analysis

Explanatory variable	Abbreviation	Units	Context
Median annual household income	AHI	South African Rands (R)	Socio-economic status
Mean Normalized Difference Vegetation Index	NDVI	Range between 0–1	Urban vegetation productivity
Patch density of urban vegetation cover	Urban veg PD	Patches per 100 ha	Configuration of urban vegetation habitat patches–index of fragmentation
Percentage coverage of urban vegetation	Urban veg cover	%	Composition of urban vegetation–index of quantity
Patch Cohesion Index for urban vegetation cover	Urban veg cohesion	%	Configuration of urban vegetation habitat patches–index of connectivity

demand for ornamental plants across different socio-economic levels. The underlying hypothesis is that areas with higher socio-economic status may have greater access to and demand for garden centres, potentially indicating a higher capacity to create and maintain bee-friendly habitats. Apart from remotely sensed layers accessed and downloaded from Google Earth Engine (Gorelick et al. 2017), all analyses were carried out using R version 4.1.2 (R Core Development Team 2023).

Bee abundance data

The analysis consisted of data collected from 347 bee hotels as some of the original participants stopped submitting data (Appendix S1). For the purposes of this analysis, we grouped all bee functional groups together to get a total measure of abundance at each hotel by summing the occurrence of new bees recorded each week over the course of the 12-week study period. The functional classification was important to help us track instances of "switching" in the hotels (i.e., a previously colonised hole was subsequently occupied by a new species from a different functional group). Specifically, we could determine when a hole previously occupied by an *Allodapula sp.* (usually nesting early in the season) was taken over by either a resin/membrane, mud or leaf cutter bee. In these cases, we added both observations to the total count, which meant that in some cases the total abundance of bees over the study period was greater than the 38 available holes (Fig. 1). Unfortunately, even though we have some functional resolution on the nesting bees the decision to combine all functional groups into a total measure of abundance was also taken due to excessive overdispersion caused by the large proportion of zeroes in some functional groups. Despite attempts to model these data with appropriate zero-inflated models we had to model abundance as a single measure for each hotel to minimise any violation to model assumptions. Furthermore, due to the nature of the citizen science initiative it is not possible to get accurate taxonomic information and abundance on the nesting bees, as this would require destructive sampling of the citizen hosted bee hotels, which we believed to be counterproductive to the engagement and educational aspects of our project.

Socio-economic and ecological covariates

Data to quantify annual household income was sourced from the most recently available South African Population Census (StatSA 2012). The data provides the annual household income for households that are spatially grouped in what is called a small area layer. The small area layer is a GIS vector layer that contains polygons of various sizes and contains census data for roughly 200 households per polygon. The size of each small area layer polygon is inversely related to population density. In each polygon of the small area layer, we calculated median annual household income from the available household census income data (see Chamberlain et al. 2019). Our Johannesburg study area comprised 8294 small area layer polygons with an average area of 32 ha (Appendix S1). We then used our circular buffers around each bee hotel at three spatial scales to get a median annual household income for each hotel location. Annual household income has been shown to be closely related to several other socio-economic variables (e.g., education level, household size, and employment) and can therefore be considered a robust measure of socio-economic status (Chamberlain et al. 2019; Anderson et al. 2020; Howes and Reynolds 2021).

We used Google Earth Engine (Gorelick et al. 2017) to calculate mean normalized difference vegetation index (NDVI) and tree cover (Appendix S5) within the circular buffers around each study site at three spatial scales. For NDVI we used the Landsat 8 Collection 1 Tier 1 8-Day NDVI Composite at a 30 m resolution (Chander et al. 2009), and for tree cover we used the Global Forest Cover Change (GFCC) Tree Cover Multi-Year Global 30 m dataset (Appendix S5). The tree cover layer contains estimates of the percentage of horizontal ground covered by woody vegetation greater than 5 m in height in each 30 m pixel (Sexton et al. 2013). For the NDVI layer we applied a temporal filter for the duration of the study period (26/08/2021 to 02/01/2022) before calculating the spatial mean. For the tree cover layer, we used the data from 2015, which was the closest available on a temporal scale (note this layer was only used in our supplementary analysis, Appendix S5).

The percentage cover, patch cohesion and patch density of urban vegetation were calculated based on the 2020 South African National Land-Cover raster layer with a 20 m resolution (SANLC 2020). The original land cover layer had a total of 73 different classes. For the purposes of our analysis, we reclassed the data into five classes: Natural vegetation, urban vegetation, wetlands, urban, and other (Appendix S2). We calculated class-level patch metrics for each of the reclassed land cover classes using *sample_lsm* function from the *landscapemetrics* R package (Hasselbarth et al. 2019). The class-level metrics for each land cover class used in our analysis included: Total class area (percentage cover), patch cohesion index (which calculates the connectedness of patches belonging to a class), and patch density (which describes the fragmentation of a class). See Table 2 for a further description of class metrics.

Bee abundance analysis

For our primary analysis we constructed a set of six models, consisting of a null model and five other models, each representing one of our hypotheses outlined in Table 1. We used zero-inflated negative binomial models with a *ziformula* parameter equal to 1, implemented with the *glmmTMB* function, to model total bee abundance as a function of our hypothesis-specific predictor variables. The regression analysis and model selection procedure were repeated for each of the three spatial scales (300 m, 2000 m, and 5000 m). We checked for pair-wise correlations and standardised all predictor variables before running the models. Following this, we carried out a model selection using the *aictab* function from the AICcmodavg R package (Mazerolle et al. 2017). After identifying the top model from the model selection process (Appendix S3), we checked for overdispersion, zero-inflation, outliers and spatial autocorrelation using functions from the DHARMa R package (Hartig and Lohse 2022). In addition to this we also checked for variance inflation of predictor variables using the *check_collinearity* function from the performance R package (Lüdecke et al. 2021). We followed an identical process for our secondary analysis (Appendix S5), which included the extra set of natural vegetation variables (i.e., tree cover, patch density of natural vegetation and water, cohesion index of natural vegetation and water, and proportion of urban land cover).

Linking garden nurseries to socio-economic status in the city

In a final analysis, we examined the relationship between socio-economic status and access to garden centres, hypothesising that higher-income areas might have greater capacity to create bee-friendly habitats. Using the Google Places API via the googleway R package (Cooley et al. 2023), we systematically identified and geocoded all garden nurseries in Johannesburg (Appendix S6). We first created a regular grid of 75 points across Johannesburg. For each point we used the *google_places* function with the search string set as “plant nursery Johannesburg”, and the search radius set at 2500 m to query the API for matching results within the buffer. The Google Places API search returned a maximum of 60 geocoded places, which we compiled after each individual point search. The original search returned a list of 89 nurseries. The raw list was screened for obvious errors, resulting in a cleaned and validated list of 74 unique nurseries. To explore the relationship between annual household income and nurseries we calculated two metrics: Distance to closest nursery, and nursery density. Distance to closest nursery was calculated for each bee hotel location using a Euclidean distance calculation on the projected coordinates of hotels and nurseries. Nursery density was calculated at each of our three spatial scales by summing the number of nurseries intersecting with each circular buffer around bee hotels. Using simple linear regression we modelled distance as a function of annual household income at all spatial scales, and density as a function of annual household income at 2000 m and 5000 m scales. We did not run the density analysis at the 300 m scale because only nine hotels contained one or more nurseries within the 300 m buffer around the study site.

Results

Bee abundance

The mean total abundance of solitary bees across the study period at each site was 16.05 with a SD of 12.85. The median total abundance was 15 across all sites. There were 45 hotels (13% of total sample) that recorded no bees throughout the study period (see Fig. 1 for frequency distribution of total abundance). The results of the model selection showed strikingly consistent results across the three spatial scales. The top model for each spatial scale identified using AIC criteria was the model that included only annual household income as a predictor variable (Table 3). The delta AIC values were all greater than two indicating a lack of strongly competing models within the model set across scales (2.98 at 300 m, 6.17 at 2000 m, and 5.68 at 5000 m). The AIC weights for the annual household income models were all high (0.67 at 300 m, 0.89 at 2000 m, and 0.88 at 5000 m) indicating that within the candidate model set, annual household income models had a high proportion of predictive power. In all models, annual household income was positively

Table 3 Results of the AIC model selection procedure for our five competing hypotheses at three different scales (300 m, 2000 m, 5000 m). K = number of model parameters; AICWt = AIC weight, and Cum.Wt = cumulative AIC weight. * Indicates an interaction between covariates. AHI = median annual household income; NDVI = mean normalized difference vegetation index; Urban veg PD = patch density of urban vegetation cover; Urban veg cover = percentage cover of urban vegetation; Urban veg cohesion = patch cohesion index of urban vegetation

Model	Hypothesis number	AIC	K	DeltaAIC	AICWt	Cum.Wt
300 m						
abundance ~ AHI	2	2581.52	4	0.00	0.67	0.67
abundance ~ Urban veg cover + NDVI	3	2584.50	5	2.98	0.15	0.83
abundance ~ Urban veg cover*AHI + NDVI*AHI	5	2585.42	8	3.90	0.10	0.92
abundance ~ Urban veg PD *AHI + Urban veg cohesion*AHI	6	2586.55	8	5.03	0.05	0.98
abundance ~ 1	1	2588.75	3	7.23	0.02	0.99
abundance ~ Urban veg PD + Urban veg cohesion	4	2590.94	5	9.42	0.01	1.00
2000 m						
abundance ~ AHI	2	2581.30	4	0.00	0.89	0.89
abundance ~ Urban veg PD*AHI + Urban veg cohesion*AHI	6	2587.46	8	6.17	0.04	0.93
abundance ~ Urban veg cover*AHI + NDVI*AHI	5	2587.90	8	6.60	0.03	0.96
abundance ~ 1	1	2588.75	3	7.45	0.02	0.99
abundance ~ Urban veg cover + NDVI	3	2590.05	5	8.75	0.01	1.00
abundance ~ Urban veg PD + Urban veg cohesion	4	2592.66	5	11.37	0.00	1.00
5000 m						
abundance ~ AHI	2	2579.67	4	0.00	0.88	0.88
abundance ~ Urban veg cover*AHI + NDVI*AHI	5	2585.34	8	5.68	0.05	0.93
abundance ~ Urban veg PD*AHI + Urban veg cohesion*AHI	6	2585.83	8	6.16	0.04	0.97
abundance ~ Urban veg cover + NDVI	3	2587.70	5	8.04	0.02	0.99
abundance ~ 1	1	2588.75	3	9.08	0.01	1.00
abundance ~ Urban veg PD + Urban veg cohesion	2	2591.77	5	12.10	0.00	1.00

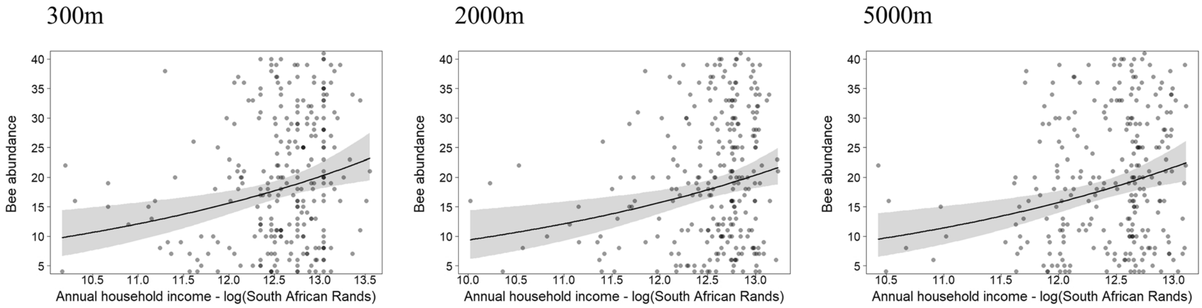

Fig. 2 Scatterplot of median annual household income (AHI) in log(South African Rands) and solitary bee abundance at three spatial scales (300 m, 2000 m, 50000 m) with regression lines and 95% confidence intervals

related to bee abundance (Fig. 2). The direction, magnitude, and significance of regression parameters of the annual household income models were consistent across scales ($\beta = 0.137$, SE = 0.045, $p < 0.01$ at 300 m; $\beta = 0.138$, SE = 0.044, $p < 0.01$ at 2000 m; and $\beta = 0.147$, SE = 0.043, $p < 0.001$ at 5000 m) (Appendix S3). These results remain consistent even when analysing a subset of data that excludes households with a log-transformed annual household income below 11.8 (where income is in South African Rands) (Appendix S4). In terms of our secondary set of models, which included additional ecological variables, the annual household income model was still the top ranked model. Similarly, to our primary model selection analysis, the delta AIC values were all greater than two indicating a lack of strongly competing models within the model set across scales (2.27 at 300 m, 4.50 at 2000 m, and 5.68 at 5000 m) (Appendix S5).

Garden nurseries in the city

Distance to closest nursery was negatively correlated with annual household income, and this relationship was significant at all spatial scales although the most prominent relationship was at the 5000 m scale (Appendix S6). Nursery density was positively correlated with annual household income at the 2000 m scale although this was strictly not significant at a 0.05 threshold (in this case $p = 0.053$). There was however, a much stronger positive relationship between nursery density and annual household income at the 5000 m scale ($\beta = 1.8$, SE = 0.45, $p < 0.001$; Appendix S6).

Discussion

Household income and solitary bee abundance across scales

Our study shows that socio-economic status is the primary predictor of solitary bee abundance across multiple spatial scales in the city of Johannesburg. Annual household income was strongly positively correlated to solitary bee abundance and was the single best predictor across all spatial scales considered. The consistent and positive relationship between increasing wealth and access to biodiversity across multiple spatial scales suggests the presence of a persistent luxury effect in this large African city and highlights the likely prevalence of environmental injustice at local, landscape and regional scales. Such a multi-scale trend suggests that the influence of wealth on biodiversity extends beyond localised environments and can produce larger scale impacts on access to biodiversity. These insights suggest that urban planning policies need to be rethought, particularly in terms of how socio-economic factors are incorporated into biodiversity conservation strategies (see Sect. 4.3 below). This is especially important given that city-wide urban greening strategies, proximity to natural habitats and tree cover have little effect on cavity nesting solitary bee abundance across multiple spatial scales, and that wealth is the sole predictor promoting the creation of habitat for solitary bees, likely in the form of gardens with floral resources.

In the context of Johannesburg's pronounced socio-economic disparity (Herbert and Murray 2015), the dominant correlation between household income and solitary bee abundance in the city emerges as a compelling finding. Other studies have similarly demonstrated that socio-economic status can be an important driver of biodiversity in urban landscapes (Chamberlain et al. 2019; Anderson et al. 2020; Baldock et al. 2020; Kuras et al. 2020; Venter et al. 2020; Reynolds and Howes 2023). However, what is striking here is that neither ecological landscape factors nor their interaction with household income had any apparent impact on solitary bee abundance, at any spatial scale in the analysis (Table 2 and Appendix S5). Even in more affluent neighbourhoods, where we expected higher socio-economic status to lead to greater investment in green infrastructure and thus interact with ecological landscape factors (Aronson et al. 2014; Wilkerson et al. 2018) (Table 1), annual household income remained the sole best predictor of pollinator abundance across all scales. These findings challenge conventional wisdom on urban greening, which suggests that improvements in urban green infrastructure, such as increasing green space and improving connectivity, are effective mechanisms for promoting urban biodiversity (Kang et al. 2015; Beninde et al. 2015; Turrini and Knop 2015; Villaseñor et al. 2022). Instead, our analysis indicates that socio-economic or development factors, especially where these gradients are pronounced, may exert a greater influence on access to urban biodiversity overall and present a significant challenge for urban planning and environmental justice (Aronson et al. 2014; Schell et al. 2020). The absence of other landscape-scale ecological mechanisms in explaining bee abundance, at any of our measured scales, suggests that conventional interventions aimed at city-wide improvements to existing green infrastructure may not adequately address social inequalities in access to biodiversity and urban ecosystem services.

The emergence of household income as the predominant predictor of solitary bee abundance in Johannesburg led us to explore the potential underlying mechanisms of this significant correlation. Given the biology of bees, the key factor may not be the sheer quantity of green space but rather its quality (Turo and Gardiner 2019; Daniels et al. 2020). Specifically, highly manicured green spaces, which are extensive across the city of Johannesburg, may lack the floral biodiversity essential for supporting robust pollinator populations (Daniels et al. 2020). Our initial attempt at understanding the mechanisms focused on including more natural elements within the urban landscape (i.e. natural vegetation, tree cover and water availability). We hypothesised that affluent households might have greater access to more natural areas, often deemed attractive living spaces (Sander and Zhao 2015; Lang et al. 2023). However, this analysis reaffirmed that annual household income remained the strongest predictor of solitary bee abundance, indicating that innate natural features are also not the primary factors influencing urban solitary bee dynamics.

Subsequently, we examined whether the behaviours of more affluent individuals, particularly their possible investment in and maintenance of gardens with elaborate floral resources (Lowenstein and Minor 2016; Blanchette et al. 2021), could be driving bee abundance. As we did not collect a measure of local floral resources from Jozi Bee Hotel Project participants, we used the density and location of plant nurseries (garden centres) as proxies for understanding how the behaviour of more affluent households could shape the availability of floral resources across our scales of interest. The data revealed that affluent neighbourhoods not only had closer proximity to but also a higher number of plant nurseries, suggesting a substantial market demand for these resources. This correlation implies that the behaviours and financial capacity of affluent individuals (Lowenstein and Minor 2016; Blanchette et al. 2021), possibly also motivated by values that associate lush gardens with prestige (Grove et al. 2006), play a significant role in enhancing solitary bee activity and in creating habitat for pollinators. This is further emphasised by the finding that increased availability and connectivity of green spaces in more affluent neighbourhoods was not correlated with higher bee abundance. This suggests that it is not just the presence of green spaces, but the specific nature and management of these spaces that matters for bee populations. Future research should verify these findings through detailed vegetation and pollen surveys in gardens along socioeconomic gradients to assess the abundance and composition of bee-preferred plants (e.g. Müller et al. 2006). The choice to utilise one's wealth for creating biodiverse environments highlights a behavioural or cultural facet in fostering urban biodiversity (Machlis et al. 1997; Goddard et al. 2013; Aronson et al. 2016; Kuras et al. 2020) but is an option more accessible to wealthy individuals. In wealthier areas in Johannesburg, a societal norm of maintaining rich floral resources appears to create favourable conditions for solitary bees, reflecting a form of socio-ecological ‘keeping up with the Joneses’. In Johannesburg, this scenario is likely exacerbated given the stark income disparity, where creation of habitat for bees is unlikely to be a priority of economically disadvantaged households.

Ecosystem services

The differential access to pollination services across the socio-economic gradient in Johannesburg revealed by our study (see also Reynolds and Howes 2023 on bird pollination) has significant implications for both biodiversity and human well-being. In areas of higher socio-economic status, increased pollinator abundance, emphasises a disparity in ecosystem service provision across Johannesburg. Pollination is crucial not only for ecological function (Guenat et al. 2019; Brom et al. 2023), but also for urban agricultural practices (Lowenstein et al. 2014), which can be a vital source of food security and nutritional diversity for low-income households (Poulsen et al. 2015; de Oliveira Alves & de Oliveira 2022). This highlights the need for policy interventions that ensure equitable access to ecosystem services, such as more inclusive urban agricultural policies. Urban agriculture is a priority for the City of Johannesburg, through its Food Resilience Policy (Cilliers et al. 2024) and the presence of appropriate pollinators may benefit these food security efforts. Lower solitary bee abundance observed in economically disadvantaged areas indicates a reduced access to this important ecosystem service, potentially exacerbating existing inequalities and reinforcing the feedback between reliance on ecosystem services and decreased access to these services (Cumming and von Cramon-Taubadel 2018; White et al. 2022).

Rethinking urban greening and the luxury effect

Our study emphasises the need for more transformative urban greening strategies that intertwine socio-economic development with biodiversity conservation and recognise socio-economic status as an influential factor in landscape ecology across multiple spatial scales. In the context of developing countries, and particularly in South Africa, the goals of enhancing human well-being, addressing poverty, and promoting equity and wealth redistribution are already paramount, but often exist in isolation from urban biodiversity conservation efforts (Cilliers et al. 2004). This disconnection is problematic, as achieving socio-economic development goals without integrating biodiversity and ecosystem services can lead to suboptimal outcomes for both human well-being and environmental health. Our own work, and that of others highlights the persistent challenges faced by impoverished urban communities (Chamberlain et al. 2019; Anderson et al. 2020; Venter et al. 2020; Reynolds and Howes 2023), despite ongoing urban greening efforts, and suggests the need for more integrated strategies. Urban greening initiatives, therefore, should not be seen as isolated environmental projects but as integral components of broader socio-economic development plans (Aronson et al. 2014; King and Shackelton 2020).

In rethinking the traditional luxury effect (Hope et al. 2003), we advocate for improving and using biodiversity to foster socio-economic development, rather than viewing it as merely an artefact of increased wealth. This framing recognises a synergistic relationship between biodiversity and socio-economic growth, suggesting that enhancing urban biodiversity can simultaneously drive, and benefit from, socio-economic development. For example, formalising and promoting community-led agricultural and greening projects can boost both public and private green spaces and provide vital employment (e.g. Kazungu et al. 2014; King and Shackelton 2020). Policy initiatives focused on securing more green collar jobs in cities can play a pivotal role in alleviating poverty in the developing world, where unemployment rates are often high. These forms of employment not only contribute to reducing poverty but also facilitate the integration of biodiversity into urban landscapes, creating a balance between ecological and economic objectives (King and Shackelton 2020). The key is to position human well-being at the core of sustainable cities (UN-SDG Goal 11, 2023), viewing both biodiversity enhancement and wealth creation as essential components contributing to this goal. In doing so we shift from viewing biodiversity and socio-economic development as separate axes to considering them as intertwined elements that, when optimized together, can lead to a more sustainable and equitable urban future.

Conclusion

That annual household income consistently emerges as the primary driver of solitary bee abundance across multiple spatial scales in Johannesburg highlights the persistent and pervasive impact of inequalities on urban biodiversity. This pattern, observed at local, landscape, and regional levels, underscores the pervasiveness of the luxury effect, transcending various scales and highlighting how socio-economic status can supersede the influence of certain key ecological factors in urban systems. This necessitates a paradigm shift in urban development, where socio-economic changes become integral to urban greening strategies. Effective urban biodiversity enhancement necessitates strategies that are not limited to ecological improvements but also address the socio-economic disparities evident across different spatial scales. This integrative approach will not only foster ecological well-being but also enhance social equity, ensuring that the benefits of biodiversity are equitably distributed and accessible to all urban residents, regardless of their socio-economic status.

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Data availability The data are held by the corresponding author and will be made avaliable on request to interested parties. All other spatial data used is already open access.

Declarations

Competing interests The authors declare no competing interests.

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