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Drivers of woody plant phylogenetic and taxonomic beta diversity across an urban density gradient

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Abstract
Urban plant diversity patterns are influenced by socioeconomic factors, yet our understanding of these relationships in Global South cities remains limited. We investigated how taxonomic and phylogenetic beta diversity of woody plants vary across Harare's socioeconomic gradient, examining patterns for indigenous and exotic species. We surveyed 300 household yards across 15 suburbs representing low-, medium-, and high-density areas, characterized by differences in property values, population density, and yard size. For combined species, both taxonomic and phylogenetic beta diversity showed significant positive relationships with property value and yard area, supporting the 'luxury effect' hypothesis. However, patterns differed when analysing species groups separately. Exotic species demonstrated strong socioeconomic filtering, with greater taxonomic diversity in wealthy areas but consistently low phylogenetic turnover across suburbs, suggesting selection of evolutionarily related species. Indigenous species showed unexpected resilience in high-density areas, maintaining greater phylogenetic diversity than affluent suburbs. While species turnover dominated overall beta-diversity patterns, phylogenetic nestedness contributed substantially more than taxonomic nestedness, particularly for exotic species. These findings challenge conventional urban ecology paradigms and highlight the importance of considering both taxonomic and phylogenetic dimensions when assessing urban biodiversity. The retention of phylogenetically diverse indigenous communities in high-density areas presents opportunities for biodiversity conservation in African cities.

Keywords Beta-diversity · Luxury effect · Novel ecosystem · Phylogenetic-diversity · Socioeconomic status

Introduction

The world population is expected to grow from about 7.68 billion to 9.6 billion by the year 2050 (United Nations 2019), a growth accompanied by increasing demand for land, with important implications for biodiversity (McKinney 2006). In particular, a greater population growth is expected in urban areas, which will displace sessile plants e.g., trees, with buildings and paved surfaces thereby altering plant diversity (Ziter et al. 2019). However, our knowledge of how woody species (trees and shrubs) composition and diversity varies across urban luxury gradients remains poorly understood, in African cities (Bigirimana et al. 2012; Muvengwi et al. 2019, 2024). Thus, gaining insight into the current implications of urbanization is increasingly important for formulating effective conservation strategies in urban landscapes (Aronson et al. 2017; Lepczyk et al. 2017).

The luxury effect hypothesis predicts that the level of biodiversity in cities is associated with wealth, where biodiversity is high in wealthy suburbs relative to poorer suburbs (Avolio et al. 2015a, b; Chamberlain et al. 2019; Hope et al. 2003). Because of this social stratification, there is high similarity in preferences of people living in the same neighbourhood (Padullés Cubino et al. 2020), leading to relative within neighbourhood habitat similarity (Bigirimana et al. 2012). Therefore, it is expected that household yards in the same neighbourhood host similar taxa, reducing dissimilarity between them.

Previous studies have looked at the urban luxury effect in relation to the diversity of mesopredator mammals, insects, birds, and trees (Shackleton 2016; Pearse et al. 2018;

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Chamberlain et al. 2019; Muvengwi et al. 2019; Cubino et al. 2020). Trees are important in the ecology of urban ecosystems through reduction of urban temperatures (Ziter et al. 2019), absorption of pollution (Nowak et al. 2006, 2018) and storm water (Bartens et al. 2009), and a variety of human health benefits such as recuperation from stress, and reduction of general mental fatigue (Houlden et al. 2018). Indeed, trees form the base of urban ecosystems because they provide food and habitat for birds, invertebrates, and mammals (Burghardt et al. 2009; Turner-Skoff and Cavender 2019). However, little has been done to understand how the diversity of woody plants varies across urban density gradients (Leong et al. 2018).

Despite being the predominant and most widely used measure of diversity, species richness has many limitations. For example, species richness does not capture the difference in species composition between sites as well as the evolutionary perspective (Jost 2006; Hughes et al. 2020; Brom et al. 2023). If two sites have different species of *Brachystegia*, e.g., *boehmii* and *spiciformis*, the close relationship of the species is not captured by taxonomic beta diversity, but by phylogenetic beta diversity (Padullés Cubino et al. 2020). Likewise, hummingbird assemblages in the northern Andes showed greater taxonomic but low phylogenetic beta-diversity, likely as a result of geographic barriers isolating closely related lineages in similar environments (Weinstein et al. 2014). Furthermore, if two sites have distantly related species, for example, *Brachystegia spiciformis* and *Sclerocarya birrea*, composition difference is captured by both taxonomic and phylogenetic beta diversity (Padullés Cubino et al. 2020). These examples show the importance of complementing taxonomic diversity with phylogenetic diversity in order to capture important information that can fully inform conservation of species diversity (O'Shaughnessy et al. 2023). Indeed, no study, if any, has considered the beta-diversity of woody plants (trees) occurring in household yards across an urban luxury gradient (Leong et al. 2018). However, plant beta-diversity has been considered in school yards along an urban density gradient (Muvengwi et al. 2019) and within and between cities (Padullés Cubino et al. 2020). Nonetheless, there is no study that we are aware of that has sought to understand the variation in tree species composition across urban density strata using the two partitioned components of beta-diversity, turnover and nestedness (Baselga 2010). Baselga (2010) developed a unified framework to statistically disentangle beta-diversity into two components: spatial turnover (species replacement) and nestedness (species loss), each reflecting distinct ecological processes.

Decomposition of beta-diversity into species turnover and nestedness components (Baselga 2010; Baselga and Orme 2012) can add another layer of important information explaining the luxury effects in urban landscapes since they can highlight different ecological processes, such as historical biogeography and human preferences, respectively. The nestedness component of beta diversity represents the level to which species-poor sites are subsets of species-rich sites (Ulrich and Gotelli 2007; Baselga 2010; Legendre 2014). Antithetical to nestedness, spatial turnover measures species composition or phylogenetic lineages between local assemblages (Ulrich and Gotelli 2007; Baselga 2010). Therefore, decomposing beta-diversity into nestedness and turnover helps understand biodiversity in space.

We therefore explored two forms of diversity, taxonomic and phylogenetic beta diversity of trees in residential yards across an urban density gradient. Indeed, encompassing more than one dimension of diversity helps establish the short- and long-term effects of urbanization (Knapp et al. 2012; Cubino et al. 2020). We examined how taxonomic and phylogenetic beta diversity vary along an urban socioeconomic gradient defined by human population density (km^2), yard area (m^2), and wealth. We expected plant species phylogenetic and taxonomic beta diversity to increase with an increase in yard area and wealth and to decrease with an increase in human population density (Chamberlain et al. 2019; Muvengwi et al. 2019, 2024).

Methods

Study site

The study was conducted in Harare, Zimbabwe, which is located between latitude 17˚60'and 18˚10'S, and longitude 30˚85'and 31˚25'E (Fig. 1). Precipitation ranges from 650 to 850 mm annually (Mbiba et al. 2021; Muvengwi et al. 2022). The mean temperature fluctuates between 16 °C and 22 °C (Mpakairi and Muvengwi 2019). Harford et al. (2009) have characterized the soil type in the area as predominantly sandy loam. The natural remnants of green spaces are primarily dominated by the widespread miombo woodland tree, *Brachystegia spiciformis*.

Socioeconomic stratification

The study was conducted across residential areas of Harare, Zimbabwe, where suburbs were categorized into three socioeconomic strata based on urban density (low, medium, and high, Fig. 2). This stratification incorporated three wealth indicators: property values, human population density, and yard sizes. Property values were determined using median prices (US$) of eight listed properties per suburb from PropertyBook's online database (source: https://www.propertybook.co.zw/accessed October 26, 2023). Population density calculations utilized the 2022 census data, computed as inhabitants per square kilometre for each suburb. While

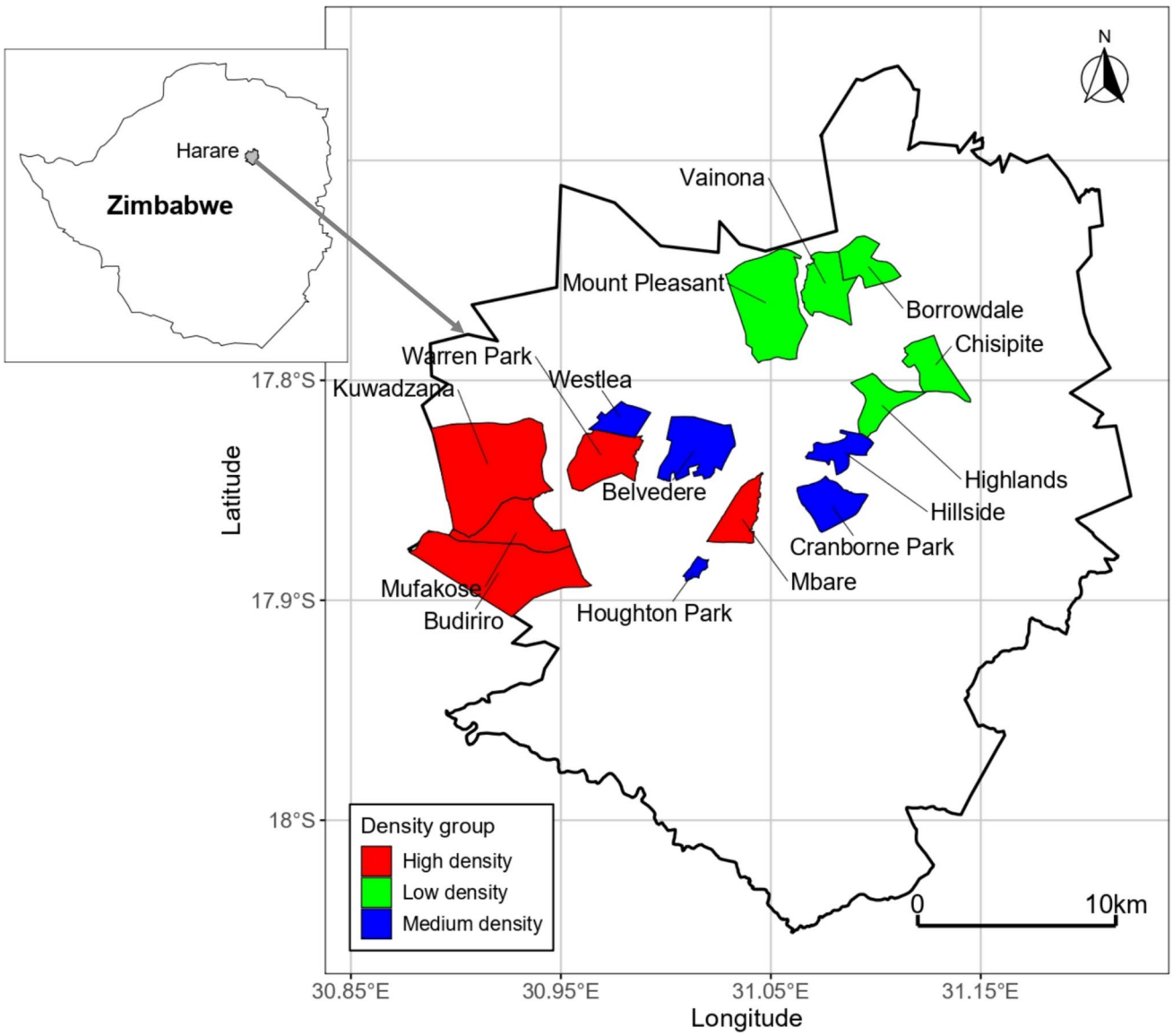


Fig. 1 Geographic location of sampled suburbs across the urban density gradient in Harare, Zimbabwe. Inset shows the location of Harare within Zimbabwe

individual yard measurements were taken during sampling, median yard area per suburb was used for stratification purposes to maintain consistency with other indicators.

Sampling design

We implemented a hierarchical sampling approach across fifteen suburbs, with five suburbs selected from each density stratum. The low-density category comprised Highlands, Vainona, Mount Pleasant, Borrowdale, and Chisipite. Medium-density areas included Westlea, Belvedere, Houghton Park, Hillside, and Cranborne, while high-density areas encompassed Mbare, Kuwadzana, Budiriro, Mufakose, and Warren Park (Fig. 1). This design ensured comprehensive coverage of Harare's socioeconomic gradient. Harare exhibits a distinct socio-economic gradient in its residential layout, with low-density affluent suburbs predominantly located in the northern and eastern parts, medium-density residential areas surrounding the central business district, and high-density suburbs concentrated in the western region of the city.

Data collection

Within each suburb, we employed a systematic sampling strategy where ten streets were randomly selected, and two households were sampled per street, yielding 20 households per suburb. This approach resulted in 100 households per



Fig. 2 Google earth images showing high density/low income- (**a**-**c**), medium density/income- (**d**-**f**), and low density/high income- (**g**-**i**) suburbs that were sampled across Harare along the urban density gradient

density stratum, totalling 300 sampled yards across the urban gradient. At each household, we conducted a comprehensive inventory of all woody plants, documenting both indigenous and exotic tree species. For analytical purposes, each suburb was treated as a discrete sampling unit, resulting in five replicates per density category.

Phylogenetic construction

The plant species list that we first recorded from the survey was standardized for botanical names based on the World Checklist of Vascular Plants using the R package *U.Taxonstand* (Zhang and Qian 2023). Our phylogeny was based on the megaphylogeny, (Cayuela et al. 2012). The phylogenetic tree was generated using *V.Phylomaker2* (Jin & Qian 2022).

Taxonomic and phylogenetic beta-diversity

Taxonomic and phylogenetic beta-diversity were assessed using the Sørensen's index (βsor) of compositional differences implemented in the betapart package (Baselga and Orme 2012). The evaluation aimed to understand nestedness (βsne) and turnover (βsim) variations between strata. Beta-diversity (βsor) was partitioned into βsim and βsne components for taxonomic and phylogenetic diversity.

To account for the inherent mathematical dependencies between species richness and beta diversity indices, we calculated standardized effect sizes (SES). SES values are crucial as they allow for more meaningful comparisons across communities with different species richness, by controlling for sampling effects that might confound raw beta diversity measures. We generated a null distribution for each diversity index by shuffling taxa labels 999 times while keeping species richness and their occurrence frequency constant. SES was then calculated using the following equation:

$$ses = \frac{\text{Observed} - \text{mean (null)}}{\text{SD (null)}}$$

This standardization helps distinguish between actual ecological processes and patterns that might arise by chance, with positive SES values indicating greater beta diversity than expected by chance, and negative values indicating lower beta diversity than expected. Furthermore, SES values enable direct comparison between our suburbs as they are measured in units of standard deviation from the null expectation.

Data analysis

We analysed the effects of human population density, property value, and yard area on taxonomic and phylogenetic beta

diversity using generalized linear models (GLMs). Model selection was conducted with the second-order Akaike Information Criterion adjusted for small sample sizes (AICc), utilizing the *MuMIn* package in R to identify the most parsimonious models for further exploration. Based on the distribution of points in the scatter plots, we applied linear regression to evaluate the relationships between each covariate and the beta diversity response variables. To verify the robustness of our models, we assessed normality and goodness of fit through diagnostic plots, using the R *performance* package (Ben-Shachar et al. 2021). We assessed the variance inflation factors (VIF) for our continuous covariates using the R *car* package, and all values were below the threshold of 10, indicating no significant multicollinearity.

Results

Taxonomic and phylogenetic beta-diversity of combined indigenous and exotic species

Our analysis revealed significant relationships between socio-economic variables and both phylogenetic and taxonomic beta diversity of woody plants across suburbs. Taxonomic beta diversity ($SEST_{\beta sor}$) of combined indigenous and exotic species showed significant positive linear relationships with both property value ($F_{1,13} = 32.80$, $p < 0.001$, $R^2 = 0.69$) and yard area ($F_{1,13} = 49.82$, $p < 0.001$, $R^2 = 0.78$). These linear relationships indicate that taxonomic diversity in more affluent suburbs deviated positively from null model expectations, as evidenced by values well above the zero reference line (Fig. 3a,c; Table 1). In contrast, human population density showed a significant negative linear relationship with taxonomic beta diversity ($F_{1,13} = 19.3$, $p < 0.001$, $R^2 = 0.57$), (Fig. 3b; Table 1).

Phylogenetic beta diversity (SESPβsor) demonstrated distinct patterns, exhibiting significant positive linear relationships with both property value ($F_{1,13} = 28.21$, $p < 0.001$, $R^2 = 0.66$) and yard area ($F_{1,13} = 26.05$, $p < 0.001$, $R^2 = 0.64$; Fig. 3d,f; Table 1). On the other hand, human population density showed a significant negative relationship with phylogenetic diversity ($F_{1,13} = 24.53$, $p < 0.001$; $R^2 = 0.63$; Fig. 3e, Table 1), indicating reduced evolutionary diversity in more densely populated areas.

Analysis of taxonomic turnover ($SEST_{\beta sim}$) for combined indigenous and exotic woody plants revealed significant

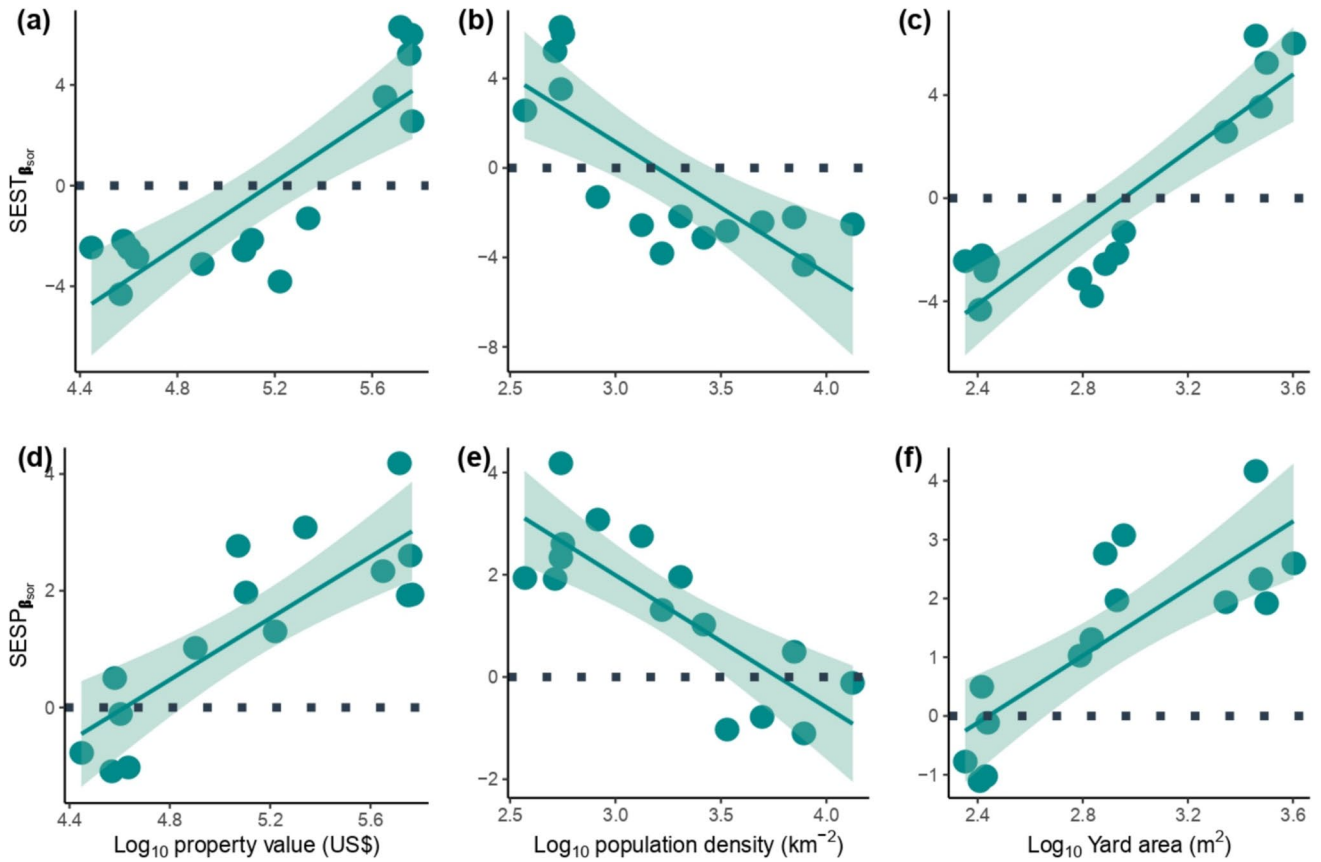


Fig. 3 Taxonomic ($SEST_{\beta sor}$ **a-c**) and phylogenetic ($SESP_{\beta sor}$ **d-f**) beta diversity of woody plants in relation to property value, population density, and yard area across Harare's urban gradient, respectively. Dotted lines represent null expectations. Shaded areas represent the 95% confidence interval

Table 1 Linear relationships between taxonomic and phylogenetic beta diversity components (Sørensen, turnover, and nestedness) and socioeconomic variables (property value, population density, and yard area) for combined indigenous and exotic woody plant species in Harare, Zimbabwe

	Model	Adj. R^2	F-value	p-value	Std. Error
Sorensen	$SEST_{\beta sor} = -33.27 + 6.43$*property value	0.89	32.8	< 0.001	1.12
	$SEST_{\beta sor} = 18.83 – 5.89$*population density	0.57	19.3	< 0.001	1.34
	$SEST_{\beta sor} = -21.93 + 7.42$*yard area	0.94	49.82	< 0.001	1.05
	$SESP_{\beta sor} = -12.17 + 2.63$*property value	0.66	28.21	< 0.001	0.50
	$SESP_{\beta sor} = 9.74 – 2.58$*population density	0.63	24.53	< 0.001	0.52
	$SESP_{\beta sor} = -6.97 + 2.86$*yard area	0.64	26.05	< 0.001	0.56
Turnover	$SEST_{\beta sim} = -42.19 + 8.55$*property value	0.79	53.48	< 0.001	1.17
	$SEST_{\beta sim} = 27.50 – 7.84$*population density	0.66	28.68	< 0.001	1.48
	$SEST_{\beta sim} = -27.03 + 9.87$*yard area	0.96	158	< 0.001	0.97
	$SESP_{\beta sim} = -2.63 – 1.05$*property value	0.19	4.20	= 0.060	0.51
	$SESP_{\beta sim} = -11.04 + 0.94$*population density	0.13	3.14	= 0.10	0.53
	$SESP_{\beta sim} = -4.49 – 1.20$*yard area	0.21	4.78	= 0.05	0.55
Nestedness	SESTβsne = 41.66–9.01*property value	0.85	78.63	< 0.001	1.02
	SESTβsne = −32.54 + 8.61*population density	0.76	45.62	< 0.001	1.28
	SESTβsne = 25.51–10.33*yard area	0.93	186.3	< 0.001	0.76
	SESPβsne = −7.15 + 3.92*property value	0.49	14.49	= 0.002	1.03
	SESPβsne = 26.20–4.07*population density	0.53	16.89	= 0.001	0.99
	SESPβsne = 0.17 + 4.39*yard area	0.51	15.85	= 0.002	1.10

positive linear relationships with both property value ($F_{1,13} = 53.48$, $p < 0.001$, $R^2 = 0.79$) and yard area ($F_{1,13} = 102.7$, $p < 0.001$, $R^2 = 0.88$; Table 2, Fig. 4a,c). These linear relationships indicate greater species turnover in wealthier suburbs with larger yards (Fig. S1). Human population density exhibited a significant negative linear relationship with taxonomic turnover ($F_{1,13} = 28.68$, $p < 0.001$; Fig. 4b), with values significantly above null model expectations in low-density suburbs, as indicated by points above the zero-reference line.

In contrast, phylogenetic turnover patterns differed markedly (Fig. S1). While neither property value nor population density showed significant relationships with phylogenetic turnover (Fig. 4d,e; Table 2), observed values were consistently below null model expectations, indicating lower phylogenetic turnover than would be expected by chance. Yard area showed a marginally significant negative relationship ($F_{1,13} = 4.78$, $p = 0.05$) with phylogenetic turnover (Fig. 4f; Table 2), suggesting that suburbs with

Table 2 Linear relationships between taxonomic and phylogenetic beta diversity components (Sørensen, turnover, and nestedness) and socioeconomic variables (property value, population density, and yard area) for exotic woody plants in Harare, Zimbabwe

	Model	Adj. R^2	F-value	p-value	Std.Error
Sorensen	$SEST_{\beta sor} = -30.93 + 5.60$*property value	0.65	26.79	< 0.001	1.16
	$SEST_{\beta sor} = 17.61 – 5.47$*population density	0.52	16.28	= 0.001	1.36
	$SEST_{\beta sor} = -20.17 + 6.87$*yard area	0.71	35.71	< 0.001	1.15
	$SESP_{\beta sor} = -18.08 + 3.59$*property value	0.79	54.03	< 0.001	0.49
	$SESP_{\beta sor} = 11.75 – 3.51$*population density	0.75	42.13	< 0.001	0.54
	$SESP_{\beta sor} = -11.14 + 3.95$*yard area	0.79	54.37	< 0.001	0.54
Turnover	$SEST_{\beta sim} = -36.98 + 7.45$*property value	0.72	37.77	< 0.001	1.21
	$SEST_{\beta sim} = 23.41 – 6.82$*population density	0.59	21.24	< 0.001	1.48
	$SEST_{\beta sim} = -23.55 + 8.51$*yard area	0.79	53.69	< 0.001	1.16
	$SESP_{\beta sim} = -8.77 + 0.49$*property value	0.02	1.34	= 0.268	0.43
	$SESP_{\beta sim} = -4.36 – 0.58$*population density	0.06	1.94	= 0.188	0.42
	$SESP_{\beta sim} = -7.66 – 0.49$*yard area	0.01	1.07	= 0.319	0.49
Nestedness	SESTβsne = 35.80–7.74*property value	0.79	53.04	< 0.001	1.06
	SESTβsne = −27.25 + 7.18*population density	0.66	28.59	< 0.001	1.34
	SESTβsne = 21.56–8.74*yard area	0.84	73.9	< 0.001	1.02
	SESPβsne = −7.36 + 3.19*property value	0.66	28.32	< 0.001	0.60
	SESPβsne = 18.28–2.86*population density	0.51	15.85	= 0.002	0.72
	SESPβsne = −1.53 + 3.61*yard area	0.71	35.2	< 0.001	0.61

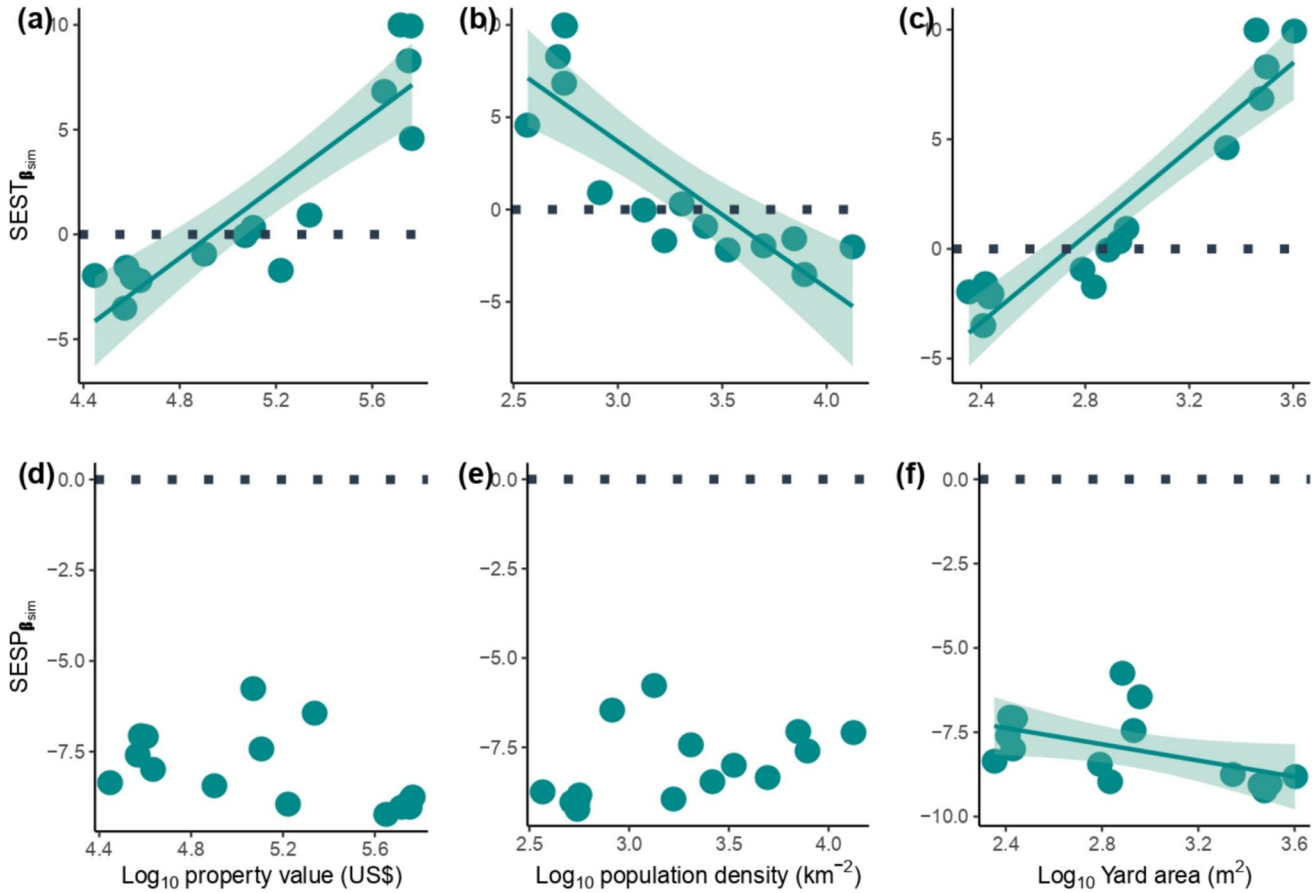


Fig. 4 Taxonomic ($SEST_{\beta sim}$ **a**-**c**) and phylogenetic ($SESP_{\beta sim}$ **d**-**f**) beta diversity of woody plants in relation to property value, population density, and yard area across Harare's urban gradient, respectively. Dotted lines represent null expectations. Shaded areas represent the 95% confidence interval

larger yards tend to harbour woody plant communities that are phylogenetically more similar than expected by chance. However, it is important to note that this relationship occurred in suburbs that are all below the null expectation.

Taxonomic beta nestedness ($SEST_{\beta sne}$) of combined woody plants showed significant negative linear relationships with both property value ($R^2 = 0.85$) and yard area ($R^2 = 0.93$; Fig. 5a,c; Table 2), indicating decreasing nestedness in wealthier suburbs with larger yards (Fig. S1). On the contrary, human population density exhibited a significant positive relationship with taxonomic nestedness ($F_{1,13} = 45.62$, $p < 0.001$), suggesting increased nested patterns in more densely populated areas (Fig. S1).

Phylogenetic beta nestedness ($SESP_{\beta sne}$) demonstrated significant relationships with all three variables, showing positive associations with both property value ($F_{1,13} = 14.49$, $p = 0.002$) and yard area ($F_{1,13} = 15.85$, $p = 0.002$), and a negative relationship with population density ($F_{1,13} = 16.89$, $p = 0.001$). Notably, all $SESP_{\beta sne}$ values were substantially above the null model expectation (zero reference line), indicating that phylogenetic nestedness was consistently greater than expected by chance across all suburbs, regardless of their socio-economic characteristics (Fig. 5d,e,f).

Taxonomic and phylogenetic beta-diversity of exotic species

Analysis of exotic woody species revealed significant positive linear relationships between taxonomic beta diversity ($SEST_{\beta sor}$) and both property value ($F_{1,13} = 26.79$, $p < 0.001$) and yard area ($F_{1,13} = 16.28$, $p = 0.001$; Fig. 6a,c; Table 2). These linear relationships indicate that affluent suburbs with larger yards harboured more taxonomically distinct exotic woody plant communities than expected by chance. In contrast, human population density showed a significant negative linear relationship with $SEST_{\beta sor}$ ($F_{1,13} = 35.71$, $p < 0.001$; Fig. 6b, Table 2), suggesting that taxonomic distinctiveness of exotic species declined in more densely populated areas.

Phylogenetic beta diversity ($SESP_{\beta sor}$) of exotic species demonstrated different patterns, showing significant positive linear relationships with both property value ($F_{1,13} = 54.03$, $p < 0.001$) and yard area ($F_{1,13} = 54.37$, $p < 0.001$;

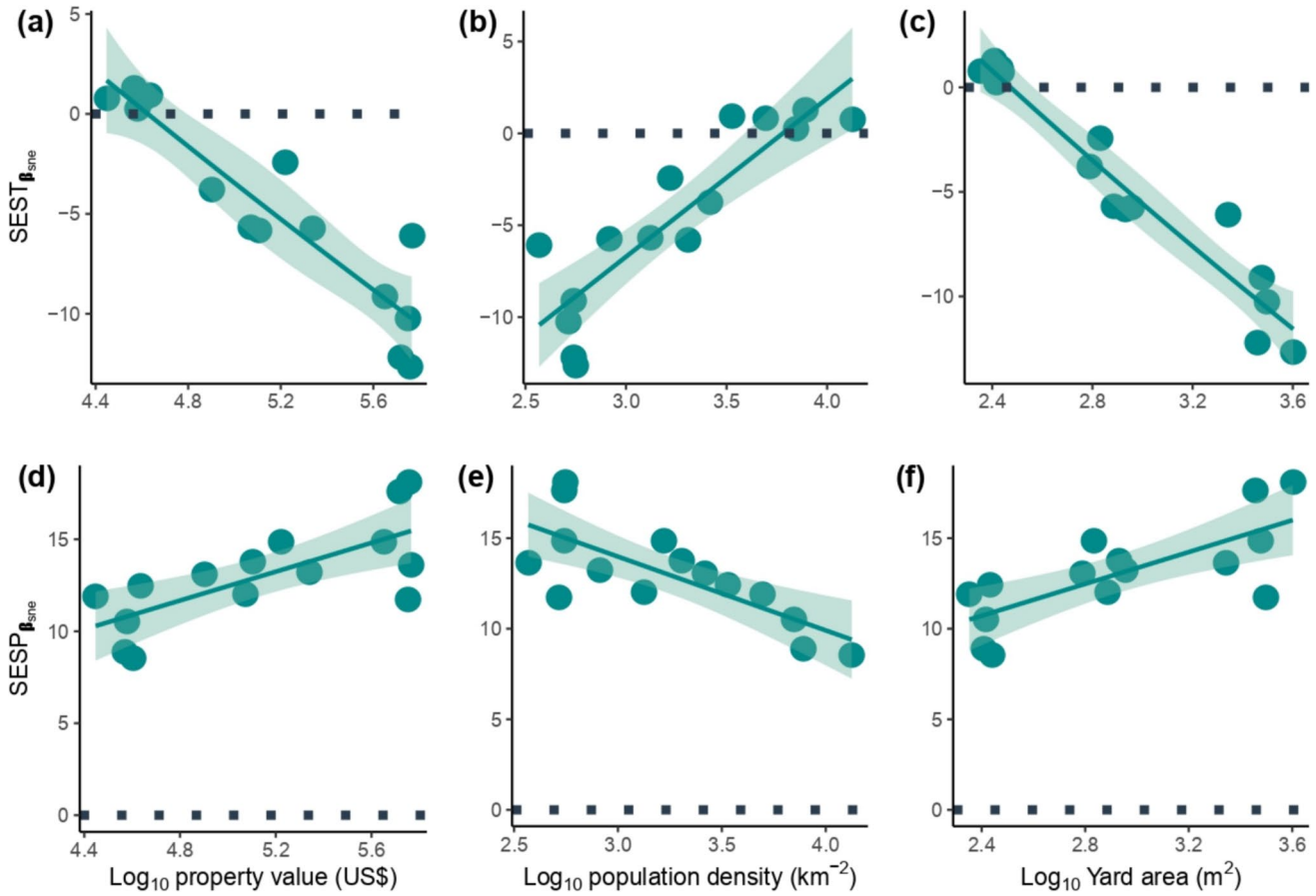


Fig. 5 Taxonomic ($SEST_{\beta sne}$ **a**-**c**) and phylogenetic ($SESP_{\beta sne}$ **d**-**f**) beta diversity of woody plants in relation to property value, population density, and yard area across Harare's urban gradient, respectively. Dotted lines represent null expectations. Shaded areas represent the 95% confidence interval

Fig. 6d,f; Table 2). However, human population density exhibited a significant negative linear relationship with $SESP_{\beta sor}$ ($F_{1,13} = 42.13$, $p < 0.001$; Fig. 6e), indicating that phylogenetic distinctiveness of exotic woody species decreased as population density increased.

Taxonomic turnover ($SEST_{\beta sim}$) of exotic species exhibited significant positive linear relationships with both property value ($F_{1,13} = 37.77$, $p < 0.001$) and yard area ($F_{1,13} = 53.69$, $p < 0.001$; Fig. 7a,c; Table 2), indicating greater species turnover in wealthier suburbs with larger yards (Fig S2). Human population density showed a significant negative linear relationship with $SEST_{\beta sim}$ (Fig. 7b; Table 2).

In contrast, phylogenetic turnover ($SESP_{\beta sim}$) showed no significant relationships with any of the socio-economic variables examined (property value, human population density, or yard area; Fig. 7d,e,f; Table 2). Notably, all suburbs, regardless of their socio-economic characteristics, exhibited $SESP_{\beta sim}$ values substantially below the null model expectation (zero reference line), indicating consistently lower phylogenetic turnover than expected by chance (Fig. S2). This pattern suggests that exotic woody plant communities across all suburbs shared more similar evolutionary histories than would be expected under random assembly.

For exotic species, taxonomic nestedness ($SEST_{\beta sne}$) showed significant negative linear relationships with both property value ($F_{1,13} = 53.04$, $p < 0.001$) and yard area ($F_{1,13} = 73.9$, $p < 0.001$; Fig. 8a,c). Values below the null model expectation (zero reference line) indicated that nestedness was less pronounced than expected by chance, particularly in wealthier suburbs with larger yards. This pattern suggests that poorer suburbs with smaller yards exhibited stronger nested subset patterns in their exotic woody plant communities (Fig. S2).

Phylogenetic nestedness ($SESP_{\beta sne}$) of exotic species demonstrated contrasting patterns. Values consistently above the null model expectation across all suburbs indicated greater phylogenetic nestedness than expected by chance throughout the urban gradient. However, the degree of phylogenetic nestedness varied with socio-economic factors, showing significant positive relationships with both property value ($F_{1,13} = 28.32$, $p < 0.001$) and yard area ($F_{1,13} = 35.2$, $p < 0.001$; Fig. 8d,f; Table 2), and a significant

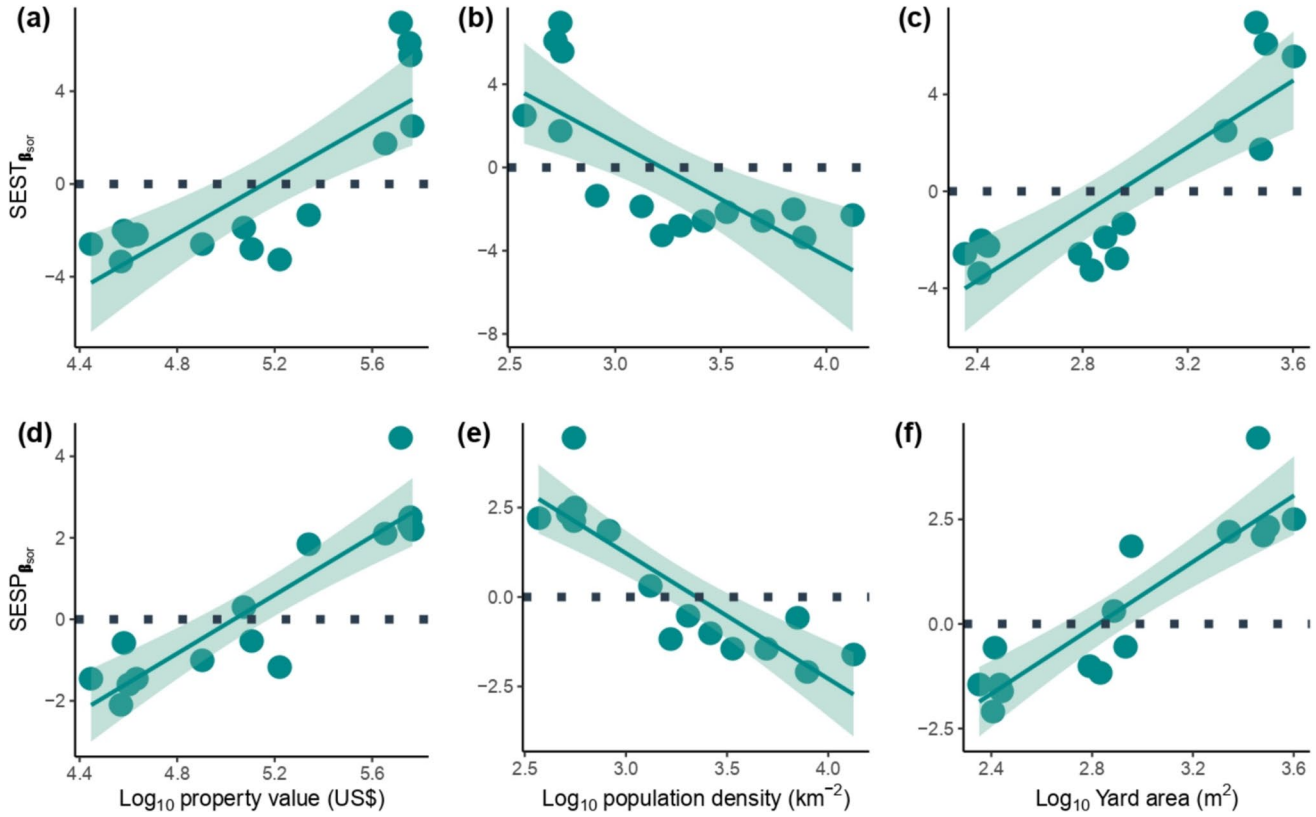


Fig. 6 Taxonomic (SEST$_{\beta sor}$ **a-c**) and phylogenetic (SESP$_{\beta sor}$ **d-f**) beta Sorensen diversity patterns of exotic woody plants in relation to property value, population density, and yard area, respectively, in Harare, Zimbabwe. Dotted lines represent null expectations. Shaded areas represent the 95% confidence interval

negative relationship with population density ($F_{1,13} = 15.85$, $p = 0.002$; Fig. 8e; Table 2). These relationships indicate that wealthier suburbs with larger yards harboured exotic woody plant communities with stronger phylogenetic nested patterns, while densely populated areas showed reduced phylogenetic nestedness.

Taxonomic and phylogenetic beta-diversity of indigenous species

Analysis of indigenous woody species revealed significant positive linear relationships between taxonomic beta diversity (SEST$_{\beta sor}$) and both property value ($F_{1,13} = 8.25$, $p = 0.013$) and yard area ($F_{1,13} = 9.93$, $p = 0.008$; Fig. 9a,c; Table 3). Although not statistically significant, human population density showed a negative trend with SEST$_{\beta sor}$ ($F_{1,13} = 4.03$, $p = 0.066$; Fig. 9b, Table 3).

Phylogenetic beta diversity (SESP$_{\beta sor}$) patterns for indigenous species showed distinct trends. All suburbs exhibited values above the null model expectation, indicating greater phylogenetic distinctiveness than expected by chance. However, the magnitude of phylogenetic diversity varied with socio-economic factors (Fig. S3). Notably, poorer suburbs with smaller yards demonstrated greater phylogenetic beta diversity (Fig. S3). This pattern was further supported by a significant positive relationship between SESP$_{\beta sor}$ and human population density ($F_{1,13} = 28.13$, $p < 0.001$; Fig. 9e, Table 3), suggesting that densely populated areas maintained more phylogenetically diverse indigenous woody plant communities.

For indigenous woody plants, taxonomic turnover (SEST$_{\beta sim}$) showed no significant relationships with either property value ($F_{1,13} = 3.76$, $p = 0.074$) or population density ($F_{1,13} = 2.75$, $p = 0.121$; Fig. 10a,b; Table 3). However, yard area exhibited a marginally significant positive relationship with SEST$_{\beta sim}$ ($F_{1,13} = 4.90$, $p = 0.045$; Fig. 10c, Table 3), suggesting slightly greater species turnover in suburbs with larger yards.

Phylogenetic turnover (SESP$_{\beta sim}$) of indigenous species demonstrated consistently lower values than null model expectations across all suburbs, as indicated by values below the zero-reference line. While property value and yard area showed no significant relationships with SESP$_{\beta sim}$ (Fig. 10d,f; Table 3), human population density exhibited a significant positive relationship with phylogenetic turnover. However, despite this positive trend with population density, SESP$_{\beta sim}$ values remained below null expectations (Fig. 10e, Table 3), indicating that indigenous woody plant

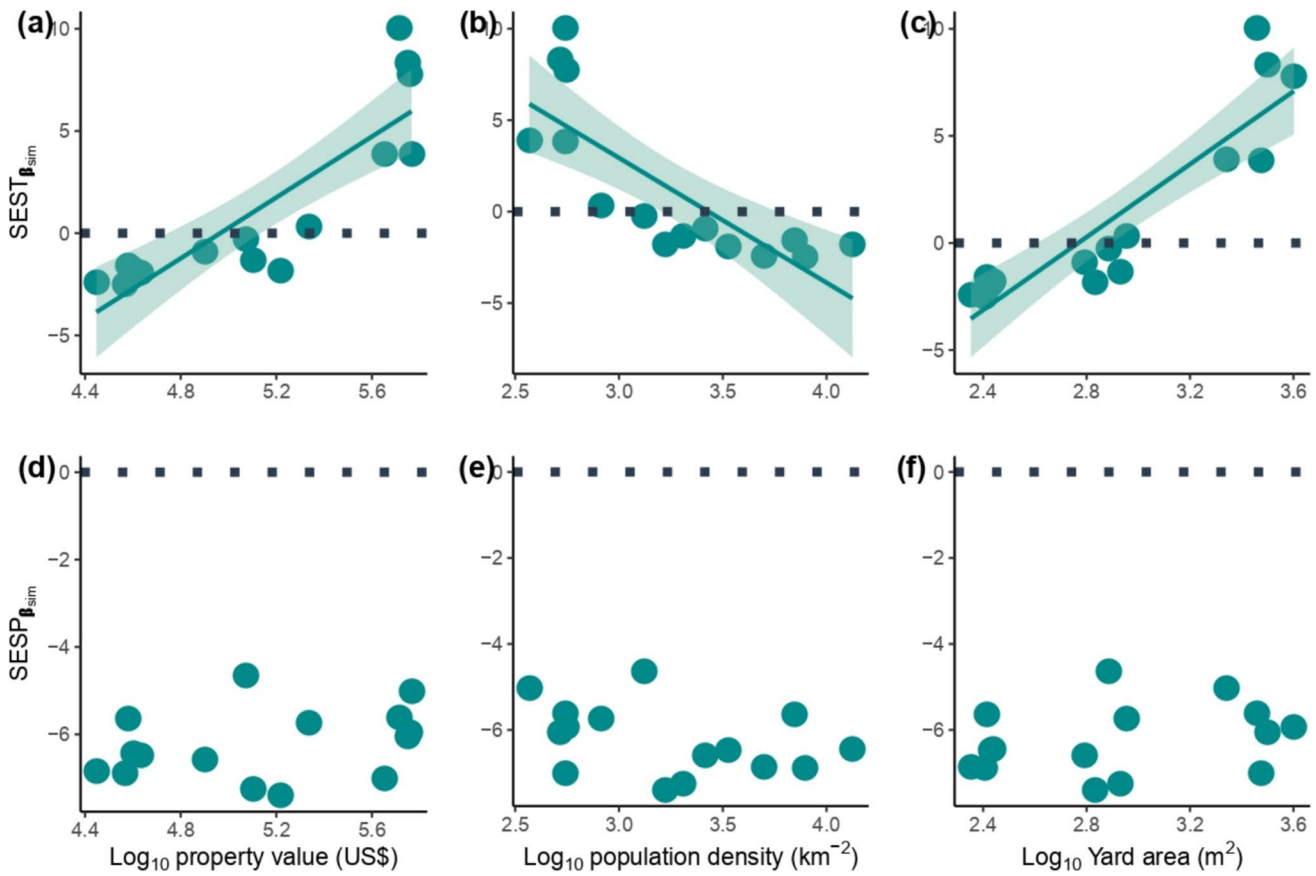


Fig. 7 Taxonomic ($SEST_{\beta sim}$ **a-c**) and phylogenetic ($SESP_{\beta sim}$ **d-f**) beta turnover diversity patterns of exotic woody plants in relation to property value, population density, and yard area, respectively, in Harare, Zimbabwe. Dotted lines represent null expectations. Shaded areas represent the 95% confidence interval

communities across all suburbs shared more similar evolutionary histories than would be expected by chance (Fig. S3).

Analysis of indigenous woody plants revealed no significant relationships between taxonomic nestedness ($SEST\beta_{sne}$) and any of the socio-economic variables examined: property value ($F_{1,13} = 2.56$, $p = 0.133$), population density ($F_{1,13} = 1.98$, $p = 0.183$), or yard area ($F_{1,13} = 3.38$, $p = 0.089$; Fig. 11a,b,c; Table 3). Values clustering around the null model expectation (zero reference line) suggested that taxonomic nestedness patterns were largely consistent with random assembly processes.

Similarly, phylogenetic nestedness ($SESP_{\beta sne}$) showed no significant relationships with property value ($F_{1,13} = 1.96$, $p = 0.185$), population density ($F_{1,13} = 0.793$, $p = 0.389$), or yard area ($F_{1,13} = 1.67$, $p = 0.219$; Fig. 11e,f,g; Table 3). However, all suburbs exhibited $SESP_{\beta sne}$ values above null model expectations, indicating consistently greater phylogenetic nestedness than expected by chance (Fig. S3). This pattern suggests that despite the lack of relationship with socio-economic variables, indigenous woody plant communities across all suburbs shared similar evolutionary histories in a nested fashion (Fig. S3).

Discussion

We examined taxonomic and phylogenetic beta-diversity patterns of woody plants across Harare's socioeconomic gradient, represented by suburbs of varying population densities. When analysing combined indigenous and exotic plant species, suburbs with low population density demonstrated greater taxonomic and phylogenetic beta-diversity, supporting our hypothesis of greater diversity in affluent areas. Exotic species showed higher taxonomic diversity in affluent areas but maintained low phylogenetic turnover across suburbs, indicating the selection of closely related species regardless of socioeconomic status. Interestingly, this pattern differed for indigenous species alone, where high-density suburbs maintained greater phylogenetic beta-diversity than their intermediate and low-density counterparts. Across all population density categories, while species turnover emerged as the primary driver of both taxonomic and phylogenetic beta-diversity, phylogenetic patterns showed a notably stronger nestedness component compared to taxonomic patterns. These contrasting patterns between combined and indigenous species assemblages, coupled with the varying

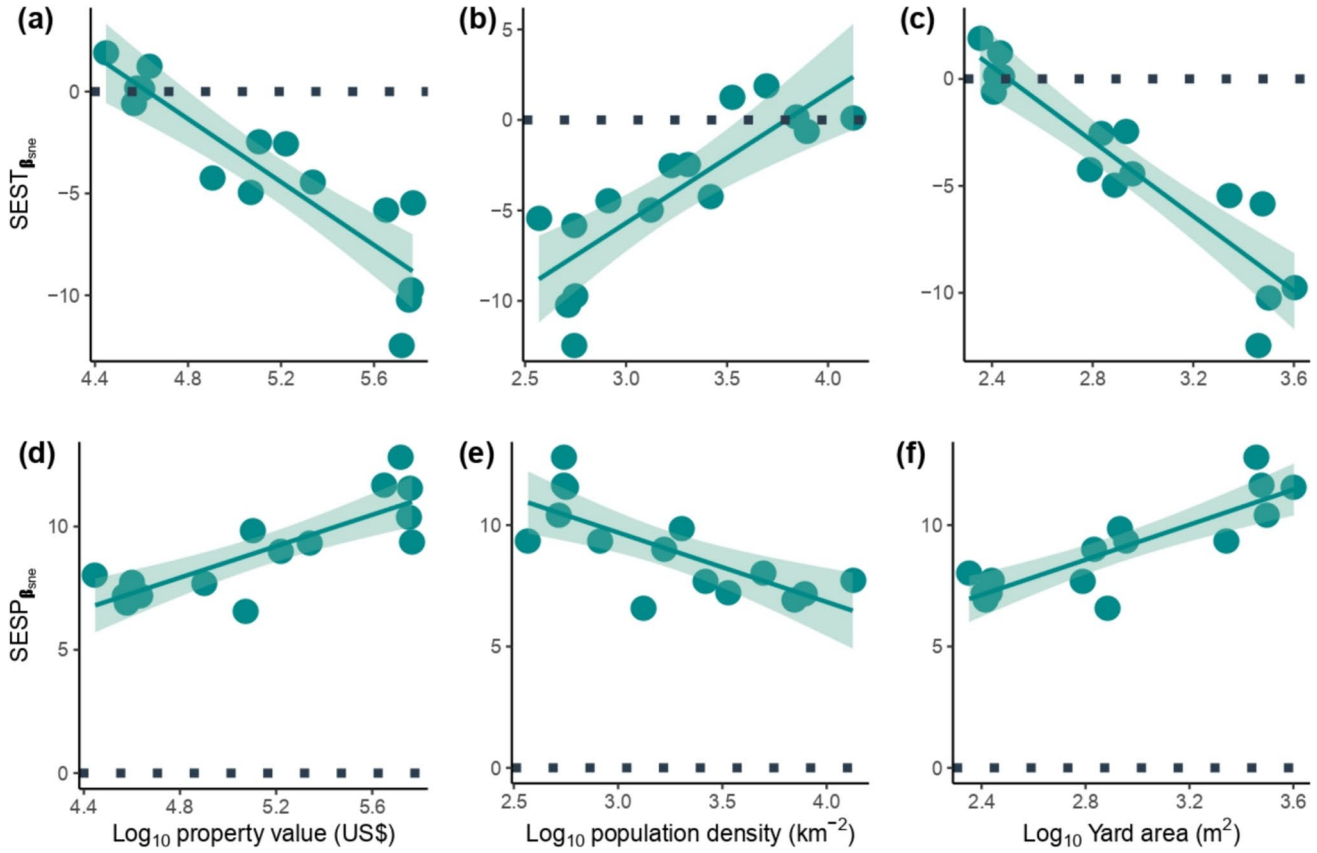


Fig. 8 Taxonomic (SEST$_{\beta sne}$ **a-c**) and phylogenetic (SESP$_{\beta sne}$ **d-f**) beta nestedness diversity patterns of exotic woody plants in relation to property value, population density, and yard area, respectively, in Harare, Zimbabwe. Dotted lines represent null expectations. Shaded areas represent the 95% confidence interval

contributions of turnover and nestedness, suggest that distinct ecological processes shape woody plant communities across Harare's urban density gradient.

Taxonomic and phylogenetic beta-diversity of all trees

Our analysis of Harare's urban landscape reveals complex interactions between socioeconomic factors and woody plant diversity patterns. The positive linear relationships between taxonomic beta diversity and both property value and yard area strongly support the'luxury effect'hypothesis (Leong et al. 2018; Chamberlain et al. 2020), particularly evident in this Global South context where socioeconomic disparities markedly influence urban vegetation structure (Cilliers et al. 2013; du Toit et al. 2018). Indeed, this social injustice to access ecosystems services has been emphasized in some previous studies (Chamberlain et al. 2019; Muvengwi et al. 2024). The negative relationship between taxonomic beta diversity and population density demonstrates the homogenizing effect of urbanization intensity (Pearse et al. 2018), likely driven by reduced planting space and standardized landscaping practices in densely populated areas (Groffman et al. 2017). Unlike, in a review of 105 studies by McKinney (2008) which showed that plant diversity (richness) was highest in moderate urbanized environments, in our study we observed a linear relationship where diversity increased with decrease in human population density. Differences between our study and the review could have emanated from the fact that the McKinney (2008) gradient included rural undeveloped areas and did not specifically sample yards, but some studies would incorporate gardens, street trees and interstitial vegetation (Pearse et al. 2018). Furthermore, in our study we used standardized effect sizes which control for differences in species richness, while McKinney (2008) study was based on species richness.

For phylogenetic beta Sørensen diversity, low-density suburbs had trees that were more distantly related supporting several previous studies suggesting the existence of a socioeconomic gradient, with more affluent areas having greater biodiversity (Bigirimana et al. 2012; Chamberlain et al. 2019; Padullés Cubino et al. 2020; Leong et al. 2018; Muvengwi et al. 2019). For phylogenetic beta nestedness, it appears there is selection of species that are closely related

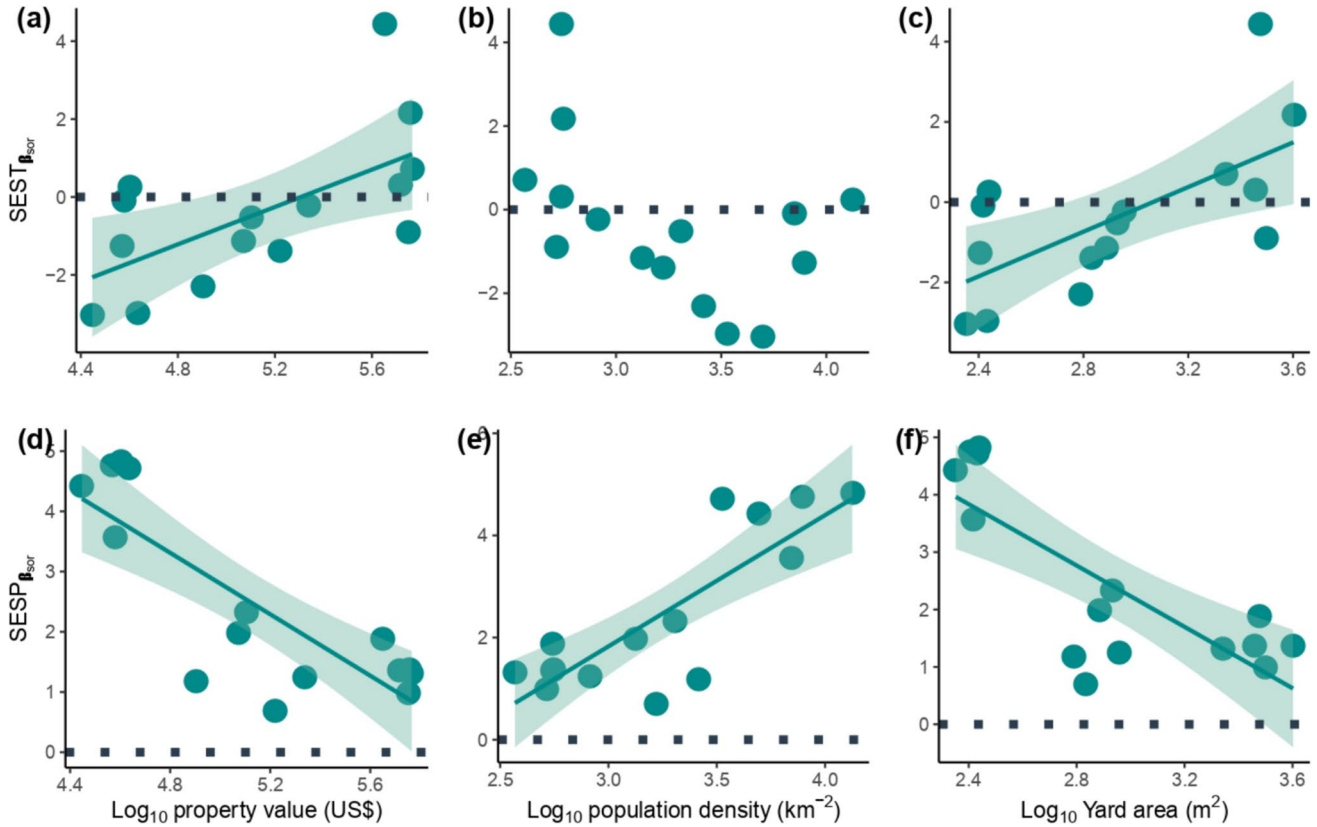


Fig. 9 Taxonomic ($SEST_{\beta sor}$ **a-c**) and phylogenetic ($SESP_{\beta sor}$**d-f**) beta Sorensen diversity patterns of indigenous woody plants in relation to property value, population density, and yard area, respectively, in Harare, Zimbabwe. Dotted lines represent null expectations. Shaded areas represent the 95% confidence interval

Table 3 Linear relationships between taxonomic and phylogenetic beta diversity components (Sørensen, turnover, and nestedness) and socioeconomic variables (property value, population density, and yard area) for indigenous woody plants in Harare, Zimbabwe

	Model	Adj. R^2	F-value	p-value	Std.Error
Sorensen	$SEST_{\beta sor} = -12.73 + 2.40$*property value	0.34	8.25	= 0.013	0.83
	$SEST_{\beta sor} = 5.69–1.88$*population density	0.18	4.03	= 0.066	0.94
	$SEST_{\beta sor} = -8.52 + 2.78$*yard area	0.39	9.93	= 0.008	0.88
	$SESP_{\beta sor} = 15.53–2.85$*property value	0.65	27.41	< 0.001	0.49
	$SESP_{\beta sor} = -5.88 + 2.57$*population density	0.67	28.13	< 0.001	0.48
	$SESP_{\beta sor} = 10.25–2.67$*yard area	0.59	20.96	< 0.001	0.58
Turnover	$SEST_{\beta sim} = -11.81 + 2.50$*property value	0.16	3.76	= 0.074	1.29
	$SEST_{\beta sim} = 8.20–2.21$*population density	0.11	2.75	= 0.121	1.33
	$SEST_{\beta sim} = -7.82 + 3.03$*yard area	0.22	4.90	= 0.045	1.37
	$SESP_{\beta sim} = 2.66–1.32$*property value	0.15	3.46	= 0.086	0.71
	$SESP_{\beta sim} = -9.66 + 1.71$*population density	0.30	7.00	= 0.020	0.65
	$SESP_{\beta sim} = -0.04 – 1.40$*yard area	0.13	3.16	= 0.100	0.79
Nestedness	SESTβsne = 9.72–2.19*property value	0.10	2.56	= 0.133	1.37
	SESTβsne = −7.85 + 1.97*population density	0.07	1.98	= 0.183	1.40
	SESTβsne = 6.39–2.69*yard area	0.15	3.38	= 0.089	1.46
	SESPβsne = 19.10–1.78*property value	0.06	1.96	= 0.185	1.27
	SESPβsne = 6.12 + 1.18*population density	−0.02	0.79	= 0.389	1.33
	SESPβsne = 15.26–1.82*yard area	0.05	1.67	= 0.219	1.41

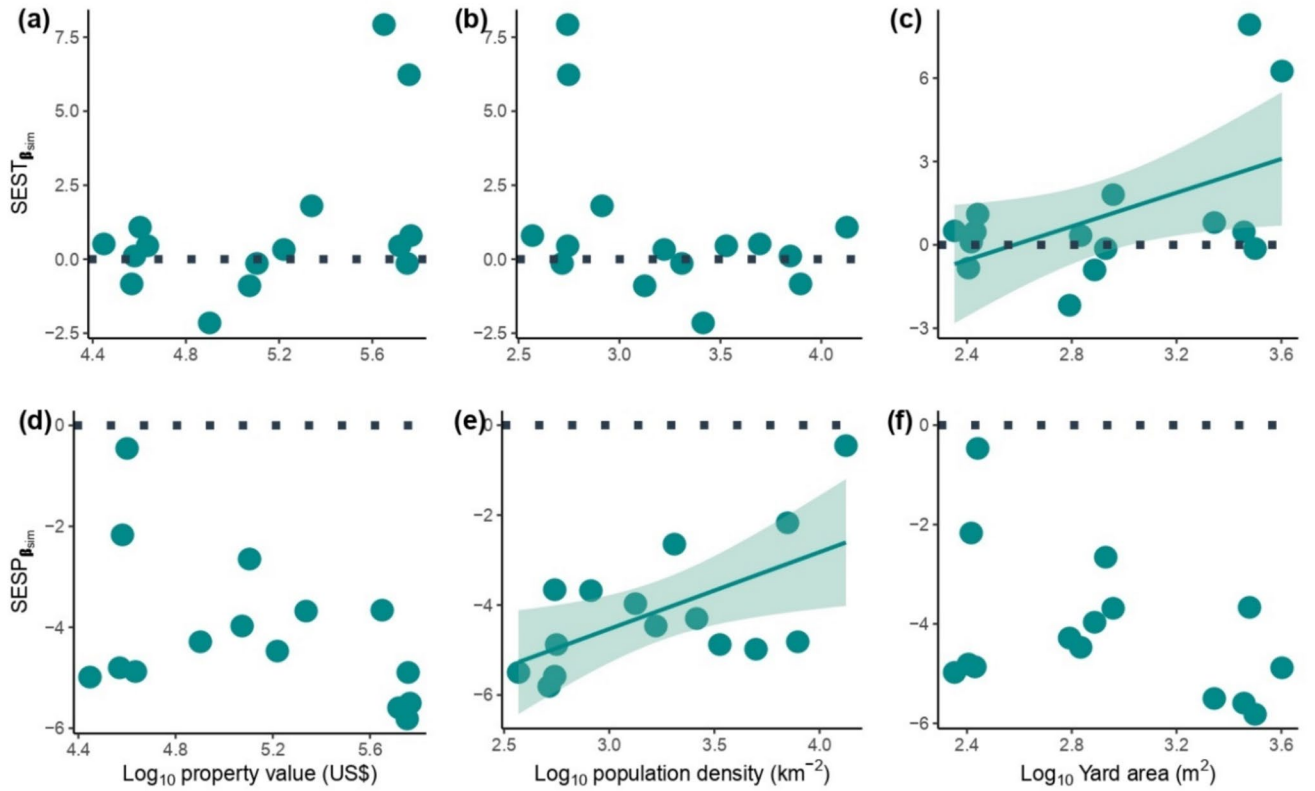


Fig. 10 Taxonomic (SEST$_{\beta sim}$**a-c**) and phylogenetic (SESP$_{\beta sim}$**d-f**) beta turnover diversity patterns of indigenous woody plants in relation to property value, population density, and yard area, respectively, in Harare, Zimbabwe. Dotted lines represent null expectations. Shaded areas represent the 95% confidence interval

across the urban density gradient, possibly resulting from similar preferences (Padulles Cubino et al. 2020). Indeed, in the city of Cape Town, South Africa, citizens were going for particular plant traits which makes the yards highly similar in species composition(Goodness 2018). Another plausible reason could be that commercial nurseries are influencing species composition of yards in all suburbs across the urban density gradient (Cavender-Bares et al. 2020) in terms of easy access to the specific plant species that they typically stock.

Taxonomic and phylogenetic beta-diversity of exotic trees

The distribution of exotic woody plants across Harare's urban landscape reveals strong socioeconomic influences on community assembly. Affluent households maintained greater taxonomic diversity of exotic species, consistent with both local patterns of alpha diversity (Muvengwi et al. 2024) and global urban biodiversity trends (Knapp et al. 2012; Avolio et al. 2015b, a; Pearse et al. 2018). This pattern reflects better access to horticultural resources and knowledge in wealthy areas (van der Walt et al. 2015; du Toit et al. 2018), while space constraints and limited access to expensive nursery stock restrict exotic species diversity in high-density suburbs (Hope et al. 2008; Bigirimana et al. 2012).

However, the phylogenetic patterns reveal more complex community assembly processes. While taxonomic turnover dominated overall taxonomic beta-diversity patterns, the strong phylogenetic nestedness component indicates that high-density households maintain a subset of the species found in low-density areas (Socolar et al. 2016). This nested pattern likely reflects both economic constraints and the'ecology of prestige' (Grove et al. 2014; Pickett et al. 2016), where residents within similar socioeconomic strata create aesthetics associated with wealth through shared landscaping preferences (Smith et al. 2006; Bernholt et al. 2009; Muvengwi et al. 2019, 2024).

While low-density suburbs showed greater-than-expected taxonomic turnover, they maintained lower-than-expected phylogenetic turnover, suggesting selection of evolutionarily related species despite diverse species choices. This pattern might reflect commercial nursery influences, where available exotic species share similar adaptive traits suitable for urban environments (Avolio et al. 2015a; Pearse et al. 2018) within any particular climate zone. However, the variation in species selection among wealthy households indicates that factors beyond wealth influence planting decisions (Leong et al. 2018; Chamberlain et al. 2019).

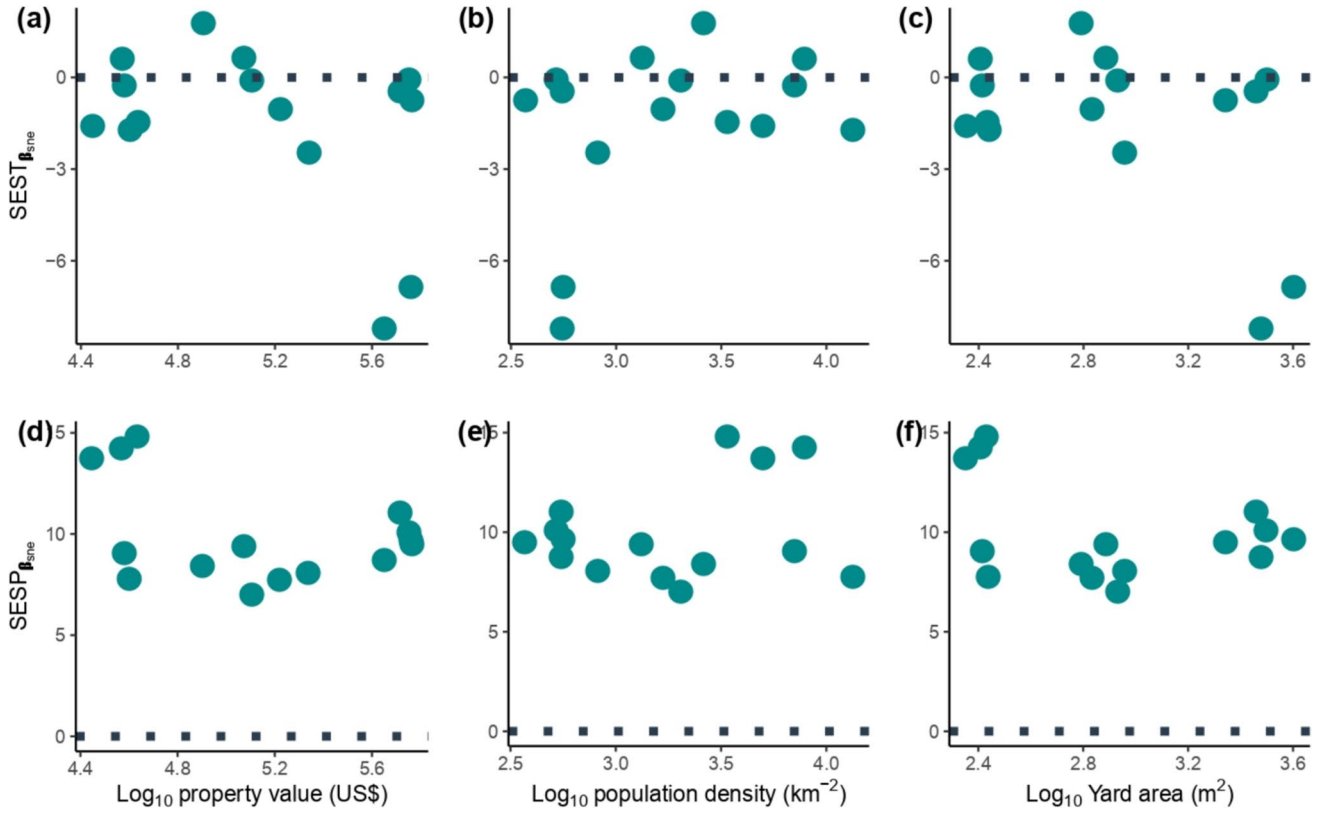


Fig. 11 Taxonomic (SEST$_{\beta sne}$**a-c**) and phylogenetic (SESP$_{\beta sne}$**d-f**) beta nestedness diversity patterns of indigenous woody plants in relation to property value, population density, and yard area, respectively, in Harare, Zimbabwe. Dotted lines represent null expectations. Shaded areas represent the 95% confidence interval

The combination of high species diversity but low phylogenetic diversity in wealthy areas presents a potential vulnerability: while these areas maintain rich exotic species assemblages, their tendency toward phylogenetically related species may reduce resilience to environmental change (Knapp et al. 2012; Schwarz et al. 2017). This pattern, driven by coordinated landscaping practices and shared aesthetic preferences (Grove et al. 2016), suggests the need for more phylogenetically diverse planting strategies in urban landscapes. This observation reinforces the need to always vary the diversity indices to have a holistic understanding (Padullés Cubino et al. 2020). Furthermore, this observation indicates that trees grown in household yards are closely related from an evolutionary perspective. Alternatively, closely related clades have traits that make them popular in urban environments, hence become more common (Goodness 2018).

Taxonomic and phylogenetic beta-diversity of indigenous trees

Indigenous woody plants demonstrate notably different patterns from their exotic counterparts. While showing some response to the luxury effect, wealthy households in Harare maintain stronger connections to indigenous flora than typically observed in Global North cities (Chamberlain et al. 2020). Particularly significant is the greater phylogenetic beta diversity of indigenous species in densely populated, less affluent areas—a pattern that challenges conventional urban ecology paradigms (Duncan et al. 2011).

The retention of phylogenetically diverse indigenous plant communities in high-density areas might reflect both cultural connections to native flora (Cousins and Witkowski 2015; Cilliers et al. 2018) and the survival of pre-urban vegetation in less-developed areas (Dyderski et al. 2017). Space availability, rather than wealth, appears to be the primary driver of indigenous species composition, contrasting with patterns typically observed in Global North cities (La Rosa et al. 2018). Although not focusing on phylogenetic diversity, a study in Helsinki showed higher diversity in the lower-income suburbs which was attributed to reduced human intervention in garden maintenance (Venn and Kotze 2014). Due to time and financial constraints, it is believed that residents in these areas engage in less intensive gardening practices, inadvertently allowing for natural ecological succession processes. This minimal intervention creates

opportunities for stenotopic plant species (those with narrow ecological tolerances) to establish themselves alongside common garden species (Venn and Kotze 2014). The resulting spontaneous vegetation recovery may lead to increased plant phylogenetic diversity, demonstrating how reduced anthropogenic management can enhance urban biodiversity through natural colonization processes.

Synthesis and conservation implications

The contrasting patterns between indigenous and exotic species highlight the unique character of urban biodiversity in Global South cities and bring attention to the need to think beyond taxonomic diversity as an indicator of ecosystem health. While exotic species follow expected socioeconomic gradients, indigenous species demonstrate unexpected resilience in high-density areas, suggesting different mechanisms driving community assembly processes. This suggests that indigenous plants have been filtered by local environmental factors such as competition, soil, rainfall and temperature while exotic species have been filtered more by resident choices of the different suburbs (Goodness 2018). Our findings have crucial implications for urban biodiversity conservation in rapidly urbanizing cities. Urban planning initiatives must simultaneously address social equity and evolutionary heritage in their design (Schwarz et al. 2017), recognizing that while high-density areas show reduced exotic diversity, they serve as important reservoirs of indigenous phylogenetic diversity worthy of conservation attention (Shackleton et al. 2017; Garekae and Shackleton 2020). Future greening initiatives should carefully balance the aesthetic appeal of exotic species with the ecological value of indigenous plants (du Toit et al. 2018), while conservation strategies must consider the entire socioeconomic gradient, acknowledging that different urban areas contribute uniquely to overall biodiversity. This holistic approach to urban conservation recognizes the complementary roles of different urban zones in maintaining both cultural preferences and ecological heritage across the urban landscape. The persistence of phylogenetically diverse indigenous communities in high-density areas suggests untapped opportunities for biodiversity conservation in less affluent neighbourhoods. This finding is particularly relevant for rapidly urbanizing African cities, where maintaining biological and cultural connections to native flora could enhance urban ecosystem resilience while preserving local ecological heritage (van Kleunen et al. 2018).

While taxonomic and phylogenetic diversity provides deeper insights into the evolutionary relationships and history of species assemblages, we recommend further studies focusing on functional diversity. Functional diversity offers a more mechanistic understanding of ecosystem processes and community assembly (Cadotte et al. 2011). Functional traits directly influence species'interactions, resource utilization, and ecosystem services, making them stronger predictors of ecosystem functioning (Díaz and Cabido 2001). Recent meta-analyses have demonstrated that functional diversity better explains ecosystem stability, resilience, and productivity across different biomes than taxonomic measures (Gagic et al. 2015). Furthermore, in the context of environmental change, communities with high functional diversity have shown greater adaptive capacity and resistance to disturbance, as functionally diverse species assemblages maintain essential ecosystem processes through complementarity and redundancy (Mori et al. 2013).

Conclusion

Our study reveals complex patterns in the distribution and assembly of woody plant communities across Harare's socioeconomic gradient, highlighting important distinctions between indigenous and exotic species. While the'luxury effect'strongly influences exotic species distribution, with wealthy areas maintaining greater taxonomic diversity, indigenous species show remarkable resilience in high-density areas, particularly in terms of phylogenetic diversity. These findings challenge traditional urban ecology paradigms and suggests that urban biodiversity patterns in Global South cities may differ fundamentally from those observed in the Global North.

The contrasting patterns between taxonomic and phylogenetic diversity metrics underscore the importance of considering multiple biodiversity dimensions in urban ecological studies. While taxonomic turnover dominates overall beta-diversity patterns, the strong phylogenetic nestedness component, particularly for exotic species, suggests that urban environments act as powerful filters of closely related lineages. This filtering appears to operate differently for indigenous and exotic species, with socioeconomic factors more strongly influencing exotic species assembly, while indigenous species patterns likely reflect both historical ecological processes and cultural connections to native flora.

Municipalities can play a proactive role by working with nurseries, particularly in wealthier suburbs, to raise awareness about the importance of phylogenetic diversity. This could include tailored education campaigns, training sessions for nursery staff, and the development of outreach materials that highlight the ecological and aesthetic benefits of offering a wider variety of native and phylogenetically diverse plant species.

These findings have significant implications for urban planning and biodiversity conservation in rapidly urbanizing African cities. The unexpected retention of phylogenetically diverse indigenous communities in high-density areas presents opportunities for biodiversity conservation

that simultaneously addresses ecological and social equity goals. Future urban greening initiatives should leverage these patterns by promoting indigenous species diversity across the socioeconomic gradient while carefully managing exotic species introduction to enhance overall urban ecosystem resilience. This approach would not only preserve local ecological heritage but also ensure more equitable access to urban ecosystem services across the social spectrum.

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Author contribution J.M and M.M collected the data, J.M compiled the initial draft, H.G.T.N, M.M, E.T.F.W, and T.N read and commended on the paper. After incoporating comments from all co-authors all authors reviewed the final draft manuscript.

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Data availability Data will be available upon request from the authors.

Declarations

Ethics approval The study was granted a human ethics approval by the Bindura University of Science Education Research and Postgraduate Centre in 2019 and certify that the study was performed in accordance with the ethical standards as laid down in the 1964 declaration of Helsinki and its later amendments. Prior consent to interview and publish the work was granted by all the interviewees that were involved in the survey.

Competing interests The authors declare no competing interests.

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