Beyond the concrete jungle: the value of urban biodiversity for regional conservation

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Keywords

Urban biodiversity, beta diversity, urban green spaces, regional biodiversity, species richness, birds

Abstract

Urbanization destroys and degrades natural ecosystems, contributing to the ongoing loss of biodiversity. Yet, on the local scale, well-managed cities can host significant biodiversity, including endemic and threatened species. Understanding the trade-off between local and regional biodiversity outcomes is limited, primarily due to the lack of comprehensive sampling across heterogeneous urban areas and adjacent regions. To address this knowledge gap and assess urban areas' value for conserving the regional species pool, we conducted an extensive bird survey across an urbanized metropolitan area and its surrounding region (>300 km^2). The survey included 11 cities, 24 rural settlements, agricultural areas, and natural habitats, employing high-resolution geographic data (e.g., 3D vegetation layer) to examine land cover effects on α- and β-diversity metrics. Our findings reveal that urban avian diversity can surpass adjacent non-urban areas, with urban green spaces among the most species-rich habitats. Most regional bird species did not avoid urban areas, indicating their significant potential for regional conservation, particularly in human-dominated areas. Across the region, local avian assemblages were highly heterogeneous, driven by species turnover rather than loss, highlighting urban biodiversity complexity. However, factors associated with urbanization negatively affected both α- and β-diversity, with synanthropic species most prevalent in urban habitats. Our findings suggest that strategic urban planning, focusing on compact development and accommodating non-synanthropic species in green spaces, can significantly contribute to regional conservation efforts.

1. Introduction

As cities around the world rapidly expand, they transform extensive areas of agricultural and natural landscapes into urban infrastructure and buildings, contributing significantly to global biodiversity declines (Czech et al., 2000). Numerous studies have investigated species diversity patterns within urban areas and across urban-to-rural gradients, consistently revealing the adverse effects of urbanization on biodiversity (reviewed by Chace and Walsh, 2004; Lepczyk et al., 2017; Mckinney, 2008). However, on a local scale, cities are often found to host significant biodiversity, including endemic, rare, and threatened species (Ancillotto et al., 2019; Aronson et al., 2014; Ives et al., 2016; Jokimäki et al., 2018; White et al., 2023). This emerging recognition of the potential role of urban environments in maintaining biodiversity has led to an increased focus on strategies to enhance urban biodiversity (Nilon et al., 2017). Yet, how cities can best be managed and developed to contribute to regional biodiversity conservation remains insufficiently known (Clergeau et al., 2006b; Colléony and Shwartz, 2019; Knapp et al., 2021; Spotswood et al., 2021). A critical gap exists in our understanding of the intricate relationships between local urban biodiversity and the broader regional species pool (Sweet et al., 2022), a gap largely due to the limited research that comprehensively samples biodiversity across entire cities and their adjacent regions (Shwartz et al., 2014).

Most studies addressing the interdependencies between urban and regional biodiversity have sampled along urbanization gradients, typically represented by transects from rural or natural areas through suburbs to city centers (Marzluff, 2017; Mcdonnell and Hahs, 2013). As expected, species richness is mostly observed to decline with increasing urbanization intensity (Mckinney, 2008). However, some inconsistencies exist (Marzluff, 2017), with peak richness sometimes observed at moderate levels of urbanization (cf. the intermediate disturbance hypothesis, Blair, 1996; Marzluff, 2005). Furthermore, the response to urbanization varies between biogeographical regions (Ferenc et al., 2014; Filloy et al., 2019; Saari et al., 2016), across spatial scales (Clergeau et al., 2001; Pautasso, 2007; Uchida et al., 2021) and depending on the urban gradient setup (Batáry et al., 2018; Sol et al., 2017). Additionally, species assemblage composition changes along these gradients, with urban centers often dominated by a small set of synanthropic species (i.e., species that thrive in human-altered environments) that replace many of the native species found in natural and rural ecosystems (Buonincontri et al., 2023; Crooks et al., 2004; Evans et al., 2018). Studies comparing urban green spaces with neighboring non-urban areas reveal similar patterns (e.g., Jokimäki et al., 2013), sometimes showing a nested arrangement of less diverse urban assemblages within richer non-urban ones (Fernández-Juricic and Jokimäki, 2001; Tena et al., 2020). However, the degree of similarity between urban and adjacent non-urban assemblages varies significantly across cities and taxa (Aronson et al., 2016; Clergeau et al., 2001; Filloy et al., 2019; Garaffa et al., 2009). Additionally, recognizing the distinct conservation role of species groups, such as synanthropic or invasive species versus non-synanthropic natives, is key to assessing urban biodiversity's value (Shochat et al., 2010).

Idiosyncrasies in biodiversity responses to urbanization can be attributed to the remarkable spatial heterogeneity of cities, arising from the interplay of natural and built elements shaped by fine-scale socio-cultural characteristics (Alberti and Wang, 2022; Cadenasso et al., 2013; Zhou et al., 2017). Urban-rural gradient studies may oversimplify the urban environment, as cities typically encompass diverse habitats, each potentially supporting distinct species assemblages (Alberti and Wang, 2022). For example, diverse urban green spaces in Zurich, Switzerland – including allotment gardens, parks, and green roofs – were shown to selectively filter distinct assemblages of species from the regional species pool (Fournier et al., 2020). This compositional difference, termed β-diversity, is a less-studied aspect of urban species diversity, with most studies focusing primarily on local α-diversity (Swan et al., 2021). β-diversity bridges local α-diversity and landscape-level γ-diversity, indicating how species composition varies between local assemblages within the landscape (Whittaker, 1972). It results from two phenomena: spatial turnover, where species are replaced due to environmental sorting, and nestedness, where species loss occurs due to environmental impoverishment (Baselga, 2012). While urban spatial heterogeneity might enhance β-diversity through turnover, urbanization typically leads to species loss, suggesting observed β-diversity in urban assemblages could be due to nestedness rather than turnover (Fernández-Juricic, 2002; Leveau et al., 2017; Marcacci et al., 2021). However, few studies have explored this phenomenon at metropolitan or regional scales. Such knowledge is important for understanding the role urban biodiversity can play in protecting the regional species pool and directly contributing to conservation efforts.

The growing interest in biodiverse and wildlife-friendly cities has motivated research on the impact of specific land cover and land use variables on urban biodiversity. These studies often focus on urban green spaces, revealing that factors such as size, connectivity, and vegetation structure are key drivers of species richness (Beninde et al., 2015). Yet, while green spaces are crucial biodiversity hubs in cities, effectively integrating conservation goals into urban planning requires identifying and characterizing processes and mechanisms that influence biodiversity throughout the entire urban mosaic (Shwartz et al., 2014; Zhou et al., 2017). Research encompassing a wider range of urban habitats highlights the importance of vegetation cover and structure, along with building properties (Morelli et al., 2021; Pellissier et al., 2012).

Integrating a broader regional approach that includes diverse urban and non-urban habitats is crucial for assessing the value of cities for conservation efforts and generating the insights needed to optimize regional and urban conservation planning.

The objective of this study is to assess the value of urban areas for regional biodiversity by (1) investigating the relationships between urban and regional γ-, α-, and β-diversity of bird species in the Tel-Aviv metropolitan area and its surrounding region, and (2) exploring the variables influencing α- and β-diversity, using high-resolution geographic datasets (e.g., 3D vegetation layer). Our study addresses the fine-scale heterogeneity of urban environments through an extensive and systematic sampling approach, involving over 2000 random point locations across the 300-km^2 region, covering a wide range of habitats. We hypothesize that urban areas will support significant biodiversity but will have distinct assemblage compositions compared to non-urban areas. Thus, we predict that regional γ-diversity will be relatively high due to the combination of both urban and non-urban species pools. We examine diversity patterns for synanthropic species, non-synanthropic residents, migrants, and all bird species collectively. We predict that a few synanthropic species will dominate urban areas, resulting in lower α-diversity and reduced species turnover, as non-synanthropic species are excluded. However, we predict nestedness to play a more significant role in built-up areas compared to agricultural and open lands. Conversely, we expect urban green spaces to act as biodiversity hubs, supporting both synanthropic and non-synanthropic species, leading to higher levels of diversity in these areas. Modeling the impact of land use and cover variables on α- and β-diversity metrics, we predict that vegetation structure and the proportion of built surfaces will be key drivers of bird diversity patterns. By identifying patterns of α- and β-diversity, we aim to highlight strategies for enhancing urban biodiversity and contributing to regional conservation efforts.

2. Methods

2.1 Research area

The study was conducted in the Tel-Aviv District metropolitan area and its non-urban surroundings, Israel (Fig. 1). Tel-Aviv District is a densely populated urban area (1,502,610 inhabitants/172 km^2), including eleven cities, of which the largest is Tel-Aviv-Yafo (492,870 inhabitants/52 km^2) (Israel Central Bureau of Statistics, 2022). The non-urban surroundings of the district include an additional 140 km^2 of largely rural and natural landscapes. Altogether the study covered an area of 312 km^2, of which approximately 50% is built-up area, including the metropolitan area and 24 rural settlements (Fig S4), 20% agricultural land, including both arable fields (~60% of agricultural area) and orchards (~40% of agricultural area), and 30% other open areas. Approximately 25% of the open area is protected natural areas, including nature reserves and national parks. The research area lies in Israel's central coastal plain region, stretching along the eastern Mediterranean coast, between Mount Carmel (north) and the semi-arid Northern Negev (south), bordered by the Judaean Mountains' foothills (east). The region features Kurkar (aeolianite) ridges and red sandy clay loam soil. It has a temperate Mediterranean climate with hot, dry summers (Beck et al., 2018), and mean annual precipitation ranging from 550 mm in the north to 390 mm in the south (Israel Meteorological Service, 2022). The natural landscapes are dominated by low Mediterranean maquis, with approximately 40% of the region urbanized. The research area covers about 30% of this region.

2.2 Regional bird survey

Relative abundance of bird species was recorded in a systematic point-count survey including an overall of 2,166 sampling points across the study area. Our sampling efforts thus were about seven sampling points per 1 km^2. To capture this mosaic-like landscape's heterogeneity, most of the sampling points (82%) were distributed at random, but the remaining points were then distributed manually in specific, rare and small habitats to avoid under-sampling them (Bibby et al., 2000). For the random distribution of sampling points, a grid of 100m x 100m cells was first defined across the research area. Then, 6% of the grid cells were sampled at random, with the constraint that no immediately adjacent cells were selected (Sutherland, 2006). At a larger sampling percentage (≥7%) this distance constraint could not be kept. We further validated the sufficient representation of socio-ecological land cover strata in the sample by comparing their distribution in the sample to their distribution across the Tel-Aviv District (see Text S1 and Fig. S1 in Supporting Information).

In the centroid of each selected grid cell, we located a single sampling point. When needed, the point's location was manually adjusted so that it was accessible for sampling. The point was relocated within the grid cell if sampling a similar habitat was possible. Otherwise, the point was moved to an adjacent cell with a similar habitat, or ultimately removed. Out of the original 6% sample (equal to 1,937 sampling points), 159 points were eventually removed due to inaccessibility. Additionally, 388 points were manually located in ecologically valuable habitats that may be underrepresented in the random sample due to their small coverage and scattered distribution. These included small nature reserves, sites recognized as urban nature sites in municipal ecological surveys, small urban green spaces, and other remnants of native vegetation, visually identified from an orthophoto.

During the bird breeding season, March-June 2021, we conducted a survey by four experienced birders, following the protocols described in Bibby et al. (2000). Weather conditions from March to June 2021 were typical based on 2000–2020 temperature and precipitation averages. May 2021 was slightly warmer, exceeding the median of historical data but remained within observed temperature ranges (data from Israel Meteorological Service, 2022). Each sampling point was visited twice at peak hours of bird activity, once during early morning hours (from sunrise and up to 3.5 hours after sunrise) and once during late afternoon hours (from 3.0 hours before sunset and up to sunset). Repeated visits to each point were at least three weeks apart (mean gap 86 ± 63 days), and the order of early morning and late afternoon visits was randomly assigned. In each visit, the observer conducted a ten-minute point count, in which all bird species seen or heard within a 100-meter radius were recorded. For each observation, observers recorded species identity, number of individuals, and interaction with the sampled grid cell (i.e., whether birds were interacting with the local habitat or just passing through). Only observations of birds in interaction with the sampled grid cell were used in the analysis.

2.3 Main land covers

We classified the research area into four main land cover categories: (1) built-up areas, comprising clusters of buildings and paved surfaces; (2) agricultural land; (3) open land, neither urban nor agricultural; and (4) urban green spaces, including all public open spaces within the built-up boundaries. These broad categories are widespread, sufficiently heterogeneous for assessing β-diversity, and clearly distinguishable within the study area. We created a vector-based polygon map to delineate these land covers through manual digitization of a recent high-resolution (0.25 m) orthophoto and several governmental and custom-made GIS layers (see Table

S1 for detailed layer information). Specifically, clusters of buildings, roads, and pavements were identified using a high-resolution (2 m) land cover raster and manually digitized; agricultural plots were extracted from a governmental GIS vector layer; and urban green spaces were identified within built-up areas based on relevant categories from OpenStreetMap, verified with municipal planning layers. All GIS analyses were conducted using ArcGIS Pro 2.9, with data projected in Israeli Transverse Mercator projection (ITM, EPSG:2039). Survey points were classified into four land covers by overlaying the 100-meter grid with the main land cover map. The coverage of each land cover within each point's grid cell was calculated, and the land cover with the highest coverage was assigned to the point. Points in urban green spaces were classified as such irrespective of the grid cell coverage. For 32 points with less than a 5% difference in land cover coverage, we visually determined the land cover at the point's location within the cell from the orthophoto.

2.4 Land use and land cover metrics

The predictor variables for modeling bird species diversity were a set of eleven land use and land cover metrics, describing the urban and non-urban environmental attributes of the research area that we expect to be most relevant for birds: buildings (*building cover* and *building height*), paved surfaces (*impervious surface cover*), agriculture (*arable field cover* and *orchard cover*), vegetation (*tree cover*, *lower vegetation cover,* and *vegetation height variance*), water (*inland water cover)*, coastal habitat (*coastal cover*) and landscape diversity (*land cover heterogeneity*). We obtained the values of each metric using the GIS layers detailed in Table S1, for a 100-meter buffer around each sampling point. To overcome resolution differences, all layers were processed into 2-meter-pixel rasters before calculation.

Building cover was calculated as the relative area of buildings within the buffer. *Building height* was the calculated average height of buildings within the buffer, derived by subtracting ground elevation from surface heights extracted from the digital surface model layer. *Impervious surface cover* was calculated as the relative area classified as either pavement, road, railway, driveway, parking, or airport in the high-resolution land cover map. *Arable field cover* was the relative area of agricultural plots of arable crops, including wheat, vegetables, flowers, etc. *Orchard cover* was the relative area of agricultural plots of citrus and deciduous trees. A total vegetation cover layer was generated through spectral signature classification of the high-resolution multispectral orthophoto (see Text S2, Figs. S2-3), enabling the incorporation of summer-dormant shrubs with low photosynthetic activity, which are prevalent in the native Mediterranean maquis vegetation. *Tree cover* was calculated as the relative area of green vegetation higher than two meters, based on the total vegetation cover layer and the digital surface model. Similarly, *lower vegetation cover*, (i.e., grasses and shrubs) was the relative area covered with all vegetation lower than two meters. *Vegetation height variance* was the calculated variance in height values of pixels classified as vegetation. *Inland water cover* was the relative area classified as either water, lake, or river in the high-resolution land cover map. *Coastal cover* was calculated as the relative coverage of an 80-meter buffer from the coastline inland. *Land-cover heterogeneity* was calculated using Shannon's diversity index formula, , where represents the proportional area of each of the following land cover classes: buildings, impervious surfaces (see above), fields, grass, trees, bare ground, inland water (see above), and sea.

2.5 Biodiversity metrics

The use of α- and β- and γ-diversity metrics requires spatial definition of the extent of local and regional biodiversity, which is often obscure in urban and natural ecosystems alike (Swan et al., 2021). Here, we use the four main land covers defined above (i.e. built-up, agriculture, open, and urban green space) to test differences in species diversity metrics across the region. Regional γ-diversity is measured for the entire research area, as well as for each main land cover separately, to assess the representation of the regional species pool in each one. Local α-diversity is defined here as the diversity measured in a single sampling point. To compare the degree of compositional variation between the main land cover types, we used 'multiple-site' β-diversity measures, suitable for quantifying β-diversity among more than two sites (i.e. sampling points) (Baselga, 2013a). For investigating how compositional dissimilarity is affected by environmental dissimilarity we used pairwise β-diversity measures (Ferrier et al., 2007). We further separated the two types of β-diversity measures into their additive components representing dissimilarity caused by either species replacement (i.e., turnover) or species loss (i.e., nestedness).

2.6 Data analysis

All analyses were conducted in R version 4.0.5 (R Core Team, 2021). *γ-diversity*: Species richness and species composition for the entire research area and each habitat type were summarized based on the pooled data from all relevant sampling points. To omit vagrant species, we only included species with a total abundance of > 5 individuals. Overlap in species identities was calculated between each combination of habitat types. All species were classified according to their synanthropic and migratory status into three categories: synanthropes, non-synanthropic residents, and migrants (see Table S2 for species classification details and sources).

α-diversity: Species richness and diversity indices (Shannon diversity, Simpson diversity) per point, were calculated based on averaged species abundances across the two visits. To determine whether α-diversity differed between habitat types, we performed an analysis of variance

(ANOVA) on the averaged values of species richness and diversity indices and compared differences between pairs of habitat types using Tukey's HSD post-hoc tests ($p<0.05$). This was performed for all species together and for each species group (i.e., synanthropes, non-synanthropic residents, and migrants). The homogeneity of variance and normality of residuals were verified to ensure model assumptions were met. We fitted a Generalized Linear Model (GLM) to predict α-diversity across the region, with all 11 land use and land cover variables as predictors, as well as latitude and longitude coordinates to account for spatial autocorrelation (Bahn and McGill, 2007). Such a model was fitted to each metric of local species richness and diversity, for all species together and of each species group separately. Models were fitted using the *stats* package in R, assuming Poisson error distribution and a Log link function. Normality and heteroscedasticity assumptions were verified by plotting the residuals, Cook's distance metrics, and leverage points. We also checked for multicollinearity with the variance inflation factor (VIF) and ensured VIF >5 (Thompson et al., 2017).

β-diversity: For each main land cover, we calculated two multiple-site β-diversity measures representing the proportion of unique species per site using the *betapart* package (Baselga and Orme, 2012). Sörensen dissimilarity was used as a qualitative measure for incidence-based total β-diversity (i.e., based on species incidence data), and Bray-Curtis dissimilarity as a quantitative measure for abundance-based total β-diversity (i.e., based on species abundances). Incidence-based β-diversity was partitioned into its turnover component (i.e., Simpson dissimilarity) and nestedness-driven dissimilarity component, the latter obtained by subtracting turnover from total β-diversity (Baselga, 2012). Abundance-based β-diversity was similarly partitioned, with its turnover component indicating that some individuals replace individuals of different species from site to site, and its nestedness component indicating that the abundance of all species declines from site to site (Baselga, 2013b). We calculated multiple-site dissimilarities repeatedly for 1,000 random samples of 50 sites at a time, to generate a distribution of each β-diversity measure using *beta.sample* R function (Baselga and Orme, 2012). ANOVA and Tukey's HSD post-hoc tests ($p<0.05$) were used to determine the significance of differences in mean β-diversity between habitat types. The homogeneity of variance and normality of residuals were verified to ensure model assumptions were met.

Generalized Dissimilarity Modelling (GDM) approach, a matrix regression technique that allows for non-linear relations (Ferrier et al., 2007) was used to investigate the patterns of β-diversity along environmental gradients across the region. In the GDM model fitting procedure, monotonically increasing I-spline functions are used to transform each of the environmental predictors, to generate together the best estimate of predicted ecological distance. The predicted ecological distance is then used to predict compositional dissimilarity between sites using a GLM with a negative exponential link function. Due to the flexible nature of I-spline functions, GDMs can account for varying rates of change in β-diversity along the environmental gradients (Mokany et al., 2022). To reduce dimensionality and aid interpretation of the main patterns of variability underlying changes in β-diversity across the study region, we used a principal component analysis (PCA, R function *prcomp*) on the full set of 11 land cover variables summarized in a 100-meter buffer around each sampling point. We identified two primary axes to be used as environmental predictors in the GDM (Table S6). We fitted GDMs using the selected PC axes and geographical distance as environmental predictors, to both incidence-based and abundance-based pairwise β-diversity indices, as well as their respective turnover and nestedness components (*gdm* package; Fitzpatrick et al., 2022).

3. Results

3.1 *γ-diversity*

Overall, 182 bird species were observed in the regional survey, with 123 species having a total abundance >5 and included in the regional species pool analysis. The urban species pool (104 species observed in built-up areas and urban green spaces) constituted 85% of the regional pool, with the remaining species primarily being water birds. Of the regional species, 97 (79%) were shared across urban, agricultural, and open habitats. When distinguishing between built-up areas and urban green spaces, only 5 species were unique to urban green spaces, while 20 were unique to built-up areas (Fig. S5). Most of these built-up area species were also observed in agricultural and open habitats, indicating few species were exclusively associated with built-up areas. Altogether, there was a high overlap in species presence among all four main land cover types.

3.2 *α-diversity*

Mean local species richness was highest in urban green space sampling points (Fig. 2, Table S3), compared to built-up, agriculture, or open area points. Differences in local species diversity between land covers, measured using Shannon's and Simpson's diversity indices, were mostly not significant but showed a trend of higher diversity in open areas and urban green spaces than in agriculture (Fig. 2a, Table S3; $0.01<\text{p-adj}<0.07$). Synanthropic, non-synanthropic, and migrant species differed in their local richness and diversity among the main land covers (Fig. 2b-d, Table S3). Synanthropic species ($N_{sp}=13$) had higher richness and diversity in urban green spaces and built-up areas compared to open and agricultural areas (Fig. 2b, Table S3). Non-synanthropic species ($N_{sp}=76$) had higher richness and diversity in open and agricultural areas and lowest in built-up areas (Fig. 2c, Table S3), with urban green spaces showing intermediate values. Migrant species (N_{sp}=92) exhibited lower richness and diversity in built-up areas than in other land covers, with significant effects in most pairwise comparisons (Fig. 2d, Table S3).

Responses to the land cover variables varied among bird species groups (Fig. 3, Table S4, Fig. S6). Urbanization-related variables (e.g., building cover, impervious surface cover), positively affected synanthropic species richness but a strongly negatively affected non-synanthropic species. Natural habitat variables (e.g., tree cover, low vegetation cover, inland water cover) positively affected non-synanthropic and migrant species richness but had no significant effect on synanthropic species. Land cover heterogeneity positively affected synanthropic and non-synanthropic species but negatively affected migrants. Agriculture-related variables negatively affected all species groups. Vegetation height variance negatively affected non-synanthropic species richness and had no significant effect on other groups. Shannon and Simpson diversity indices responded similarly to land cover variables as species richness (Fig. S6).

3.3 -diversity

Multiple-site total -diversity was high across all land covers, for both incidence-based (Sörensen dissimilarity) and abundance-based (Bray-Curtis dissimilarity) -diversity measures (Fig. 4). Pairwise comparisons between land covers were less significant for abundance-based than for incidence-based diversity, but trends were similar, with slightly higher -diversity in agriculture and urban green spaces than in open and built-up areas (Fig. 4, Table S5). Partitioning -diversity indices into turnover and nestedness components revealed that species turnover was the largest contributor to overall -diversity in all land covers. Nestedness-driven dissimilarity was generally much lower than turnover but was highest among built-up points (Fig. 4, Table

S5). Incidence-based nestedness was higher in urban green space than in open and agricultural areas (Fig. 4). However, abundance-based nestedness did not significantly differ between land covers.

A PCA on the 11 land use and land cover variables resulted in two primary PC axes explaining 51% of the variance: (a) PC1, explaining 37%, was positively correlated with low vegetation cover and negatively with urbanization-related variables such as building cover, building height, impervious surface cover, and land cover heterogeneity; (b) PC2, explaining an additional 14%, was mostly negatively correlated with tree cover and agricultural orchard cover (Table S6; Fig. 5a). The axes represent (a) urbanization to lower vegetation and (b) tree cover gradients. GDMs explained 17.3% of the deviance in pairwise abundance-based turnover and 22.3% in incidence-based turnover. The I-spline curves for both PCA axes indicated they highly contributed to -diversity between sites, while geographic distance had a much smaller contribution (Fig. 5b-d). The function describing the -diversity change along the urbanization to lower vegetation gradient (PC1) was non-linear, with a sharp increase in turnover at higher gradient values, i.e., in points with lower urbanization intensity and higher shrub and grass cover (Fig. 5c). Along the tree cover gradient (PC2), -diversity increased most strongly at very high or very low tree coverage, indicating that points with medium tree cover were more similar (Fig. 5d). GDMs for total -diversity indices showed similar patterns to turnover GDMs (Fig. S7). GDMs for nestedness components of -diversity explained very little deviance (0.008%) and I-spline curves could not be fitted.

4. Discussion

Understanding the role urban areas can play in conserving regional biodiversity is becoming crucial, as cities continue to grow globally (Knapp et al., 2021; Shwartz et al., 2014; Spotswood et al., 2021). Our results indicate that urban bird diversity can be nearly as rich and diverse as that of adjacent non-urban areas. Notably, urban green spaces emerged as some of the region’s most biodiverse habitats, while bird communities in built-up areas were less diverse and more homogenous. These findings demonstrate the significant potential for urban biodiversity conservation at a regional scale, reflected in both γ- and α-diversity patterns.

Substantial overlap between urban and regional species pools shows that in our region most bird species do not avoid the city, indicating a higher urban representation than previously reported (Caula et al., 2010; Ferenc et al., 2014; Sweet et al., 2022). Despite Tel-Aviv's intermediate size and southern Mediterranean location, its biodiversity patterns align with larger or higher latitude cities (Ferenc et al., 2014). Locally, α-diversity metrics reveal urban communities, particularly in green spaces, to be relatively species-rich and ecologically even, compared to non-urban communities. Urban green spaces are commonly described as biodiversity hubs in the built-up matrix, but usually they are not as biodiverse as non-urban habitats (Knapp et al., 2008). While synanthropic species significantly contribute to the richness of urban green spaces, as previous research has shown (Crooks et al., 2004; Sandström et al., 2006), this increase does not lead to reduced evenness, contrary to expectations of competitive exclusion of non-synanthropes (Shochat et al., 2010). Regarding migrant species, our findings support the importance of urban green spaces to contribute to migrant species conservation (Leveau, 2021). It should be noted that the observed high species richness of urban green spaces in our study area might be tied more to the low quality of non-urban habitats. This can be attributed to the region’s landscapes being mostly human-modified, with small, fragmented natural areas. Thus, we assess urban areas' value against these already degraded ecosystems. Yet, this situation is not uncommon, especially in cities expanding into agricultural hinterlands with similar fragmentation.

Biotic homogenization in cities, characterized by “few winners replacing many losers” (Clergeau et al., 2006a; McKinney and Lockwood, 1999), is expected to lead to nested species assemblages where highly disturbed habitats are subsets of less disturbed ones (Fernández-Juricic, 2002; Sorace and Gustin, 2008; Tena et al., 2020). While some studies show that gradual species loss promotes nestedness (Leveau et al., 2017; Marcacci et al., 2021), others find that replacement by urban specialists drives turnover-dominated β-diversity along urbanization gradients (Leveau et al., 2017; Sol et al., 2017). Generally, turnover is the primary component of β-diversity in most ecosystems (Soininen et al., 2018). In our study, avian communities in the Tel-Aviv metropolitan area and its surroundings were highly heterogeneous, primarily due to species replacement with similar abundances. Although nestedness was higher in urban habitats, its overall contribution to total β-diversity was small. Thus, species turnover, rather than species loss or decreased abundances, is the main driver of β-diversity in this region.

Species turnover in the region was primarily affected by land use and land cover variables, rather than geographical distance, indicating that habitat connectivity is not a major constraint. However, this may not apply to other taxa that are less mobile. Higher turnover rates were observed in the least urbanized and least densely forested areas. Non-urban sampling points had a greater prevalence of rare species, which is driving the increased change in composition in non-urbanized vegetated areas. Despite the overall heterogeneity in urban bird communities and minimal species loss, the least common species—which contribute to the β-diversity of non-urban assemblages—are mostly absent in urban settings, indicating a subtle homogenization effect of urbanization on avian biodiversity.

Considering this homogenization, examining the influence of urban design on α-diversity is essential for enhancing bird diversity in cities. While extensive building cover and impervious surfaces significantly decreased non-synanthropic species richness–a well-documented effect (e.g., Morelli et al., 2021)–building height had a minor impact–an understudied variable (Amaya-Espinel et al., 2019). These results contribute to the compact vs. sprawling urban growth debate, suggesting increased building cover, rather than height, drives bird diversity declines, thus favoring compact development (Lin and Fuller, 2013). Vegetation and habitat features such as tree cover, lower vegetation, and freshwater presence were positively related to non-synanthropic species richness, supporting previous research (Aronson et al., 2014; Beninde et al., 2015; Morelli et al., 2021). Lower vegetation, characteristic of the region's native low Mediterranean maquis, also enhanced β-diversity, highlighting its role in designing urban green spaces suitable for native species. The significance of shrub cover in urban green space for bird richness, as indicated by previous studies (Morelli et al., 2021; Sandström et al., 2006), was also observed in Tel-Aviv's urban parks (Paker et al., 2014). Similarly, integrating floodwater retention in urban green spaces could further enhance urban biodiversity. Our findings indicate that freshwater positively impacts non-synanthropic and migrant species richness, with most regional bird species that were absent in the city being water birds. This approach is particularly relevant given the historical loss of wetlands in the coastal plain region due to urbanization (Levin et al., 2009). Altogether, our regional analyses confirm prior research on urbanization's biodiversity impacts, showing it may lead to homogenization (McKinney and Lockwood, 1999), diminish richness (Mckinney, 2008), and favor synanthropic species (Crooks et al., 2004; Evans et al., 2018), but also highlighting the high species diversity in urban green spaces (Beninde et al., 2015; Nilon et al., 2017). Our study utilizes a more robust approach than the common practice of sampling along urban gradients or solely in green spaces, a method criticized for oversimplifying urban complexity (Alberti and Wang, 2022; Mcdonnell and Hahs, 2013; Zhou et al., 2017). By examining patterns across a wider habitat spectrum with high-resolution land cover and biodiversity data, we provide stronger support for previous findings.

However, a main limitation of our study is its temporal scope, confined to a single breeding season. While we focused on increasing the spatial scale and resolution of biodiversity sampling, this approach limits our ability to understand changes over time. This is important for two reasons. First, species assemblages change throughout the year; while we focus on breeding and migrating species, wintering species were not surveyed. Second, long-term urban bird research suggests that urban bird communities are dynamic and experience significant changes in species composition over time (Fidino and Magle, 2017; Fraissinet et al., 2023). Future research can benefit from expanding the analysis to include multiple seasons across several years to better represent temporal dynamics. Additionally, differences between managed and unmanaged urban green spaces, as well as finer aspects of green space management (e.g., mowing frequency, deadwood removal), were not addressed due to the broader scope of this study. These elements are also important for a comprehensive understanding of urban ecology (Shwartz et al., 2013) and future research can benefit from integrating such local scale factors to explore additional pathways for enhancing biodiversity in cities.

5. Conclusions and implications

Our study reveals a complex relationship between urban and regional diversity in urbanized regions. Despite an evident negative effect of urbanization-related variables on biodiversity, the overall diversity in urban habitats is on par with that of non-urban habitats. These findings highlight the potential of urban nature conservation as a significant component of regional conservation, especially in human-dominated landscapes where pristine habitats are scarce and opportunities for biodiversity conservation are diminishing. In such regions, urban biodiversity efforts could be as effective as those in rural settings. However, our findings also indicate that this potential is not fully realized, with lower diversity metrics in built-up areas and the diversity in urban green spaces being partly due to synanthropic species. This implies two main strategies to improve urban biodiversity. The first is the greening of the city's built-up matrix, using trees and lower vegetation associated with the increased richness of non-synanthropes. This can be achieved through nature-based solutions like green roofs, walls, and ecologically designed public spaces, which have demonstrated local biodiversity benefits (e.g. Mühlbauer et al., 2021; Partridge & Clark, 2018) and could scale to city-wide impacts. The second strategy focuses on supporting non-synanthropic species in urban green spaces, potentially by integrating elements from native habitats in the region known to increase bird diversity. In Tel-Aviv, these may include native shrubs and herbs, and floodwater retention basins. As our research demonstrates the importance of studying urban biodiversity in its context, future studies should explore the effect of such strategies not just locally, but within the wider regional context, to optimize their conservation impact.

Acknowledgments

We wish to thank the birdwatchers who participated in the bird survey: Yohay Wasserlauf, Yotam Lenard, and Yehonatan Ben-Aroya. We also thank Dr. Avi Bar-Massada, Achiad Sade, and Guy

Steenekamp for their assistance with GIS analyses, and Dr. Ronit Cohen-Seffer for her invaluable support throughout the project. This project has received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation program (grant agreement No. 852633-ERC).

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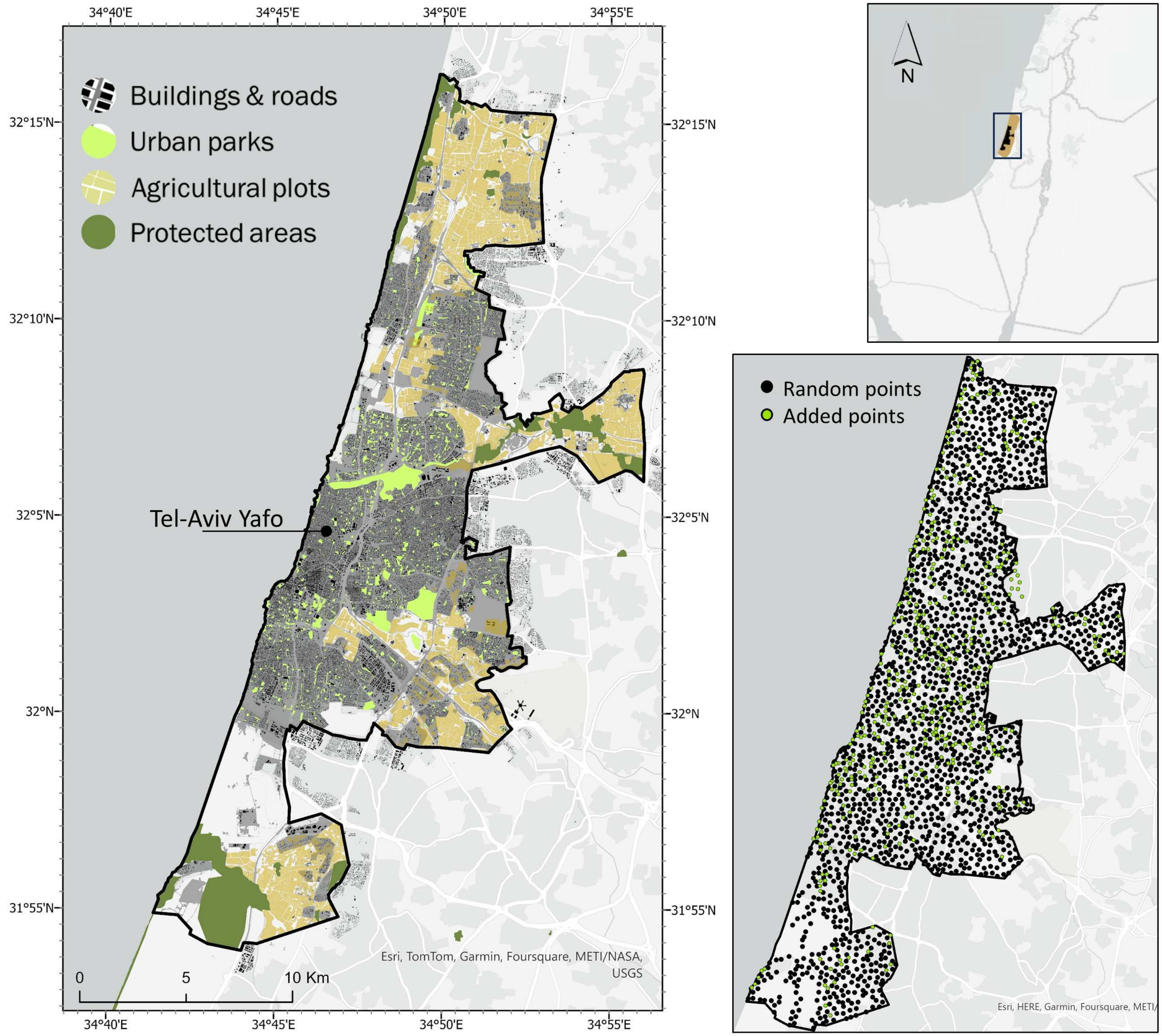
Figure : The extent of the research area, including the Tel-Aviv District metropolitan area and additional non-urban area in its surroundings. (A) The distribution of land covers and uses: buildings and roads, urban green spaces, agriculture, and protected areas. (B) regional bird survey sampling points (n=2,166), black circles: randomly located points (n=1,937), green circles: additional points manually located at specific habitats (n=388).

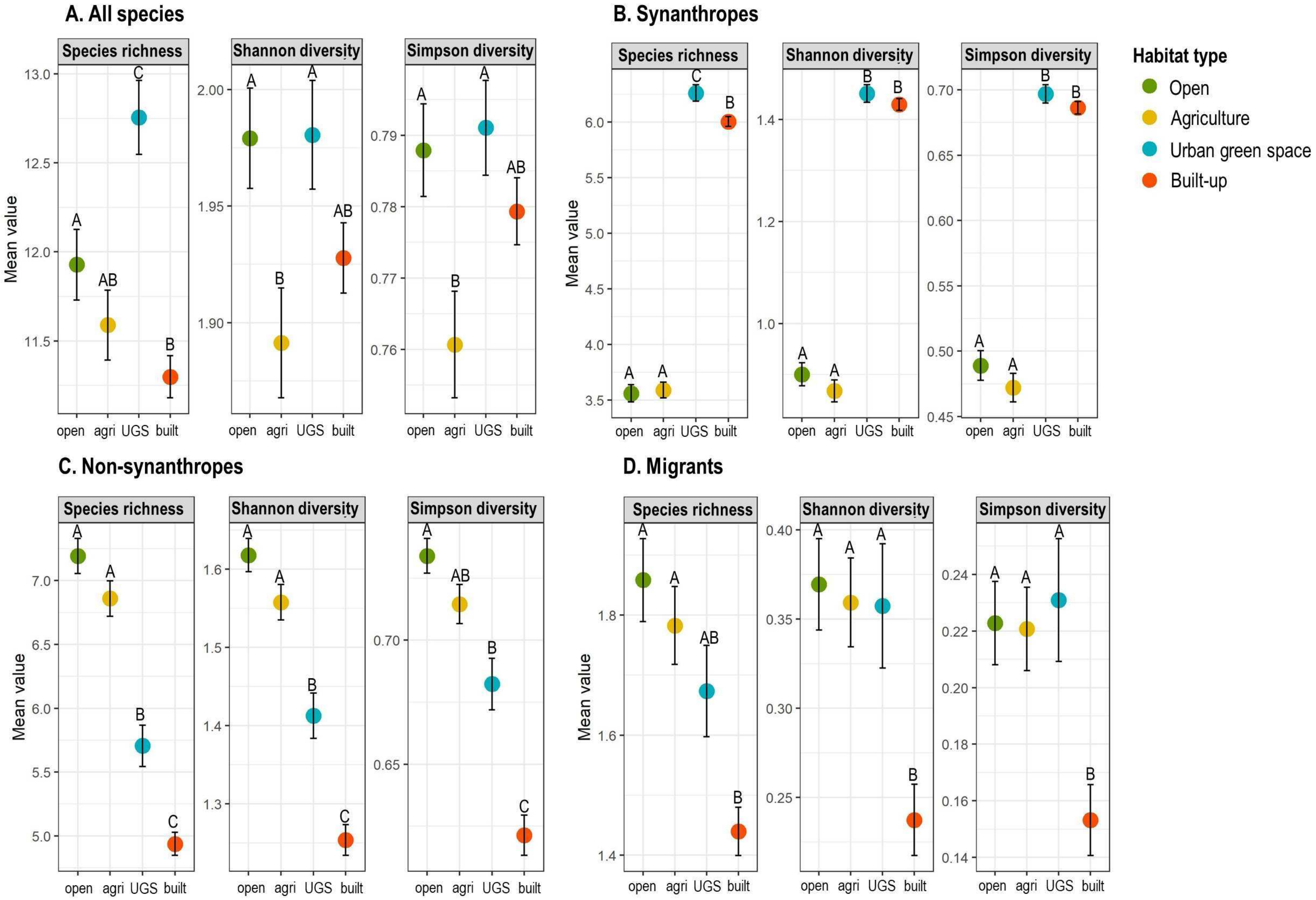
Figure 2: Mean values (±SE) of α richness and diversity measures. For: (A) all species, (B) synanthropes, (C) non-synanthropic residents and (D) migrants, in main regional land covers: open land, agriculture, built-up and urban green space. Significant differences were found among habitats in all three measures in ANOVA ($p<0.001$; Table S2). Letters indicate whether pairwise comparisons were statistically significant (p-adj<0.05) based on Tukey's-HSD post-hoc tests.

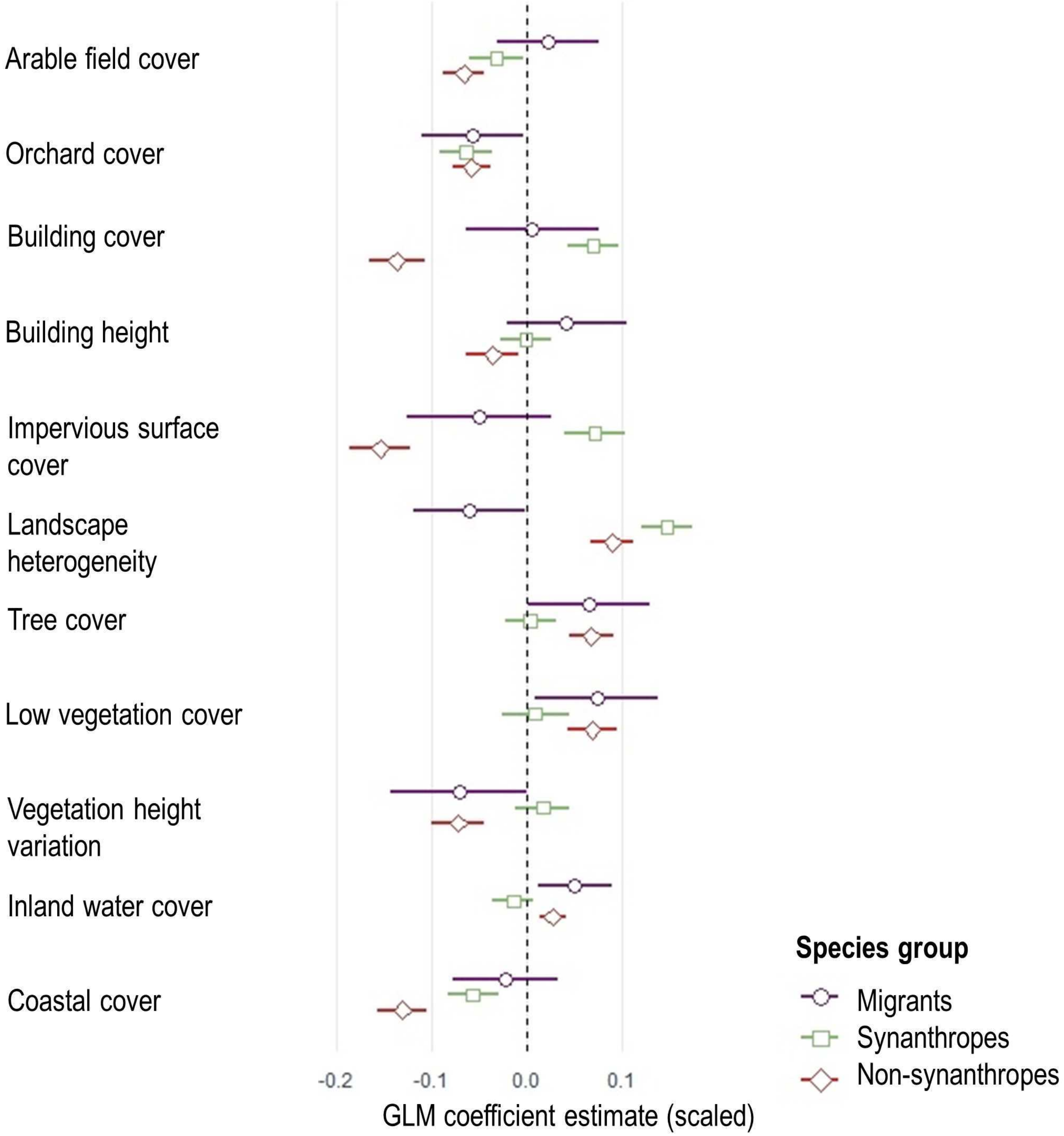
Figure 3: Standardized coefficient estimates (±0.95 CI) for local land cover predictor variables. Coefficients for each variable are estimated in three GLMs, each fitted for α species richness of a different species group (synanthropes, non-synanthropic residents and migrants). See Table S3 for full model results.

Figure 4: Measures of multiple-site total β-diversity and their turnover and nestedness components. β-diversity is measured in main regional land covers: open land, agriculture, built-up and urban green space. a. Sorensen index; b. Bray-Curtis index. Boxplot lower and upper hinges correspond to the first and third quartiles, notches indicate 95% confidence interval for comparing medians. Significant differences were found among habitats in all measures using ANOVA ($p<0.001$; Tab. S4). Letters indicate significant pairwise comparisons (p-adj<0.05) based on Tukey's-HSD post-hoc tests.

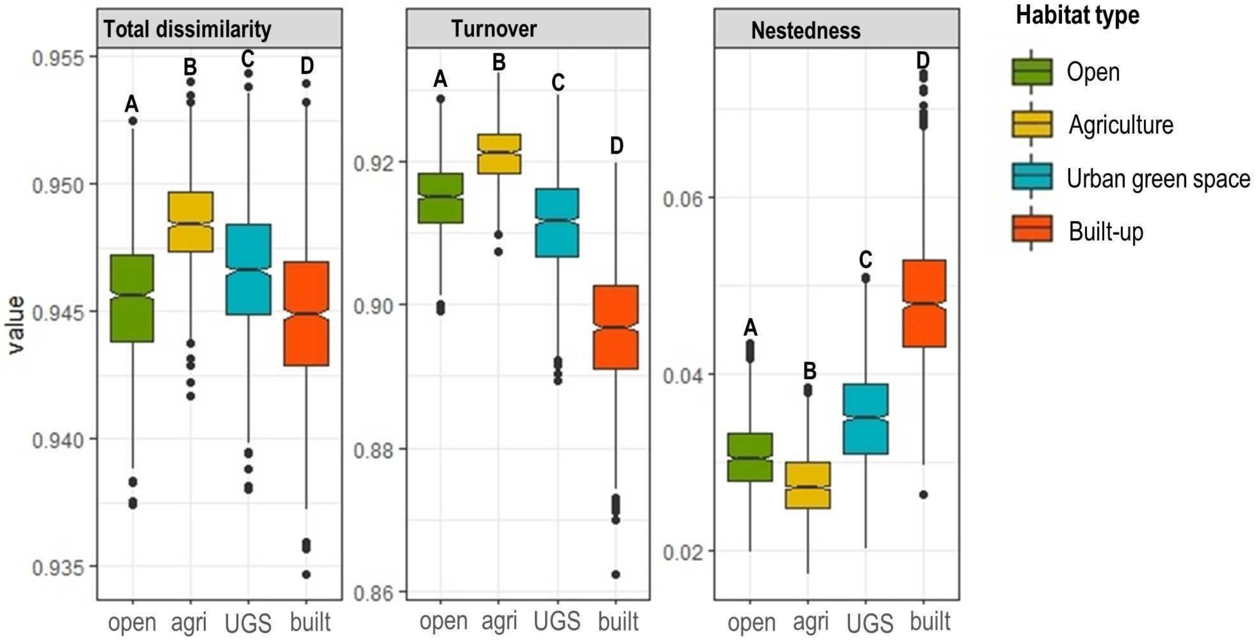
Figure 5: Generalized Dissimilarity Model (GDM) using PCA axes of local land cover variables used as predictor variables. (A) Two primary axes of local land cover variables PCA, magnitude and direction of each variables' contribution to the axes is indicated by arrow length, color, and direction. PC1 is mostly correlated with urbanization-related variables (negative) and low vegetation cover (positive), while PC2 is mostly correlated with tree cover (negative).)B-D) GDM's fitted I-splines, corresponding to the magnitude of effect of environmental variables on beta-diversity (partial ecological distance), using two turnover indices: abundance-based (blue solid) and the occurrence-based (red dashed). Variables are: (B) Geographical distance, (C) PC1: urbanization to lower vegetation gradient, (D) PC2: decreasing tree cover gradient. Error bands represent model uncertainty. Curve height indicates the variability explained by each predictor, while the slope provides an indication of how the rate of compositional turnover varies along each predictor's range.


34°40'E
34°45'E
34°50'E
34°55'E
32°15'N
32°10'N
32°5'N
32°N
31°55'N
Buildings & roads
Urban parks
Agricultural plots
Protected areas
Tel-Aviv Yafo
0
5
10 Km
Esri, TomTom, Garmin, Foursquare, METI/NASA, USGS
N
● Random points
● Added points
Esri, HERE, Garmin, Foursquare, METI/

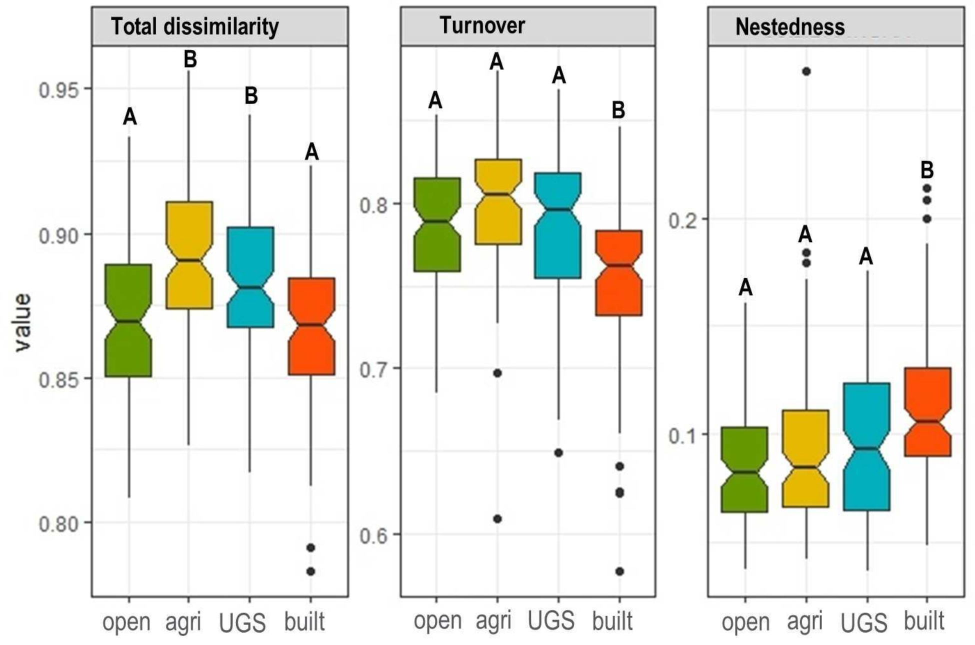

A. All species
Species richness
Shannon diversity
Simpson diversity
Mean value
13.0
12.5
12.0
11.5
C
A
AB
B
2.00
1.95
1.90
A
A
B
AB
0.79
0.78
0.77
0.76
A
A
B
AB
open agri UGS built
B. Synanthropes
Species richness
Shannon diversity
Simpson diversity
Mean value
6.0
5.5
5.0
4.5
4.0
3.5
A
A
C
B
1.4
1.2
1.0
A
A
B
B
0.70
0.65
0.60
0.55
0.50
0.45
A
A
B
B
Habitat type
● Open
● Agriculture
● Urban green space
● Built-up
C. Non-synanthropes
Species richness
Shannon diversity
Simpson diversity
Mean value
7.0
6.5
6.0
5.5
5.0
A
A
B
C
1.6
1.5
1.4
1.3
A
A
B
C
0.70
0.65
A
AB
B
C
D. Migrants
Species richness
Shannon diversity
Simpson diversity
Mean value
1.8
1.6
1.4
A
A
AB
B
0.40
0.35
0.30
0.25
A
A
A
B
0.24
0.22
0.20
0.18
0.16
0.14
A
A
A
B
open agri UGS built

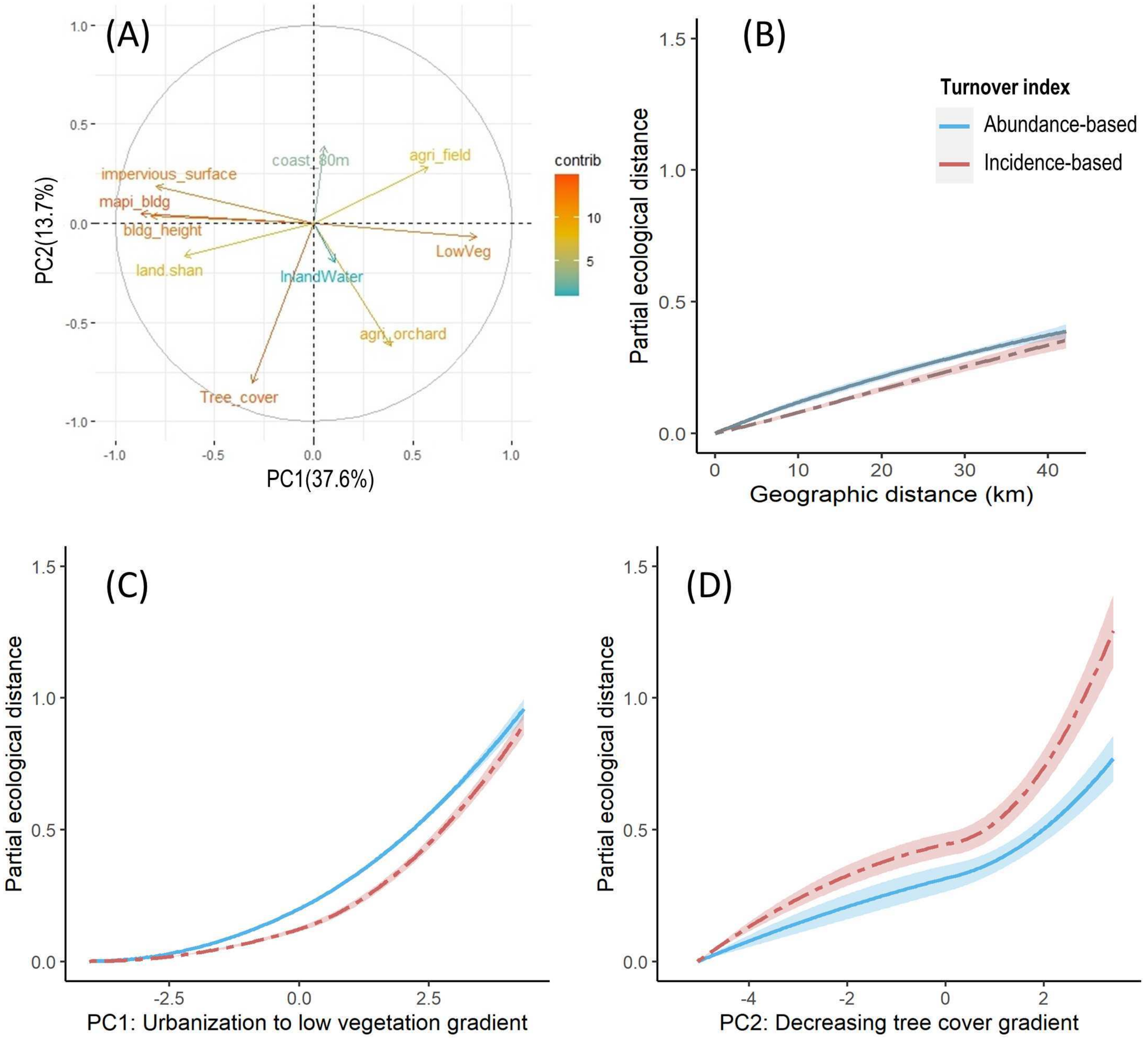

Arable field cover
Orchard cover
Building cover
Building height
Impervious surface cover
Landscape heterogeneity
Tree cover
Low vegetation cover
Vegetation height variation
Inland water cover
Coastal cover
-0.2
-0.1
0.0
0.1
GLM coefficient estimate (scaled)
Species group
Migrants
Synanthropes
Non-synanthropes

A. Sørensen index



B. Bray-Curtis index




(A)
PC2(13.7%)
PC1(37.6%)
1.0
0.5
0.0
-0.5
-1.0
-1.0
-0.5
0.0
0.5
1.0
coast_80m
agri_field
impervious_surface
mapi_bldg
bldg_height
land.shan
InlandWater
LowVeg
agri_orchard
Tree_cover
contrib
10
5
(B)
Turnover index
Abundance-based
Incidence-based
Partial ecological distance
1.5
1.0
0.5
0.0
0
10
20
30
40
Geographic distance (km)
(C)
Partial ecological distance
1.5
1.0
0.5
0.0
-2.5
0.0
2.5
PC1: Urbanization to low vegetation gradient
(D)
Partial ecological distance
1.5
1.0
0.5
0.0
-4
-2
0
2
PC2: Decreasing tree cover gradient

Supporting Information

Text S1: Validation of land cover representation in randomly distributed survey points

We used a clustering procedure of six environmental variables to form a typology of socio-ecological land cover strata, to validate that randomly distributed sample of 6% of the 100 m grid cells in the research area is representative of the socio-ecological heterogeneity in Tel Aviv District. We used a preliminary assessment of six environmental variables, all processed into 100 x 100 m resolution rasters. The variables included (sources of GIS layers detailed below): building cover, agricultural field cover, orchard cover, mean neighborhood building cover in a 500 x 500 m moving window, road cover score calculated by summarizing road per pixel, weighted according to the road class (e.g. highway, residential, etc.), and mean NDVI (normalized difference vegetation index; a proxy for vegetation cover). All variables were rescaled between 0 and 1.

Classification was performed using unsupervised random forest classification with k-means clustering. The procedure included three stages: (1) using the randomForest package[1] unsupervised random forest classification model to generate pairwise proximity values among a random sample of 1000 pixels[2]; (2) cluster the proximity values using k-means into a predetermined number of clusters; (3) use the clustering results as labels to train another random forest model, that is then used to predict the classification of the entire dataset. The main advantage of this clustering procedure is that it enables the use of random forest classification on large non-labeled dataset. Random forest is a highly efficient machine learning classification algorithm suitable for large datasets, that can detect non-linear relationships among variables[3]. Simple k-means and hierarchical clustering were tested as well as alternative clustering methods, but failed to identify some important land use features, such as roads. We determined the optimal number of clusters (k) as k=8 based on the average silhouette width and a visual examination of the classification results for k values of 3 to 10, in relation to each of the environmental variables and to a satellite image. We concluded that lower k value did not allow distinction between important socio-ecological features that we could visually identify, and higher values did not yield additional meaningful clusters. Since one cluster has comprised NA values that occur outside the research area boundaries, the classification ultimately included 7 land use clusters (fig. S1a 错误：引用源未找到). Finally, we compared the distribution of land cover classes in the sample to that of the entire district using a Chi-squared test and found them to be similar (fig. S1b; χ^2= 2.01, p-value = 0.92).

Sources of GIS layers: Buildings and roads extracted from OpenStreetMap GIS Layered data[4]; Agricultural field and orchard: vector-based layer of agricultural plots and their main crops produced by the Israeli Ministry of Agriculture (retrieved October 2019); NDVI calculated from a Sentinel-2 4-band multi-spectral satellite image from February 2019, with original resolution of 10 m[5].

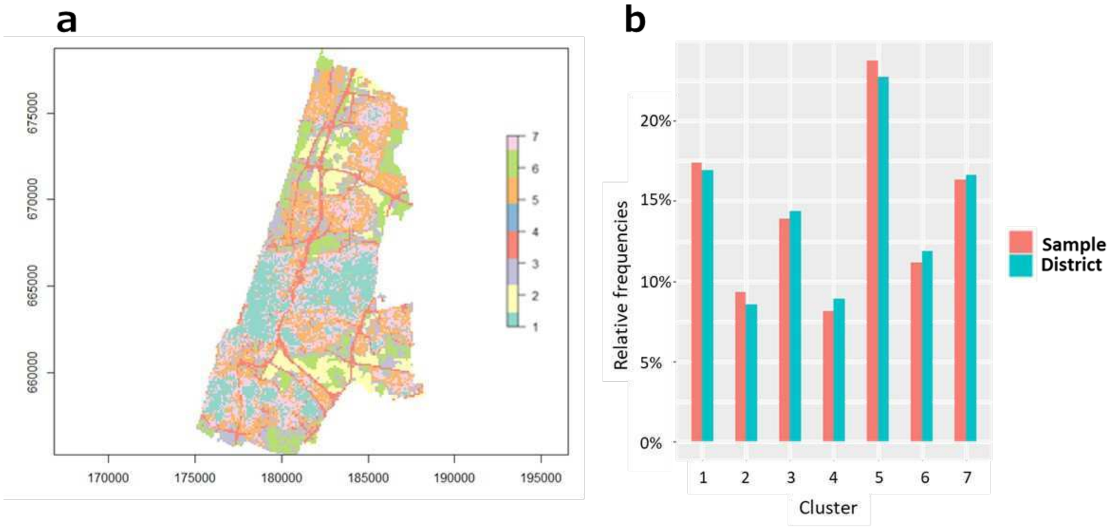


Figure S: a) The seven main land cover classes produced by an unsupervised random forest classification of multiple environmental variables with k-means clustering; **b)** The distribution of land cover classes in the randomly sampled grid cells, compared to their distribution in the entire district (χ^2= 2.01, p-value = 0.92).

Text S2: Vegetation cover and height layers

In order to identify vegetation cover in different photosynthetic states (i.e. both actively photosynthetic plants and dormant summer-deciduous shrubs), we performed a spectral signature classification using a high-resolution (0.25 m) 4-band multispectral orthophoto (red, green, blue and near infra-red) taken during April-June 2020. We first used spectral angle mapping with the R function "*sam*" from the "RStoolbox" package, to classify spectral signatures of different land cover types in the research area. The classification yielded five land cover types differing in their spectral signature (Fig. S2). Examining a sample of 100 pixels from each signature showed that while pixels classified as green vegetation were clearly distinct in their spectral signature from other land cover types, pixels classified as brown vegetation were somewhat overlapping with pixels classified as bare ground. Therefore, we manually corrected the classification of brown vegetation pixels that were less than 15% dissimilar from bare ground, as bare ground. Based on the updated pixel sample, the mean signature for each class is generated for each spectral band (Fig. S3). We manually identified and characterized the spectral signature of asphalt surfaces to provide an additional out-group that can improve the distinction between ground and brown vegetation. To validate the classification, we tested the classification of a sample of 518 points randomly distributed across the research area. As we were only interested in identifying vegetation, we visually examined whether the classification of vegetation (either green or brown) vs. non-vegetation was correct. Out of 518 points, 30 points could not be clearly identified visually and were therefore excluded. Of the remaining 488 points, 9 were classified incorrectly, therefore we determined a 98% accuracy of the classification.

The vegetation height layer was generated based on the vegetation cover layer, combined with a 3D point cloud representing surface height, derived from stereo imagery in a 0.25 m resolution. To assess vegetation canopy height, we: (1) estimated terrain height by identifying the minimal height within a coarser grid of 15 m^2 pixel size, (2) obtaining total surface height by identifying the maximal height in a finer grid of 1 m^2 pixel size, (3) subtracting the terrain height from the surface height in each 1 m^2 pixel classified as vegetation, to achieve canopy height[6].

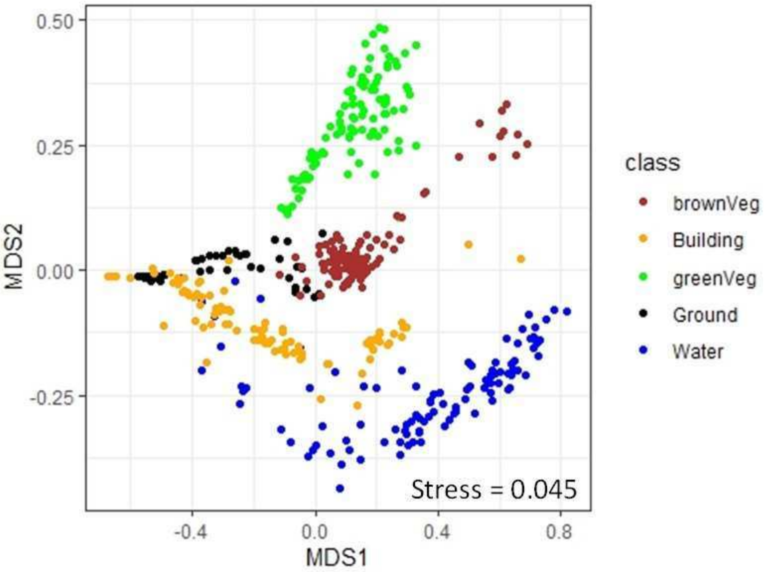


Figure S: Non-metric multidimensional scaling (NMDS) plot of a random sample of 100 pixels drawn from the multispectral orthophoto, showing their classification into five spectral classes determined through the spectral angle mapping procedure.

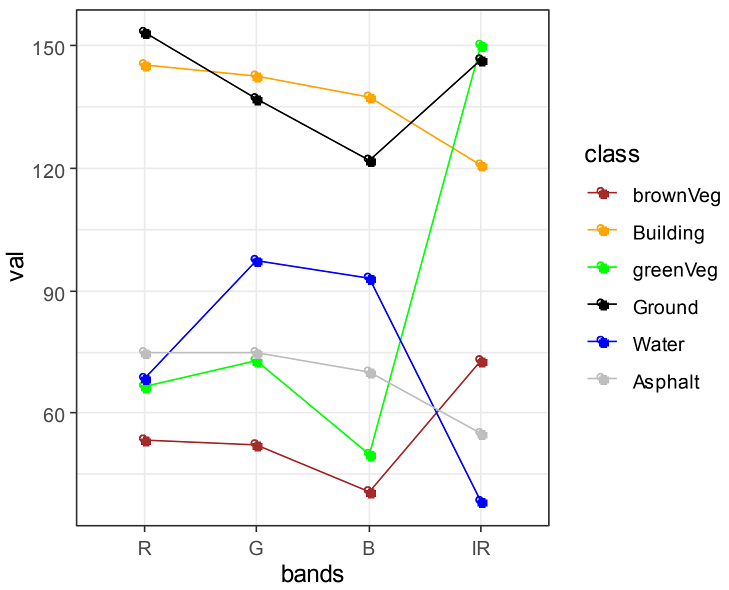


Figure S: The spectral signature, i.e. mean values of each spectral band, for the six land cover classes, including five classes identified the spectral angle mapping procedure and one identified manually to improve classification (Asphalt)

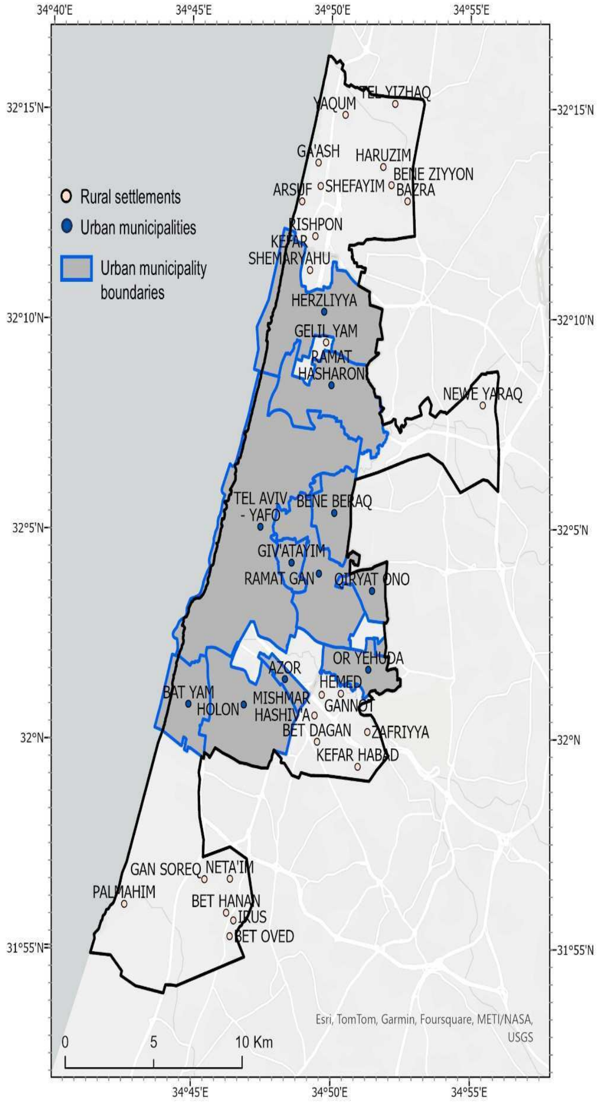


Figure S4: Map of the research area with names of cities and rural settlements

Table S1: Details of GIS layers and databases used in spatial analyses. All layers and databases were obtained for the extent of the research area.

Table S2: Species observed in the regional survey and their affiliation into one of three main species groups: synanthropic species (i.e., alien and urban exploiters), non-synanthropic species (i.e., urban adapters and avoiders) and migrants. Migrant species were determined based on the primary population status in Tel-Aviv region according to Shirihai (1996). Species synanthropy was determined following Shwartz et al. (2008) and Kark et al. (2007).

Species	**Group**
Accipiter brevipes	Migrant
Accipiter nisus	Non-synanthropic
Acridotheres burmannicus	Synanthropic (alien)
Acridotheres tristis	Synanthropic (alien)
Acrocephalus arundinaceus	Migrant
Acrocephalus schoenobaenus	Migrant
Acrocephalus scirpaceus	Migrant
Acrocephalus stentoreus	Non-synanthropic
Actitis hypoleucos	Migrant
Alauda arvensis	Migrant
Alcedo atthis	Non-synanthropic
Alectoris chukar	Non-synanthropic
Alopechon aegyptius	Synanthropic (alien)
Anas clypeata	Non-synanthropic
Anas crecca	Non-synanthropic
Anas platyrhynchos	Non-synanthropic
Anas querquedula	Migrant
Anas strepera	Non-synanthropic
Anthus campestris	Migrant
Anthus cervinus	Migrant
Anthus godlewskii	Migrant
Anthus pratensis	Non-synanthropic
Anthus spinoletta	Non-synanthropic
Anthus trivialis	Migrant
Apus affinis	Migrant
Apus apus	Synanthropic
Apus pallidus	Migrant
Aquila clanga	Non-synanthropic
Ardea cinerea	Migrant
Ardea purpurea	Migrant
Ardeola ralloides	Migrant
Asio flammeus	Migrant
Athene noctua	Non-synanthropic
Aythya nyroca	Non-synanthropic
Bubulcus ibis	Non-synanthropic
Burhinus oedicnemus	Non-synanthropic
Buteo (buteo) vulpinus	Migrant
Buteo buteo	Non-synanthropic
Buteo rufinus	Migrant
Cairina moschata	Synanthropic (alien)
Calandrella brachydactyla	Migrant
Calidris alpina	Non-synanthropic
Calidris minuta	Migrant
Calidris temminckii	Migrant
Caprimulgus europaeus	Migrant
Carduelis carduelis	Non-synanthropic
Carduelis chloris	Non-synanthropic
Cercopis daurica	Migrant
Cercotrichas galactotes	Migrant
Ceryle rudis	Non-synanthropic
Cettia cetti	Non-synanthropic
Charadrius dubius	Migrant
Charadrius hiaticula	Migrant
Chlidonias hybrida	Migrant
Ciconia ciconia	Migrant
Circaetus gallicus	Migrant
Circus aeruginosus	Non-synanthropic
Circus cyaneus	Non-synanthropic
Circus pygargus	Migrant
Cisticola juncidis	Non-synanthropic
Clamator glandarius	Non-synanthropic
Columba livia domestica	Synanthropic
Coracias garrulus	Migrant
Corvus cornix	Synanthropic
Corvus frugilegus	Non-synanthropic
Corvus monedula	Non-synanthropic
Coturnix coturnix	Migrant
Crex crex	Migrant
Cuculus canorus	Migrant
Cygnus atratus	Synanthropic (alien)
Delichon urbicum	Migrant
Dendrocopos syriacus	Non-synanthropic
Egretta garzetta	Non-synanthropic
Elanus caeruleus	Non-synanthropic
Emberiza caesia	Migrant
Emberiza calandra	Non-synanthropic
Emberiza hortulana	Migrant
Erithacus rubecula	Non-synanthropic
Falco naumanni	Migrant
Falco peregrinus	Non-synanthropic
Falco subbuteo	Non-synanthropic
Falco tinnunculus	Non-synanthropic
Ficedula albicollis	Migrant
Ficedula semitorquata	Migrant
Fringilla coelebs	Non-synanthropic
Fulica atra	Non-synanthropic
Galerida cristata	Non-synanthropic
Gallinago gallinago	Migrant
Gallinula chloropus	Non-synanthropic
Garrulus glandarius	Non-synanthropic
Halcyon smyrnensis	Non-synanthropic
Himantopus himantopus	Non-synanthropic
Hippolais olivetorum	Migrant
Hirundo rustica	Non-synanthropic

Carduelis spinus	Non-synanthropic
Carpodacus erythrinus	Migrant
Casmerodius albus	Non-synanthropic
Species	**Group**
Lanius minor	Migrant
Lanius nubicus	Migrant
Lanius senator	Migrant
Larus armenicus	Non-synanthropic
Larus cachinnans	Non-synanthropic
Larus genei	Migrant
Larus michahelis	Non-synanthropic
Larus ridibundus	Non-synanthropic
Locustella luscinioides	Migrant
Luscinia luscinia	Migrant
Luscinia megarhynchos	Migrant
Luscinia svecica	Migrant
Merops apiaster	Non-synanthropic
Merops persicus	Migrant
Milvus migrans	Non-synanthropic
Motacilla alba	Non-synanthropic
Motacilla citreola	Migrant
Motacilla flava	Migrant
Muscicapa striata	Migrant
Myiopsitta monachus	Synanthropic (alien)
Nectarinia osea	Non-synanthropic
Nycticorax nycticorax	Non-synanthropic
Oenanthe cypriaca	Migrant
Oenanthe hispanica	Migrant
Oenanthe isabellina	Migrant
Oenanthe oenanthe	Migrant
Oriolus oriolus	Migrant
Otus scops	Non-synanthropic
Pandion haliaetus	Migrant
Parus major	Non-synanthropic
Passer domesticus	Synanthropic
Passer hispaniolensis	Migrant
Phalacrocorax carbo	Non-synanthropic
Phalacrocorax pygmeus	Non-synanthropic
Philomachus pugnax	Migrant
Phoenicurus ochruros	Non-synanthropic
Phoenicurus phoenicurus	Migrant
Phylloscopus collybita	Migrant
Phylloscopus humei	Non-synanthropic
Phylloscopus inornatus	Migrant
Phylloscopus orientalis	Migrant
Phylloscopus sibilatrix	Migrant
Phylloscopus trochilus	Migrant
Platalea leucorodia	Migrant
Plegadis falcinellus	Non-synanthropic
Porzana parva	Migrant
Prinia gracilis	Non-synanthropic
Psittacula eupatria	Synanthropic (alien)
Psittacula krameri	Synanthropic (alien)
Pycnonotus xanthopygos	Non-synanthropic
Riparia riparia	Migrant

Iduna pallida	Migrant
Jynx torquilla	Migrant
Lanius collurio	Migrant
Species	**Group**
Streptopelia senegalensis	Synanthropic (alien)
Streptopelia turtur	Non-synanthropic
Sturnus roseus	Migrant
Sturnus vulgaris	Non-synanthropic
Sylvia atricapilla	Migrant
Sylvia borin	Migrant
Sylvia cantillans	Migrant
Sylvia communis	Migrant
Sylvia crassirostris	Migrant
Sylvia curruca	Migrant
Sylvia melanocephala	Non-synanthropic
Sylvia nisoria	Migrant
Sylvia rueppelli	Migrant
Tachybaptus ruficollis	Non-synanthropic
Tachymarptis melba	Migrant
Tadorna ferruginea	Non-synanthropic
Tringa glareola	Migrant
Tringa nebularia	Migrant
Tringa ochropus	Migrant
Tringa stagnatilis	Migrant
Tringa totanus	Migrant
Turdus merula	Non-synanthropic
Turdus philomelos	Non-synanthropic
Upupa epops	Non-synanthropic
Vanellus spinosus	Non-synanthropic

Saxicola maurus	Migrant
Saxicola rubetra	Migrant
Saxicola rubicola	Non-synanthropic
Serinus serinus	Non-synanthropic
Sterna albifrons	Non-synanthropic
Streptopelia decaocto	Non-synanthropic

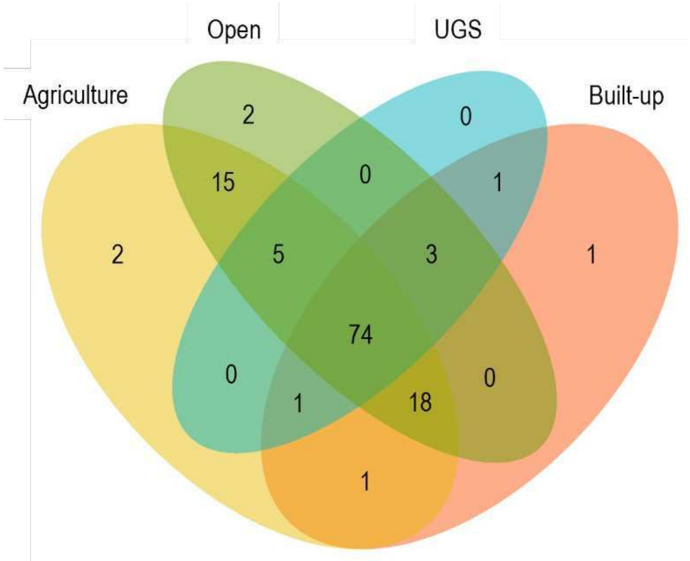


Figure S5: Overlap in species identities across the region’s four main habitats.

Table S3: ANOVA results for comparisons of mean α-diversity measures across the regions' main land covers. Adjusted p-values for differences in the observed means between pairs of land covers were determined using Tukey's HSD post-hoc tests (significance levels: * p < 0.05, ** p < 0.01, *** p < 0.001).

Species group	**α-diversity measure**	**F-statistic**	**Habitat mean difference**					
			built-agri	open-agri	UGS-agri	open-built	UGS-built	UGS-open
All species	Species richness	16.4***	-0.29	0.34	1.17***	0.63*	1.46***	0.83*
	Shannon diversity	11.3***	0.04	0.09*	0.09*	0.05	0.05	0.001
	Simpson diversity	9.3***	0.02	0.03*	0.03*	0.01	0.01	0.003
Synanthropic species	Species richness	556.9***	2.42***	-0.03	2.67***	-2.45***	0.26*	2.70***
	Shannon diversity	361.1***	0.56***	0.03	0.58***	-0.59***	0.02	0.55***
	Simpson diversity	228.2***	0.21***	0.02	0.22***	-0.20***	0.01	0.21***
Non-synanthropic resident species	Species richness	82.7***	-1.92***	0.33	-1.15***	2.25***	0.77***	-1.49***
	Shannon diversity	61.7***	-0.30***	0.06	-0.15**	0.36***	0.16***	-0.21***
	Simpson diversity	40.9***	-0.09***	0.02	-0.03	0.11***	0.06***	-0.05**
Migrants	Species richness	10.6***	-0.34***	0.07	-0.11	0.42***	0.23	-0.19
	Shannon diversity	7.3***	-0.12**	0.01	-0.002	0.13***	0.12*	-0.01
	Simpson diversity	6.4***	-0.07**	0.002	0.01	0.07**	0.08*	0.01

Table S4: GLM coefficient estimates for effects of local land cover variables (100-m scale), on species richness of different bird species groups (significance levels: * p < 0.05, ** p < 0.01, *** p < 0.001).

	All species	Synanthropic species	Non-synanthropic resident species	Migrants
Arable field cover	–0.183***	–0.128*	–0.260***	0.087
Orchard cover	–0.287***	–0.331***	–0.300***	–0.254*
Building cover	–0.289***	0.567***	–1.145***	–0.073
Building height	–0.002	–0.0001	–0.004*	0.004
Impervious surfaces	–0.317***	0.400***	–0.872***	–0.290
Landscape heterogeneity	0.227***	0.365***	0.219***	–0.141*
Tree cover	0.390***	0.033	0.582***	0.503
Low vegetation cover	0.273***	0.038	0.302***	0.321*
Vegetation height variation	–0.016***	0.007	–0.033***	–0.004
Inland water	0.404***	–0.304	0.551***	0.833*
Coastal cover	–0.849***	–0.437***	–1.062***	–0.254
X coordinate	0.318*	0.471	0.298	0.255
Y coordinate	0.248**	0.438**	0.178	–0.239

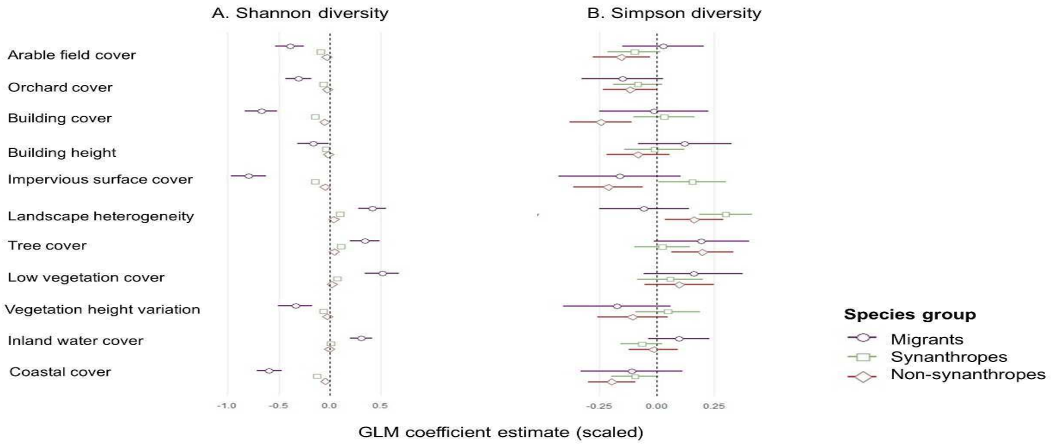


Figure S6: Standardized coefficient estimates (±0.95 CI) for local land cover predictor variables in six GLMs, each fitted for two α-diversity indices: (A) Shannon and (B) Simpson, of each of the three species group (synanthropes, non-synanthropic residents and migrants)

Table S5: ANOVA results for comparisons of mean β-diversity measures across the regions' main land covers. Adjusted p-values for differences in the observed means between pairs of land covers were determined using Tukey's HSD post-hoc tests (significance levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

β-diversity measure	**β-diversity component**	**F-statistic**	**Habitat mean difference**					
			built-agri	open-agri	UGS-agri	open-built	UGS-built	UGS-open
Sørensen	Total dissimilarity (β_{sor})	399.6***	-0.003***	-0.003***	-0.002***	0.001***	0.002***	0.001***
	Turnover (β_{sim})	2603.4***	-0.02***	-0.006***	-0.009***	0.018***	0.015***	-0.003***
	Nestedness (β_{sne})	2854.1***	0.021***	0.003***	0.008***	-0.018***	-0.013***	0.005***
Bray-Curtis	Total dissimilarity (d_{BC})	18.9***	-0.025***	-0.022***	-0.009	0.003	0.016***	0.013**
	Turnover ($d_{BC\text{-}bal}$)	18.5***	-0.043***	-0.013	-0.012	0.030***	0.021***	0.001
	Nestedness ($d_{BC\text{-}gra}$)	10.2***	0.018**	-0.008	0.003	-0.026***	-0.015*	0.011

Table S6: PCA variable loadings of local land cover variables for the two primary PC axes.

	PC1 (37.6%)	PC2 (13.7%)
Arable field cover	0.297718	0.243063
Orchard cover	0.20016	–0.52659
Building cover	–0.44915	0.043166
Building height	–0.42342	0.031363
Impervious surfaces	–0.40912	0.161041
Landscape heterogeneity	–0.33711	0.13909
Tree cover	–0.15964	–0.68746
Low vegetation cover	0.424195	–0.0583
Inland water	0.055689	–0.16759
Coastal cover	0.027032	0.333782

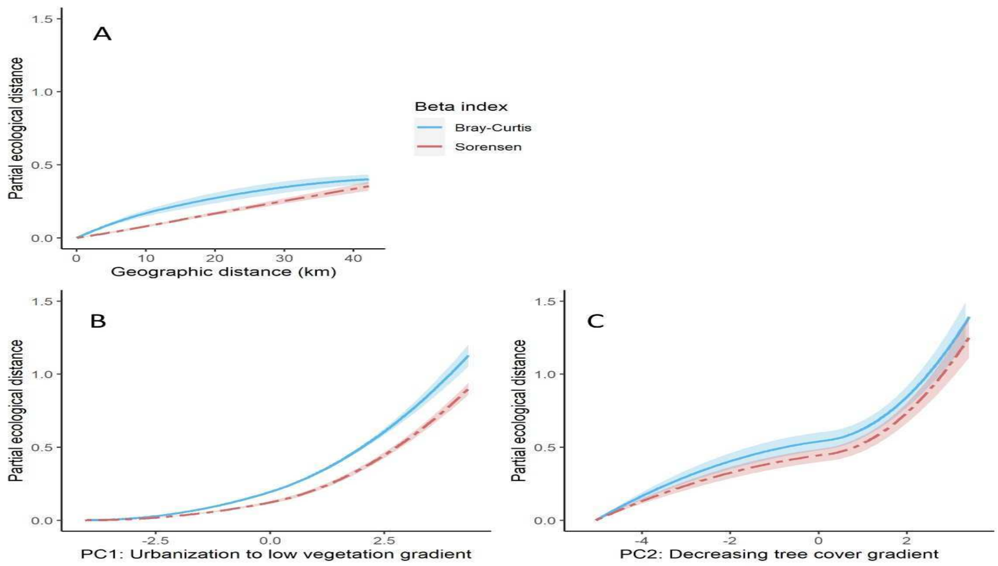


Figure S7: Generalized Dissimilarity Models' (GDM) fitted I-splines, corresponding to the magnitude of effect of environmental variables on beta-diversity (partial ecological distance), using two total β-diversity indices: Bray-Curtis (blue solid) and Sorensen dissimilarity (red dashed). Variables are: (B) Geographical distance, (C) PC1: urbanization to lower vegetation gradient, (D) PC2: decreasing tree cover gradient. Error bands represent model uncertainty. Curve height and slope are similar to those obtained in GDMs based on turnover components of these two β-diversity indices (Fig. 6).

Table S7: Relative occurrence of rarely occurring species in each of the regions' main land covers, for different "rarity" thresholds (i.e., percentage of points in which the species was recorded).

	Species occurring in <10% of points	Species occurring in <5% of points	Species occurring in <2.5% of points	Species occurring in <1% of points
Open	0.22	0.13	0.09	0.04
Agriculture	0.22	0.13	0.08	0.04
Built-up	0.07	0.03	0.02	0.01

UGS	0.13	0.07	0.04	0.02

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