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Disentangling the drivers of urban bird diversity in the non-breeding season: A general synthesis

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Abstract

Current knowledge about the impacts of urbanisation on bird assemblages is based on evidence from studies partly or wholly undertaken in the breeding season. In comparison, the non-breeding season remains little studied, despite the fact that winter conditions at higher latitudes are changing more rapidly than other seasons. During the non-breeding season, cities may attract or retain bird species because they offer milder conditions or better feeding opportunities than surrounding habitats. However, the range of climatic, ecological and anthropogenic mechanisms shaping different facets of urban bird diversity in the non-breeding season are poorly understood. We explored these mechanisms using structural equation modelling to assess how urbanisation affects the taxonomic, phylogenetic and functional diversity of avian assemblages sampled worldwide in the non-breeding season. We found that minimum temperature, elevation, urban area and city age played a critical role in determining taxonomic diversity while a range of factors—including productivity, precipitation, elevation, distance to coasts and rivers, socio-economic (as a proxy of human facilitation) and road density—each contributed to patterns of phylogenetic and functional diversity. The structure and function of urban bird assemblages appear to be predominantly shaped by temperature, productivity and city age, with effects of these factors differing across seasons. Our results underline the importance of considering multiple hypotheses, including seasonal effects, when evaluating the impacts of urbanisation on biodiversity.

KEYWORDS
biodiversity loss, bird assemblages, city age, migration, minimum temperature, urbanisation, winter ecology

1 | INTRODUCTION

More than half of the human population now resides in cities, with continued migration from rural to urban communities expected over the coming decades (United Nations, 2022). The speed and intensity of urban growth varies across geographic regions, and much of this land-use change is occurring in biodiversity hotspots (Cincotta et al., 2000). Consequently, urbanisation is considered one

of the major global drivers affecting biological diversity (Aronson et al., 2014), eco-evolutionary processes (Bonnet-Lebrun et al., 2020; Shochat et al., 2006) and ecosystem services (Marzluff et al., 2001). Previous analyses of urbanisation have rarely considered its wider effects on macroecological patterns in biodiversity. Most of our understanding of such patterns is based on studies conducted in natural- or seminatural sites (Gómez de Silva & Medellín, 2001; Hawkins, Field, et al., 2003; Hawkins, Porter, & Diniz-Filho, 2003). However, general patterns and processes observed in natural environments cannot be fully applied to urban areas (Aronson et al., 2014; Shochat et al., 2006), suggesting that a reconsideration of macroecological mechanisms is required, particularly as urban areas now cover an increasing proportion of the land (Batáry et al., 2018; Beninde et al., 2015; Marzluff et al., 2001).

Birds offer a well-established study system for assessing broad-scale impacts of urbanisation on species assemblages and their associated ecological functions, given the volume of data available from urban bird surveys worldwide, coupled with comprehensive phylogenetic and functional trait datasets for birds (Sol et al., 2017, 2020; Tobias et al., 2022). In natural habitats, previous studies have identified a range of macroecological patterns and processes structuring avian assemblages (Hawkins, Field, et al., 2003; Mittelbach et al., 2001). For instance, avian taxonomic diversity is positively related to Net Primary Productivity (NPP), providing a mechanistic explanation for the latitudinal diversity gradient (Pigot et al., 2016). Similarly, functional diversity correlates with NPP, as well as with land-use diversity (Martínez-Núñez et al., 2023). Different mechanisms may shape phylogenetic diversity, which appears to be related to historical factors (long-term climate stability) and topography (Voskamp et al., 2017). Whether these mechanisms explain urban macroecology remains uncertain, not least because bird assemblage data used in previous analyses were primarily sampled in the breeding season, and it is not clear whether they are generalisable to non-breeding birds (Rosenzweig, 1995). This cannot be assumed, since patterns of biodiversity appear to be seasonally dynamic rather than static (Newton, 2008; Somveille et al., 2015), with different mechanisms operating in the breeding and non-breeding seasons (Echeverría-Caro et al., 2022; Lepczyk et al., 2017; Neate-Clegg et al., 2023).

In temperate and Arctic regions, winter is the most critical season for many taxa, constraining their geographic distributions and causing mortality due to low food availability (Dinh et al., 2023; Järvinen & Väisänen, 1980; Root, 1988; Williams et al., 2015). Furthermore, winter temperatures have been increasing faster than spring temperatures over recent decades, especially at higher latitudes (IPCC, 2023). Accordingly, bird species' abundances and distributions have responded even more rapidly to changes to winter climatic conditions than to changes in summer conditions (Lehikoinen et al., 2021), causing a recent reorganisation of non-breeding avifauna (Quimbayo et al., 2024). However, previous analyses have focussed largely on populations in natural environments, while a growing body of evidence suggests that climatic or productivity-based constraints on bird distributions and abundances could be further altered in urban environments. In particular, climatic impacts could be ameliorated or intensified because cities are warmer than surrounding habitats (the "urban heat island" effect; de Albuquerque, Bateman, Boehme, Allen & Cayuela, 2021; Shochat et al., 2006; Tan & Li, 2015), and provide access to additional food resources during winter—including berry-bearing ornamental shrubs or trees and bird feeding stations—that are rare or even absent in more natural areas (Jokimäki & Suhonen, 1998).

As with macroecological analyses, most urban studies have focussed mainly on breeding bird assemblages (Aronson et al., 2014; Oliveira Hagen et al., 2017; but see Leveau et al., 2021), or on non-breeding assemblages in a specific restricted region (Leveau, Jokimäki, & Kaisanlahti-Jokimäki, 2017; Murthy et al., 2016; Tryjanowski et al., 2015). Importantly, urbanisation has been shown to decrease the taxonomic diversity of breeding assemblages from local (Katuwal et al., 2018; Tzortzakaki et al., 2018) to global scales (Aronson et al., 2014; Sol et al., 2014). In conjunction with overall species loss, urban environments often show a decrease in phylogenetic diversity (Ibáñez-Álamo et al., 2017; Morelli et al., 2016; Sol et al., 2017) and functional diversity (Matuoka et al., 2020; Sol et al., 2020). However, the wider impacts of urbanisation on the structure and function of non-breeding bird assemblages are still inadequately understood (Lepczyk et al., 2017; Neate-Clegg et al., 2023).

To explore the effects of urbanisation on the taxonomic, phylogenetic and functional diversity (hereafter, multifaceted diversity) of bird assemblages in the non-breeding season, we used published and unpublished community-level data on non-breeding landbirds observed in heavily urbanised areas worldwide, as well as corresponding data obtained from surrounding non-urban habitats. Landbird assemblages have been previously reported to be good bioindicators of the urbanisation continuum (Martin et al., 2012; Marzluff, 2017), they have a marked annual cycle that allows the study of temporal variation in community structure (Bonnet-Lebrun et al., 2020; Moreno-Contreras et al., 2019; Newton, 2008), and their non-breeding assemblages have been well-characterised, at least in the temperate zone (Hensley et al., 2019; Jokimäki et al., 2002; Quimbayo et al., 2024; Tryjanowski et al., 2015). Quantifying patterns in phylogenetic and functional diversity in cities at a macroecological scale allows us to test whether urbanisation has facilitated the presence of certain clades (Ibáñez-Álamo et al., 2017; Sol et al., 2017) or traits (Neate-Clegg et al., 2023; Sol et al., 2020). We used the world's cities as a replicated framework to study ecological and geographical variation in the non-breeding season (Martin et al., 2012). To understand the differences between urban and regional bird assemblages in multifaceted non-breeding avian diversity, we used a piecewise structural equation modelling framework (Lefcheck, 2016). We hypothesised that urbanisation would change non-breeding bird assemblages reducing multifaceted diversity relative to regional species pools. Overall, we tested a series of well-established macroecological hypotheses of the factors influencing multifaceted bird diversity in urban environments (Table 1). Identifying the worldwide impacts of urbanisation on the spatial patterns of multifaceted

TABLE 1 Main macroecological hypotheses assessed to explain the multifaceted diversity in non-breeding avian assemblages inhabiting urban habitats worldwide, their predictions, theoretical explanations, and predictors.

Hypothesis	Prediction	Explanation	Predictors
H1: Productivity (Benedetti et al., 2023; Hawkins, Field, et al., 2003; Hawkins, Porter, & Diniz-Filho, 2003)	Urban centres with higher productivity (available in the form of food) should harbour higher multifaceted diversity than low-productivity urban centres	Urban sites with higher energy support larger population sizes and carrying capacity, promoting higher chance of incidence for migratory species, and lower local extinction rates for permanent resident species	NDVI
H2: Energy-water balance (Batáry et al., 2018; Hawkins, Field, et al., 2003; Hawkins, Porter, & Diniz-Filho, 2003)	Urban centres with higher productivity (represented in form of food) and water availability should harbour higher multifaceted diversity than low-productivity urban centres with limited water availability	Urban sites located near migratory flyways with more energy resources and bodies of water (within or nearby) allow larger population sizes and carrying capacity, promoting higher speciation and seasonal colonisation events at lower cost, and with lower local extinction rates	NDVI + Precipitation + Distance to rivers + Distance to coasts
H3: Freezing tolerance (Hawkins, Porter, & Diniz-Filho, 2003; Root, 1988; von Humboldt, 1808)	Urban areas with higher temperatures and moderate precipitation at southern latitudes should support higher multifaceted diversity than urban centres with lower temperatures and high precipitation at northern latitudes throughout the winter season	The joint effects of temperature and precipitation limit the distributional ranges of species via physiological constraints and, in endotherms, limits the energy available for reproduction and migration. Overall, both variables would influence population sizes, allowing incidence of species with greater functional specialisation and phylogenetic divergence, and promoting higher extinction rates for lineages not adapted to urban life during winter conditions	Minimum temperature + Precipitation
H4: Elevation (Aronson et al., 2014; McCain, 2009; Montaño-Centellas et al., 2020)	Urban areas with more elevational heterogeneity should have higher multifaceted diversity with a wide window of functional specialization, compared to urban areas with more homogenous elevation. On the contrary, cities with homogeneous elevation levels tends to present lowest values of phylogenetic diversity	Elevational heterogeneity promotes colonisation events for year-round species and migrant birds, favouring functional divergence and specialization of phylogenetically close species at different elevation levels	Elevation + Distance to mountains
H5: Verdant old city (Aronson et al., 2016; Beninde et al., 2015; Echeverría-Caro et al., 2022; Kinnunen et al., 2022; Murgui, 2007; Norton et al., 2016)	Older and greener urban areas with compact shapes (e.g., perfect circle) and close to bodies of water should hold higher multifaceted diversity than younger urban areas with non-compact shapes (e.g., elongated shape) and limited water availability	Older urban areas in proximity of bodies of water tend to have remnant native and introduced vegetation, and have had more time to lessen the adverse impacts of urbanisation than younger cities with a low number of green and blue spaces due to anthropogenic pressures. These factors support larger population sizes of species adapted to urban life in greenish old cities in close proximity to coasts and rivers, promote lower extinction rates for year-round species, and increase seasonal colonisation events for migratory species. Coupled with that, any deviation from circularity will greatly decrease the amount of higher quality habitat for species occupying urban core areas	NDVI + Road density + Urban area + Urban shape + City age + Distance to rivers + Distance to coasts
H6: Human facilitation (Aronson et al., 2016)	Urban areas with more economic resources (in gross domestic product terms) should harbour higher multifaceted diversity than urban centres with lower economic conditions	Adequate social and economic management of urban areas will promote more structurally complex landscapes. Therefore, this pro-environmentally oriented governance in cities would facilitate colonization events to lineages with different evolutionary trajectories and functional specializations	Gross domestic product (GDP)
This study (an ad-hoc hypothesis)	Younger and moderately old urban areas with non-uniform temperature regimes at mid-elevation levels should exhibit higher taxonomic and phylogenetic diversity than very old urban areas at low or high elevational levels with homogeneous temperature regimes	Urban areas with favourable climatic regimes will have lower local extinction rates than urban areas with homogeneous climatic settings during the non-breeding season, if surrounding habitats harbour harsh environmental conditions. Increasing temperature (resulting from either heat island phenomenon or poor landscape management) will also reflects an increasing effect on energy resources (natural and human-provided food supplies) in cities	Minimum temperature + Elevation + City age + Urban area

(Continues)

TABLE 1 (Continued)

| Hypothesis	Prediction	Explanation	Predictors
	Furthermore, if these cities are both in close proximity with coasts and inland migratory flyways would have higher phylogenetic diversity	Coupled with that, if these urban centres are in relatively close proximity to the coasts and other inland migratory flyways, they would allow colonization events for migratory lineages adapted to urban life	Taxonomic diversity + Minimum temperature + Precipitation + Elevation + Road density + Gross domestic product + Distance to rivers + Distance to coasts
	In turn, if these urban centres have an elevated landscape complexity associated with both road density and higher productivity areas, they will have lower functional divergence	Nonetheless, since urbanisation favours certain functional traits allowing colonization events and decreasing local extinction rates, there will be a constraining effect on functional divergence	sesMPD + NDVI + Road density
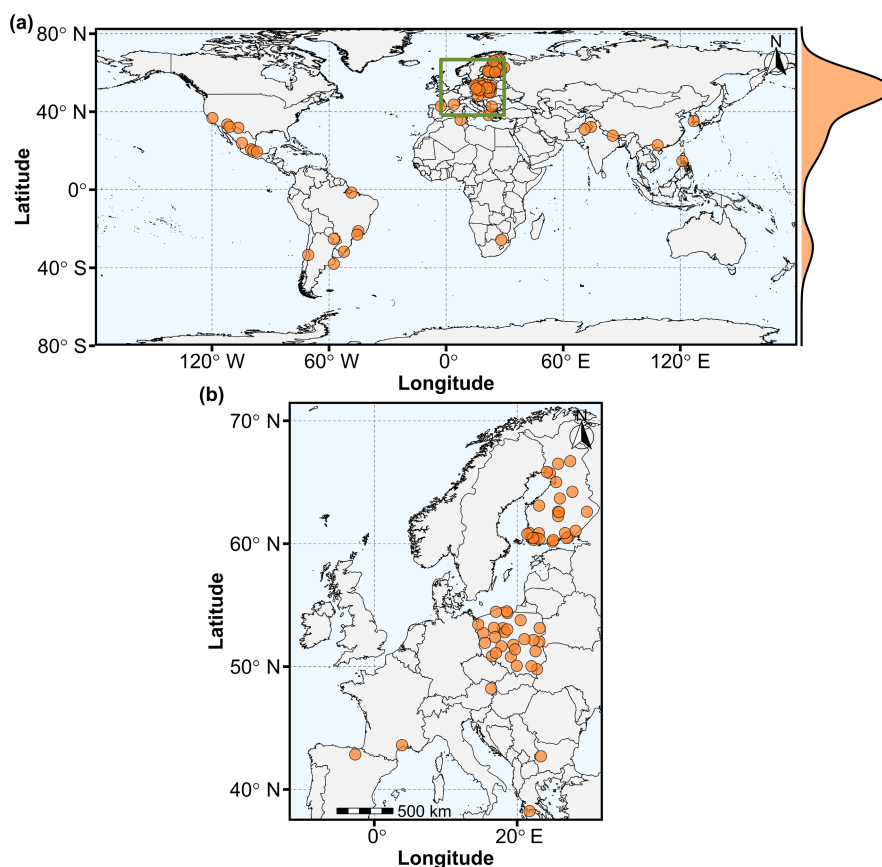
FIGURE 1 Geographic sampling of bird assemblages in cities (n = 81; see Table S1). (a) The ridge line on the right side shows the density of cities sampled as a function of latitude. The lower map (b) shows denser sampling of European cities.

diversity of non-breeding birds may assist in understanding macro-ecological patterns and processes both in human-dominated and more natural landscapes.

2 | MATERIALS AND METHODS

2.1 | Bibliographic search and selection of studies

We conducted literature searches following the guidelines of the Preferred Reporting Items for Systematic Reviews and Meta-analyses (PRISMA) 2020 statement for systematic reviews (Page et al., 2021). We used Web of Science, Scopus and Google Scholar to identify sources published in 2000–2020. For Web of Science, we performed a search on 4 March 2021 (in English language, reviewing both Spanish and English titles or abstracts) using an advanced Boolean operator string: TS = ((*urban* NOT disturbance* OR city OR cities OR town) AND (bird OR avian OR avifauna) AND (community* OR assemblage* OR biodiversity OR "species richness" OR richness OR diversity OR composition) AND (winter* OR temporal* OR seasonality*)). For the Scopus search engine (English language), we extracted published papers on 7 March 2021 using the query string: TITLE-ABS-KEY (urban* AND bird* OR avian* AND winter* OR seasonality* AND NOT disturbance). To complement those

sources, we also conducted targeted searches for relevant studies relating to two major regions for which few studies of urban ecology (Africa, India) using two languages (Spanish and English).

We also extracted sources from Google Scholar on 6 March 2021 using the following search string combination: (1) urban* bird* "species richness" community* (winter* OR temporal* OR seasonal* OR seasonality) -disturbance; (2) urbanisation urban city winter OR seasonality "bird communities" OR "avian assemblages" "India" -disturbance -virus; (3) urbanisation urban city winter OR seasonality "bird communities" OR "avian assemblages" "Africa" -disturbance -virus; (4) urbanización* OR urbano* OR "áreas urbanas" OR "ambientes antrópicos" OR ciudad* invierno* OR estacionalidad* "comunidades de aves" OR "diversidad de aves" OR composición "Aves" -disturbio -virus. The searches were restricted to peer-reviewed journal papers or book chapters as well as graduate theses. The search for the three main sources was restricted to the title, abstract, and keywords.

In addition to these exhaustive searches, we reviewed ornithological journals (*Emu*, *Ostrich*, *Huitzil*, and *Revista Brasileira de Ornitologia*) gathering urban ecology studies that were not captured by the aforementioned search engines. Studies had to meet four specific criteria to be included in the systematic review (Appendix S1). Then, we conducted a snowballing search strategy on the selected papers and pioneering macroecological studies (Aronson et al., 2014) to identify additional species lists. We contacted authors to request raw community-level data when it was not available in the publications. Finally, we retained a total of 29 articles which were identified to contain suitable data for our analyses (PRISMA flowchart in Figure S1). Additionally, we used our unpublished data from 18 Finnish cities, resulting in a total sample of 81 cities worldwide (Figure 1a; Table S1).

2.2 | Compiling avian assemblages from the non-breeding season

We included data from non-breeding species collected at any time within the non-breeding season, which we defined as December–February for the Northern Hemisphere and June–August for the Southern Hemisphere. The non-breeding season in the Northern Hemisphere coincides with the winter season, which at high (Finland) and mid-latitudes (North American cities) consist of snow cover and near-freezing temperatures (Williams et al., 2015), while the conditions in the Southern Hemisphere tend to be less severe (Dingle, 2008). In tropical regions, where precipitation varies much more strongly than temperature (Newton, 2008), the non-breeding season may coincide with dry periods. The timing of the dry season varies greatly across different tropical regions, and there may be more than one dry season per year. Our sampling included eight tropical cities (10%): seven in South America (e.g. Mar del Plata) and one in Africa (Pretoria). For a sake of comparison, we assigned tropical cities to non-breeding season based on online meteorological data from Weather Spark (2024).

The urban assemblages included all species recorded during surveys conducted between 2000 and 2016 (which coincides with the period of the environmental variables), that used standardised survey methods (e.g. atlas, point counts) over at least one non-breeding season (Table S2). The survey method was not included in the analyses because the spatial regressions used cannot include categorical variables. Avian assemblages represented species lists observed only from urban areas (percentage of built-up area >50%, building density >10 ha^{-1}, residential human density >10 ha^{-1}; defined by Marzluff et al., 2001) to make them as comparable as possible. Urban species lists were from heavily urbanised areas of each study city, and they did not contain data from species-rich suburban habitats. We excluded aquatic species (e.g. Anseriformes, Aequorlitornithes; Prum et al., 2015) from our analyses because these species were not consistently sampled, and because their occurrence is more dependent on wetland availability than factors related directly to urbanisation. We generated species accumulation curves to quantify inventory completeness (Figure S2a,b).

To evaluate whether there are differences between urban and regional assemblages, we did employ the "before-after control-impact" test (La Sorte et al., 2018). We considered both "before" and "control" conditions as the regional pools (an approximation of natural ecosystems), while "after" and "impact" conditions refer to urban pools (the impacts of urbanisation on structure and function of avian assemblages). By doing so, we estimated each city's regional species assemblages of non-breeding birds by using a fixed area surrounding the core area of the city (12,452 km^2; La Sorte et al., 2018). For this purpose, we used distributional maps of the world's birds (BirdLife International & Handbook of the Birds of the World, 2019) and the global avian invasions atlas (Dyer et al., 2017). The geoprocessing steps are described in Appendix S1.

To assess statistical differences ($p < .05$) in taxonomic diversity between urban and regional pools, we performed paired t tests in "stats" v.3.6.2 (R Development Core Team, 2021). We also analysed how the composition of species by avian Order changed (Δ) between urban and regional assemblages (methods described in La Sorte et al., 2018; Appendix S1).

2.3 | Phylogenetic diversity

To assess the impacts of phylogenetic uncertainty, we considered two avian phylogenetic trees to obtain phylogenetic divergence metrics (Tucker et al., 2017). We used phylogenetic tree distributions from BirdTree (Jetz et al., 2012) to generate consensus trees. We sampled 300 "Hackett backbone" (Hackett et al., 2008) stage 2 trees (9993 species). Then, we ran "TreeAnnotator" v.2.6 (Bouckaert et al., 2019) on the CIPRES Science Gateway portal to generate a maximum clade credibility (MCC) tree, applying the infer branch lengths option by setting node heights equal to the "common ancestor" node heights of the target tree. In addition, we used the recently published avian phylogeny based on next-generation sequencing data from Prum et al. (2015) to build alternative consensus trees for our species list. Following Cooney

et al. (2017), we merged the species-level taxonomic treatment of Jetz et al. (2012) to the backbone phylogeny derived from Prum et al. (2015) to build an additional MCC tree. Finally, we pruned both MCC trees to generate distributions for species in our data set ($n = 2175$ species). We calculated one dimension of phylogenetic information (Tucker et al., 2017): divergence (standardised effect size of mean pairwise distance [sesMPD]; Webb et al., 2002). A detailed account of the quantification of phylogenetic divergence (sesMPD) is provided in Appendix S1. To assess differences ($p < .05$) in phylogenetic divergence between regional pools and urban pools, we performed paired t tests in "stats" v.3.6.2 (R Development Core Team, 2021).

2.4 | Functional diversity

To characterise functional diversity in the context of assemblage divergence (in terms of community structure arraignment, either overdispersion or clustering trends; Webb et al., 2002), we quantified the standardised effect size of functional mean pairwise distance (sesFMPD) following a dendrogram-based approach (Podani & Schmera, 2006). Functional divergence metrics have been particularly useful in determining the impacts of urbanisation on avian assemblages (Oliveira Hagen et al., 2017). Therefore, we used different data sets consisting of morphological traits such as beak length, depth and width, wing chord, first secondary feather length, tarsus length, tail length, and hand-wing index (Tobias et al., 2022), geographic range size (BirdLife International & Handbook of the Birds of the World, 2019), and diet type and foraging strata traits (Wilman et al., 2014). Further details of our functional trait dataset and associated methods is provided in Appendix S1.

We also assessed differences ($p < .05$) in functional divergence between urban and regional species pools using paired t tests in "stats" v.3.6.2 (R Development Core Team, 2021). To quantify functional differences between species pools, we performed an analysis of the 12 functional traits in which we averaged the values for each raw trait across species for each urban and regional assemblage (La Sorte et al., 2018; Appendix S1).

2.5 | Environmental predictors

To test our hypotheses about the influence of environmental predictors on multifaceted non-breeding avian diversity, we extracted values for several predictors. We used the CHELSAcruts dataset to obtain raster layers of monthly minimum temperatures (°C) and precipitation (mm) over the period 2000–2016 (1 km^2 of resolution; Karger et al., 2017). We converted the raw raster layers to matching units for monthly minimum temperatures (divide degrees Celsius values by 10) and precipitation (kg m^{-2} into mm), respectively.

Monthly estimates of Normalised Difference Vegetation Index (NDVI) were downloaded from the Terra Moderate Resolution Imaging Spectroradiometer Vegetation Indices (MOD13A3) v.6 (resolution 1 km^2; Didan, 2015). For NDVI data, values ranged between −0.1 and 0.9 (the higher the value, the greener the land). Areas with no data were excluded for analytical purposes. To ensure that our inferences are directly comparable to the results of previous macroecological studies conducted in cities (Pautasso et al., 2011), we use NDVI instead of the Net Primary Productivity Index (NPPI). NDVI is well-established as the most widely used index to detect changes in vegetation characteristics at different spatial scales (Benedetti et al., 2023; Leveau et al., 2020; Nieto et al., 2015).

The elevation values were obtained using a digital elevation model (USGS, 2021). We used elevation in our modelling procedure because it is a major determinant of climate and biodiversity (McCain, 2009; Montaño-Centellas et al., 2020). Also, elevation has also commonly used in urban birds' studies to infer "topographic heterogeneity" (Aronson et al., 2014).

In the case of urban attributes, we downloaded the global vector data set of current road infrastructure (Meijer et al., 2018). This shapefile was converted into a road density raster at the same resolution as the other GIS layers. The city age was the difference between the establishment year of a city (e.g. year founded, obtaining of city rights) and the year in which the bird surveys finished in its respective published study. We gathered the dates at which each city was established or founded from Encyclopedia Britannica (Britannica, 2022), other internet sources, and published literature. For a proxy of socio-economic factors influencing urban diversity (Aronson et al., 2016), we used the annual GDP (gross domestic product) layers (Chen et al., 2022). We averaged the values across the pixels within each city polygon for the annual rasters corresponding to the years during which the city was surveyed for birds. All spatial data were converted into the Behrmann projection (~900×900 m of resolution in the case of rasters) for downstream analyses. Environmental values for each city were sampled by averaging the values across the pixels within each city polygon for the months corresponding to the months surveyed in its respective study.

Urban area and urban shape were calculated using R-custom scripts and raster layers (both population grid and built-up surface) retrieved from the Global Human Settlement Layer project (Florczyk et al., 2019). Both rasters (~250×250 m of resolution) were converted into binary maps using a conservative threshold (values >59.37). They were subsequently merged to obtain a single map for each city. Since many of the cities have been established in convenient locations (near bodies of water), we decided to include (Euclidean) distance-based predictors. Consequently, distance (km) to the rivers and coasts (Natural Earth; Kelso & Patterson, 2009), and global mountain regions (Rahbek et al., 2019) were calculated by measuring the distance from the geographic coordinates of a city to the nearest polygons of the corresponding vector layer.

All geoprocessing and visualisation steps of spatial data were done using ArcGIS v.10.4.1 (ESRI, 2015), QGIS v.3.16.9 (QGIS Development Team, 2021), and the following geospatial packages in R v.4.1.0 (R Development Core Team, 2021): "ggmap" v.3.0.0 (Kahle & Wickham, 2013), "ggplot2" v.3.4.3 (Wickham, 2016), "raster" v.3.4-13 (Hijmans, 2021), "rgeos" v.0.5-5 (Bivand & Rundel, 2020), "rgdal" v.1.5-23 (Bivand et al., 2021) and "sf" v.1.0-14 (Pebesma, 2018).

2.6 | Structural equation models

To account for the hierarchical nature of direct and indirect effects, we used piecewise structural equation modelling (pSEM) to investigate the relationships among multiple response and predictor variables using the R-software v.4.1.0 (R Development Core Team, 2021). pSEM allows the simultaneous evaluation of multiple causal relationships in a single hypothetical network in which the variables could be interrelated (García-Andrade et al., 2021; Lefcheck, 2016; Skeels et al., 2020). We used pSEM to analyse the direct effects of environmental factors on taxonomic diversity (TD~environment), as well as the indirect effects of the environment, TD, and sesMPD under two scenarios (Figure S3): via direct effects of TD and environment on sesMPD (sesMPD~TD+environment), and direct effects of sesMPD and environment on sesFMPD (sesFMPD~sesMPD+environment). Minimum temperature (Zuckerberg et al., 2011) and primary productivity (NDVI; Leveau et al., 2018) are thought to influence the structure of urban bird assemblages during the non-breeding conditions. Thus, we fitted two additional equations where we assessed the indirect effects of environment on any diversity metric (Figure S3). Specifically, we evaluated direct effects of environment (abiotic and urban physical factors) on minimum temperature (TMIN~environment), and on NDVI (NDVI~environment).

Taxonomic diversity itself may also have an influence on sesMPD beyond the direct statistical expectations outlined above (Yaxley et al., 2023). Therefore, even though we have corrected for the direct effect of species richness on MPD and FMPD by using standardised effect sizes, it is still expedient to investigate its direct effects on phylogenetic and functional metrics (Yaxley et al., 2023). Additionally, there are good reasons to assume that functional traits are phylogenetically conserved for urban avian assemblages (Callaghan et al., 2019), so we included sesMPD as a predictor for sesFMPD in our modelling approaches. Details on treatment of environmental variables (Table S3), spatial correlations between predictors and diversity metrics (Tables S4–S6), pSEM theoretical background (Figure S3), and simultaneous autoregressive models (SARs, Dormann et al., 2007; Table S7) are provided in Appendix S1.

The final pSEM consisted only of theoretical relationships supported as significant by our analyses. Both theoretical and final pSEM were plotted using the *grViz* function in "DiagrammeR" v.1.0.6.1 (Iannone, 2020). We calculated the total standardised effect size of explanatory variables on predictors as the sum of direct and indirect effects for each variable (Shipley, 2000). Indirect effect sizes were obtained by multiplying the standardised coefficients of indirect paths on each explanatory variable (Shipley, 2000). For those predictors with more than one indirect path, we calculated the total indirect effect as the sum of its partial effects (Shipley, 2000). Once the minimum model was obtained, we evaluated this hypothesis (in terms of AIC and performance [Nagelkerke pseudo-R^2]) against other macroecological hypotheses (Table 1) using the same SARs parameters that led us to the final pSEM for a better comparison.

3 | RESULTS

3.1 | Compilation of community-level data

Most of the data were from the Northern Hemisphere (Figure 1a; Table S1). Specifically, Europe contained the largest number of samples in the present study ($n=58$, Figure 1b), while Africa was underrepresented ($n=2$). There were no studies conducted in Oceania that met our criteria.

3.2 | Taxonomic diversity

For the 81 cities, we recorded 548 landbird species, 303 genera, 70 families and 14 Orders during the non-breeding season. The most species-rich families were Emberizidae ($n=43$) and Tyrannidae ($n=40$). The most species-rich Orders were Piciformes ($n=33$) and Columbiformes ($n=25$). Details on the effects of survey methods (Table S2) and sampling effort (Figure S2a,b) are available in Appendix S1.

Taxonomic diversity differed broadly among regional pools (mean=96.123, SD=87.236, range=36–449) and urban pools (mean=21.506, SD=18.845, range=6–83). The urban pool showed lower species richness compared to the regional pool ($t_{80}=8.698$, $p<.001$; Figure 2a). The difference in the percentage of species varied in 23 Orders between urban and regional assemblages ($F_t=43.758$, $p<.001$; Figure 3). Relative to regional assemblages, urban assemblages had on average lower proportions of Galliformes (land fowl), Strigiformes (owls), Accipitriformes (raptors), Piciformes (woodpeckers) and Falconiformes (falcons), whereas a higher proportion of Columbiformes (pigeons and doves) and Passeriformes (perching birds) was detected in urban than regional assemblages.

3.3 | Phylogenetic diversity

We found a significant positive correlation in the sesMPD calculated using Hackett's versus Prum's backbones ($r=.983$, $t=69.158$, $p<.05$, df=160, $n=162$). Therefore, all downstream analyses were performed using Prum's backbone. The regional pools had higher values (mean=−0.582; SD=1.707, $n=81$) of sesMPD than the urban pools (mean=−2.012; SD=1.193, $n=81$; $t_{80}=9.092$, $p<.001$; Figure 2b). The regional pools generally showed a random phylogenetic composition, whereas the urban pools showed a clustering phylogenetic composition (Figure 2b).

3.4 | Functional diversity

Regional species pools had higher sesFMPD values (mean=0.896; SD=0.901, $n=81$) than urban species pools (mean=−0.754; SD=0.789, $n=81$; $t_{80}=16.688$, $p<.001$; Figure 2c). In broad terms, we found a generalised clustering pattern for urban assemblages.
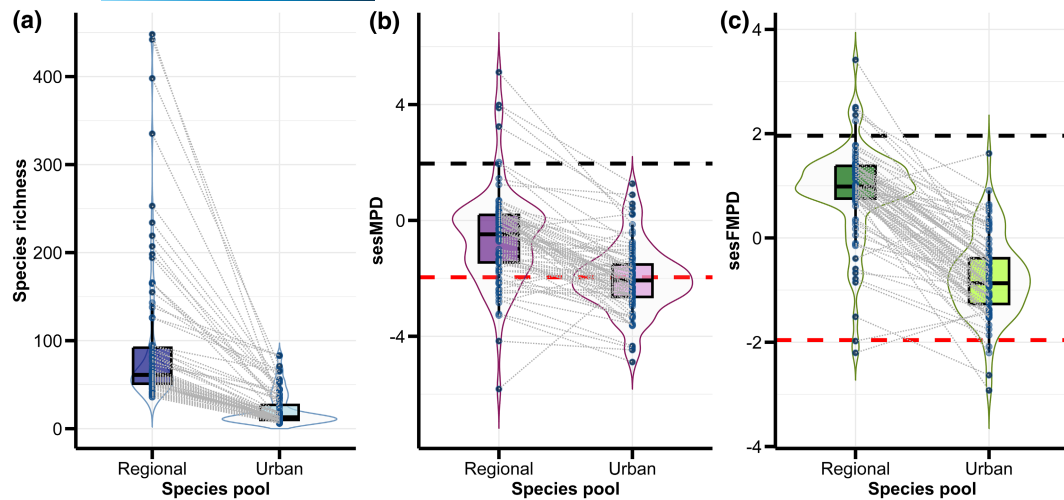
FIGURE 2 Boxplots depicting (a) taxonomic diversity (species richness), (b) phylogenetic divergence (sesMPD), and (c) functional divergence (sesFMPD) of the regional and urban species pools during the non-breeding season. The dashed lines indicate the thresholds for patterns of overdispersion (black) and clustering (red) of species assemblages.

Mean body mass for species of regional assemblages (mean = 329.66 g, SD = 120.21 g, $n = 81$) was higher than in urban assemblages (mean = 151.02 g, SD = 53.45 g, $n = 81$; $t_{80} = -13.481$, $p < .001$). Mean distribution range size was greater for species in urban assemblages (mean = 32,254,124 km^2, SD = 11,878,134 km^2, $n = 81$) relative to regional assemblages (mean = 23,879,541 km^2, SD = 8,167,852 km^2, $n = 81$; $t_{80} = 12.399$, $p < .001$). Difference in the mean variation of the morphological traits between the two assemblages varied among the eight diet categories ($F_t = 34.569$, $p < .001$; Figure 4a). The difference in the mean percentage diet composition between urban and regional assemblages varied among categories ($F_t = 94.426$, $p < .001$; Figure 4b). Urban assemblages presented on average significantly higher mean percentage diet composition of carrion, fruit, nectar and seeds (Figure 4b). The difference in the mean percentage use of foraging strata between urban and regional assemblages varied among foraging categories ($F_t = 17.734$, $p < .001$; Figure 4c). Urban assemblages had on average lower mean prevalence of below water surface and water surface, but a higher mean percentage use of understorey.

3.5 | Structural equation models

Based on our best-fitting pSEM using SARs (Fisher's $C = 69.893$, df = 58, $p = .136$, AIC = 141.893; Figure 5a), four explanatory variables had significant direct standardised effect sizes (values within parentheses) on taxonomic diversity: minimum temperature (0.511), elevation (0.398), urban area (0.304) and city age (−0.140). Only precipitation, GDP, and the distance to coasts had an indirect effect on taxonomic diversity, mediated by their direct effects on minimum temperature (Figure 5b; Table S8).

In the case of the sesMPD (Figure 5a), the environmental variables that explained the highest positive direct scores were minimum temperature (0.318), distance to coasts (0.278), road density

(0.222) and distance to rivers (0.140). Moreover, elevation, GDP, taxonomic diversity, and precipitation had direct negative relationships with sesMPD (Figure 5a). sesFMPD had a direct positive relationship with sesMPD (0.604) and road density (0.228), but a negative relationship with NDVI (−0.248) (Figure 5a). Total effect sizes for each diversity metric are provided in Figure 5b–d (Table S5). Detailed relationship between multifaceted diversity and some relevant predictors, respectively, are given in the Figures S4–S7. Results of minimum models against macroecological hypotheses is available in the Tables S8–S11.

4 | DISCUSSION

Our results provide quantitative evidence of the various ways that urbanisation decreases and constrains the worldwide distribution of multifaceted non-breeding avian diversity. Urban taxonomic diversity followed a well-defined latitudinal pattern, decreasing around 40–60°N. Meanwhile, phylogenetic and functional diversity showed clustering for urban assemblages. Harsh climate conditions (minimum temperature), urbanisation-related features (road density, city age, or urban area) and proximity to bodies of water (long distance to coasts or rivers) were the main environmental drivers of spatial variation of taxonomic, phylogenetic, and functional diversity during the non-breeding season. Productivity (NDVI) had a direct effect on functional divergence, but not on other diversity metrics. Our results differ partly from the results obtained earlier from more natural areas and breeding season. These studies have indicated that evapotranspiration is the most relevant factor influencing on avian diversity in natural areas (Hawkins, Porter, & Diniz-Filho, 2003), and temperature seasonality and NDVI seasonality have been suggested to be the most important factors shaping the diversity of migrant assemblages during the breeding season (Somveille et al., 2015).
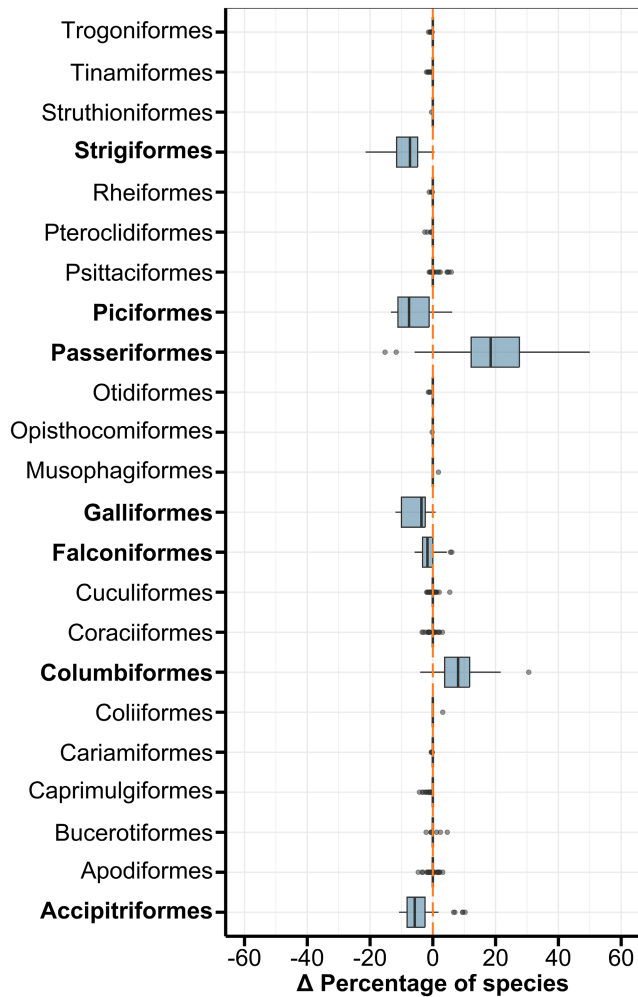
FIGURE 3 The difference in the percentage of species in 23 avian Orders between urban and regional assemblages from 81 cities (Table S1). Positive values indicate that urban is greater than regional, and negative values indicate that urban is less than regional. The avian Orders in bold text contain distributions that differ significantly from zero on average based on one-sample t tests ($p < .001$).

FIGURE 4 The difference in the mean percentage use of (a) eight morphology-based categories, (b) ten diet categories, and (c) seven foraging strata categories between urban and regional species assemblages for 81 cities (Table S1). Positive values indicate that urban is greater than regional, and negative values indicate that urban is less than regional. The functional traits in bold text contain distributions that differ significantly from zero on average based on one sample t tests ($p < .001$).

4.1 | Taxonomic diversity

In overall, 25% of the species of the regional pools was detected in urban area. This proportion is greater than observed in corresponding breeding season study (20%; Aronson et al., 2014). Probably, milder micro-climate and more predictable and abundant anthropogenic resources attract birds to settle in cities especially during the non-breeding season (Jokimäki & Kaisanlahti-Jokimäki, 2012).

Our results indicated that urbanisation represented a disadvantage for several groups (e.g. Galliformes, Strigiformes) during the non-breeding season. These results differ from previous urban global-scale analyses focussing on the breeding season. La Sorte et al. (2018) indicated that Galliformes was the only landbird group negatively affected by urbanisation. However, that study did not consider nocturnal birds in their analyses, making the comparison between breeding and non-breeding assemblages difficult. In our
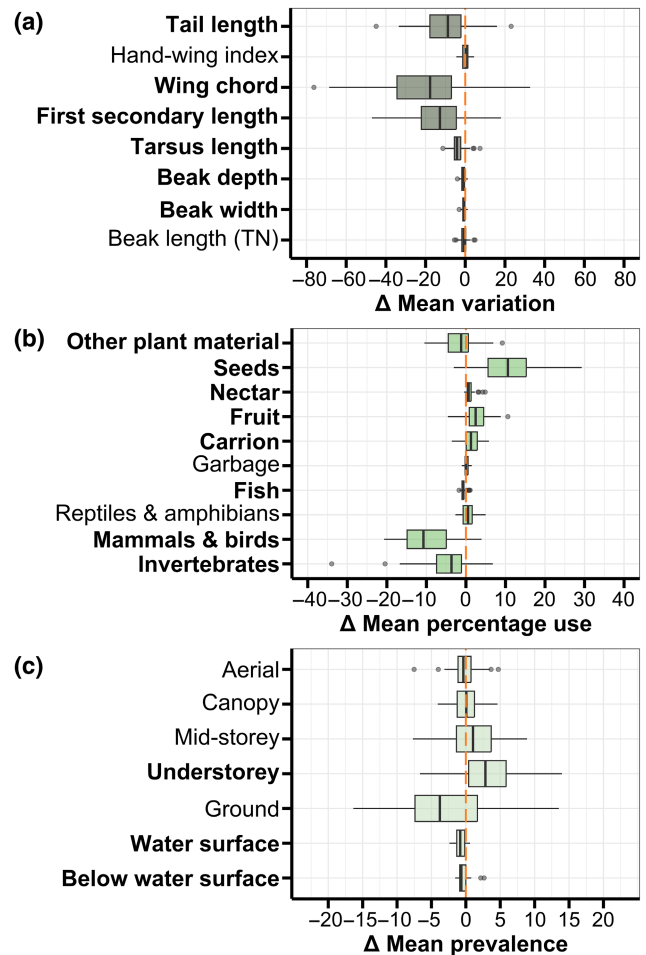
study, one potential reason why the owl assemblages (Strigiformes) were negatively impacted in cities is that heavily built urban areas do not have suitable hunting areas for them (Dziemian et al., 2012). As most owls are nocturnal species, light-pollution will reduce their foraging possibilities (Orlando & Chamberlain, 2023). Besides, urban noise will be disadvantage for predators using sense of hearing when hunting (Fröhlich & Ciach, 2019). Urbanisation has been detected to impact negatively on diurnal raptors (Accipitriformes and Falconiformes) diversity and abundance partly due to habitat loss and collisions (Hogg & Nilon, 2015; Sorace & Gustin, 2009). However, we think that the situation will be changed in the near future. Some raptor species will inhabit cities because they are not persecuted therein anymore, and they have there an adequate food supply (Chace & Walsh, 2006). Yet, their occurrence in highly urbanised areas depends on their surrounding population density (Leveau et al., 2022). Due to stable urban food and
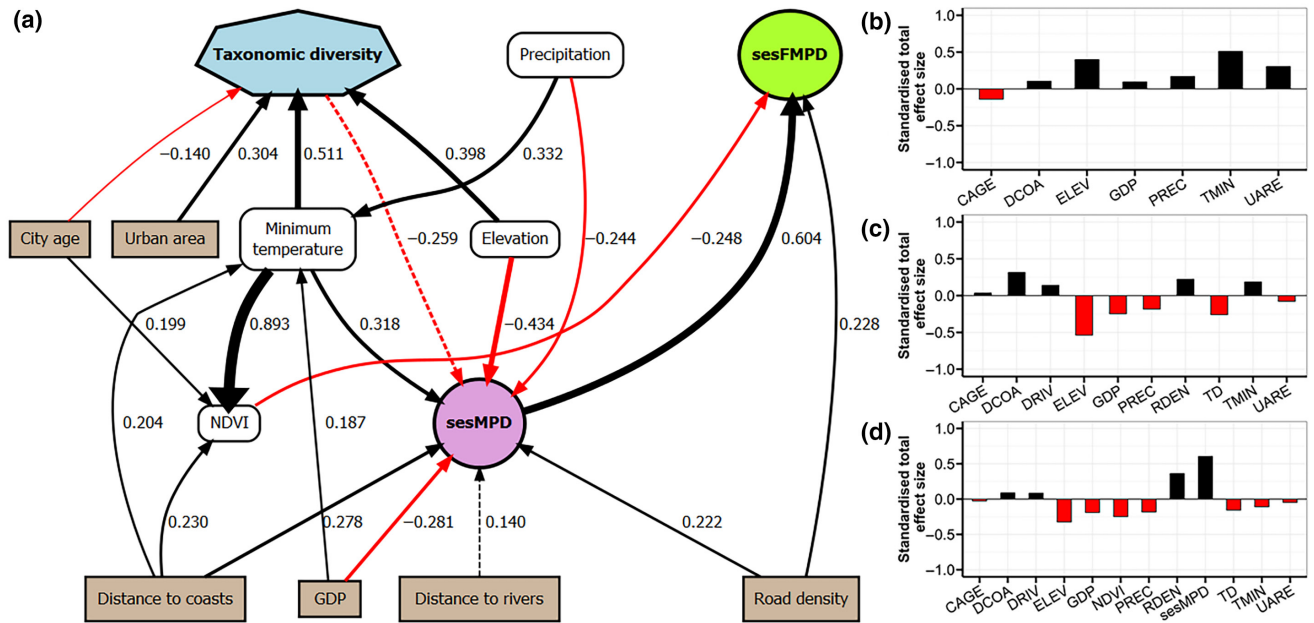
FIGURE 5 (a) Final piecewise structural equation model for drivers of non-breeding landbird assemblages in cities worldwide. Single-headed arrows represent causal pathways. Black arrows indicate positive effects and red arrows negative effects. Solid lines represent the significant paths ($p < .05$) and dashed lines indicate non-significant paths ($p > .05$). Numbers denote the standardised prediction coefficients for each causal path, and arrow thickness is proportional to their magnitude. The standardised total effect size of every variable on the (b) taxonomic diversity, (c) phylogenetic divergence, and (d) functional divergence was calculated as the sum of the direct and indirect path coefficients. CAGE, city age; DCOA, distance to coasts; DRIV, distance to rivers; ELEV, elevation; GDP, gross domestic product; NDVI, Normalised Difference Vegetation Index; PREC, precipitation; RDEN, road density; sesFMPD, standardised effect size of functional mean pairwise distance; sesMPD, standardised effect size of mean pairwise distance; TD, taxonomic diversity; TMIN, minimum temperature; UARE, urban area.

nesting conditions as compared to rural ones, the urban life habits may locally provide superior alternatives than the rural ones (Solonen, 2008). Urbanisation also filters woodpeckers by limiting habitat-specialists due to scarcity of dead wood resources in cities (Fröhlich et al., 2022). Conversely, the overrepresentation of some groups in cities could be related to their trophic characteristics. For example, some avian families, such as Passeridae (Old World sparrows, snowfinches, and relatives), include many seed eaters whose diets are likely supplemented by the availability of seeds in cities due to artificial feeding of birds during the non-breeding season (Jokimäki & Suhonen, 1998). Typical urban-exploiters (Blair, 1996) such as the Rock Pigeon (*Columba livia*, Columbiformes) and House Sparrow (*Passer domesticus*, Passeriformes) showed the highest proportions in cities, matching with reports from the breeding season in urban environments (La Sorte et al., 2018).

We found a decrease in species richness relative to their respective regional pools, coinciding with the earlier studies at multiple spatial scales (global scale: Aronson et al., 2014; Pautasso et al., 2011; Sol et al., 2014; local scale: Katuwal et al., 2018; Tryjanowski et al., 2015; Tzortzakaki et al., 2018). Species richness during the non-breeding season showed a decreasing ceiling with increasing latitudes towards Northern Hemisphere ($n = 81$ cities, Figure S4a). The trend in Asia appears also to be negative although the sample size is too small to draw any firm conclusions ($n = 6$, 15–35°N). The results of previous urban ecology studies differ in

terms of the relationships between latitude and urban avian species richness. In North America, winter taxonomic diversity decreased towards the north (Murthy et al., 2016), while across European cities the pattern was in the opposite direction, with species richness increasing with latitude (Ferenc et al., 2014). Still other studies have found no appreciable latitudinal gradient in species richness in non-breeding assemblages across European cities (Jokimäki et al., 1996; Tryjanowski et al., 2015) or in breeding assemblages across South American cities (Bellocq et al., 2017). The situation can be different outside Europe. Unfortunately, we are unable to find any studies from Asia that have analysed latitudinal trend of taxonomic diversity at city-level. Albeit, Chen and Wang (2017) found a positive relationship between latitude and phylogenetic diversity for cities in China. One potential explanation for this a disparity of outcomes is that effects are scale-dependent, such that different factors control taxonomic diversity at different spatial scales (when comparing cities of different biogeographic provinces, Leveau, Jokimäki, & Kaisanlahti-Jokimäki, 2017). Thus, considering urbanisation at a worldwide scale is more likely to detect differences in effect size between species-poor biogeographic provinces in the Northern Hemisphere, where detrimental effects are expected to be more accentuated, versus similar latitudes in the Southern Hemisphere, where effects are expected to be relatively milder. Unfortunately, our data did not include enough cities south of 40°S latitude to provide a robust test of this hypothesis.

The urban species pools had an asymptote-like relationship relative to the regional pools (Figure S5i), increasing up to a regional richness of ~100 species and urban richness of ~40 species, and then remaining stable. This asymptotic relationship is suggestive of saturated assemblages in cities, where it is hypothesised that biotic interactions (usually competition) limit community richness (Cornell & Lawton, 1992; Ricklefs & Schluter, 1993). This pattern contrasts with the proportional relationship between avian local and regional species pools ("type I," unsaturated expectation) that is generally found under natural conditions (Cornell, 1993).

Several characteristics of urbanised ecosystems make them likely to show saturated assemblages. First, they represent a semi-permeable barrier to invasion by species from surrounding areas, such that some species are able to advance toward the city centre—either gradually or as a function of well-defined thresholds to specific variables—while others are excluded (MacGregor-Fors, 2010). Second, they have a relatively high probability of being colonised by a few core generalist species (Suhonen et al., 2022) that tend to monopolise the majority of artificial energy inputs, to the detriment of rare and common migratory and winter visitors. Finally, positive interactions such as flocking facilitate the use of aggregated resources in urban areas and vigilance against possible predators such as cats, dogs, or approaching humans (Callaghan et al., 2019; Croci et al., 2008). To the best of our knowledge, our finding is the first study to report saturated (as opposed to unsaturated) assemblages in urban environments during any season.

4.2 | Phylogenetic and functional diversity

Our findings indicate that non-breeding urban bird assemblages were associated with small-sized species (fewer large bodied species, fewer long-billed species), and fewer species with narrow or restricted distributions than their surrounding regional assemblages. At the same time, there was significant presence of diet-related traits that were favoured by urban ecosystems during the non-breeding season: high incidence of granivores, nectarivores, frugivores, scavengers and species that forage in the understorey. This coincides, in part, due to species able to use feeding sites are abundant during winter in Finnish cities (Jokimäki & Suhonen, 1998). Nonetheless, this finding contrasts as those expected, as it is often stated that urbanisation favours omnivorous birds (Walker & Shochat, 2010). This was also contrary to our expectation, since it has been previously reported that the tree canopy is a preferred feeding stratum for wintering birds inhabiting cities (Amaya-Espinel & Hostetler, 2019). Furthermore, our results also contrast with findings for breeding bird assemblages, where urban assemblages had on average higher mean percentage use of understorey, mid-storey, canopy and aerial strata than regional counterparts (La Sorte et al., 2018). There are only a few studies that evaluate vertical habitat use by birds in cities (Antikainen, 1992; Mikami et al., 2022), and it is possible that vertical use differs between seasons.

Supporting our predictions, cities exhibited significantly lower phylogenetic and functional diversity than chance, which denoted a generalised clustering pattern. We expected urban species to be filtered from the regional pools, allowing closely related species to co-exist and adapt to the prevailing environmental conditions in cities. Most non-breeding birds have broad distributional ranges and are often considered habitat generalists (Somveille et al., 2015), which facilitates occurrence in poor-vegetated areas such as urban ecosystems (Amaya-Espinel & Hostetler, 2019; Martin et al., 2012). This is also well supported by global-scale analyses comparing urban assemblages with paired non-urban (natural or agricultural; Ibáñez-Álamo et al., 2017; Sol et al., 2020; but see Oliveira Hagen et al., 2017) or regional counterparts (La Sorte et al., 2018). However, the avian assemblages of many South American cities had a pattern of dispersed structure. Tropical areas are characterised by hosting phylogenetically overdispersed assemblages, in contrast to those of temperate regions, which are mainly phylogenetically clustered (Yaxley et al., 2023). In general, old lineages occur more frequently in the Neotropical and Afrotropical regions (Voskamp et al., 2017), which harbour large numbers of old taxa. Our results partially support a previous city-level analysis that showed phylogenetic randomness and functional clustering patterns during the breeding season (Leveau, 2021). In addition, we found support for studies that report phylogenetic clustering during the non-breeding season (Lees & Moura, 2017).

4.3 | Piecewise structural equation modelling

Our pSEM-based results are generally in line with pioneering studies of urban breeding assemblages (Aronson et al., 2014; Oliveira Hagen et al., 2017; Pautasso et al., 2011), although it is difficult to draw direct comparisons because of important methodological differences. In our study, four predictors (minimum temperature, elevation, urban area and city age) drove the spatial variation of the non-breeding taxonomic diversity in urban areas. At a global scale, temperature has long been recognised as a driver of species richness in natural environments (Hawkins, Porter, & Diniz-Filho, 2003); minimum temperature, specifically, limits the distributions of wintering birds throughout the Northern Hemisphere (Zuckerberg et al., 2011).

Applying a robust linear regression framework, Aronson et al. (2014) reported that anthropogenic features (landcover, city age), rather than abiotic conditions, are the main drivers of bird species within cities. Although that study used the species density as a dependent variable and extracted the temperature values at a coarser resolution, they also detected a positive relationship between both variables. Parallel to findings under natural conditions (Hawkins, Porter, & Diniz-Filho, 2003; von Humboldt, 1808), we suppose that temperature is one the most important predictors of diversity patterns in urban environments, regardless of the season of the year.

Our results fit in part with the "freezing tolerance" hypothesis, which proposes that climatic factors (temperature and precipitation) directly influence on taxonomic diversity (Hawkins, Porter, & Diniz-Filho, 2003), whereas precipitation had indirect effects only on this metric in our study. Warmer temperatures in temperate and Arctic cities thin the snow despite harsh conditions persisting in surrounding areas, allowing non-breeding birds easier access to food resources (Møller, 1983). Furthermore, long-distance migrants tended to spend the winter in warmer climate niches (Dufour et al., 2020). It is important to highlight that most of the cities in our study were located in latitudes ranging from 19 to 66°N, where a high concentration of non-breeding species richness has been documented (Karr, 1980; Somveille et al., 2015).

Disentangling the impacts of primary productivity and climatic constraints is challenging (Gaston & Blackburn, 2000; Rosenzweig, 1995). The current literature shows contrasting and biogeography-dependent results. On the one hand, it is generally thought that occurrence and abundance of birds in specific geographical areas during the non-breeding season is mainly dependent on food availability, especially at northern latitudes (Jokimäki et al., 1996; Jokimäki & Kaisanlahti-Jokimäki, 2012; Tryjanowski et al., 2015). Urban areas provide a large amount of artificial food resources that are not available in more natural environments (Norton et al., 2016), which could result in an increasing incidence of certain clades and functional groups (small-sized granivorous birds; Ciach & Fröhlich, 2017).

Minimum temperature and food resources appears be more important during the non-breeding season especially in Europe than breeding season. At northern low temperature and short winter days, the role of finding enough food is important. For example, in Finland (>64°N), birds have high survival rates if they have enough food to compensate for low temperatures during winter (Broggi et al., 2021; Jokimäki et al., 1996; Jokimäki & Suhonen, 1998). This pattern also fits cities of Britain, as the number of feeders provided in a garden had a greater influence on taxonomic diversity than either winter temperature or local habitat factors (Plummer et al., 2019). On the other hand, in a regional-scale feeding site study conducted in North America (38–50°N) indicated that minimum temperature was a more important factor than supplemental food sites in modifying wintering bird distributions in urban settings (Zuckerberg et al., 2011). Notably, most species were more likely to visit supplemental food stations at warmer sites that were characterised by less snow cover and lower urbanisation (Zuckerberg et al., 2011). Coinciding with Pautasso et al. (2011), our study provides evidence that minimum temperature is more important than NDVI during the non-breeding season in urban environments worldwide, at least under a taxonomic diversity perspective (Fraixedas et al., 2015).

In accordance with our predictions, NDVI only had a negative impact on sesFMPD when sesMPD was included as a predictor in the model. Assuming that NDVI represents a food supply (natural and anthropogenic sources) for non-breeding birds, it is possible that the increased energy supply allows for better thermoregulation.

Consequently, this thermoregulation allowing them to survive harsh climates by ingesting food resources that are abundant in the cities. Our finding did not support previous results for breeding birds from European (Benedetti et al., 2023) and South American (Leveau et al., 2020) cities, or other global-scale analyses (Oliveira Hagen et al., 2017). Broad-leafed trees and shrubs drop their leaves during autumn at higher latitudes (Suhonen & Jokimäki, 2019), which it possibly limits energy supply in urban ecosystems. Besides, highly urbanised areas with entirely impervious surface cover are expected to have a net primary production near zero (Shochat et al., 2006). In this context, we found little support for a latitudinal diversity gradient based on NDVI alone as previously reported for breeding assemblages in natural ecosystems (Hawkins, Field, et al., 2003; Hawkins, Porter, & Diniz-Filho, 2003) or urban ecosystems at continental-scale (Benedetti et al., 2023). Nonetheless, NDVI has been associated with an increase of non-breeding avian taxonomic diversity in tropical urban areas (Leveau et al., 2018), coinciding with our analyses testing the "productivity" hypothesis (Tables S9–S11). The role of NDVI is probably masked by the anthropogenic food resources in urban environments, and therefore we assume that NDVI will influence negatively only for functional divergence during the non-breeding season.

City age had a negative influence on taxonomic diversity as expected (Aronson et al., 2014). As the city gets older, then more areas will be built during the years, leading for loss and fragmentation of green areas, and consequently, leading to species loss. Also, when the city area enlarge, green areas in cities will be more isolated from the surrounding natural areas. So, young cities might have more species than old cities. There can be also a time-lag effect in species disappearing in young cities. However, mature vegetation is predominant in old cities, and this might correspondingly increase resources and species richness (Norton et al., 2016).

Urban features can also dictate functional diversity metrics (Oliveira Hagen et al., 2017). Our outcomes are partially aligned with this premise, given that road density positively influenced a functional clustering pattern for non-breeding assemblages. As the road network is more complex, it tends to lead to greater fragmentation of available habitat within a city. Greater road density would also increase the local temperature ("urban heat island"; Trombulak & Frissell, 2000), potentially favouring plants (understorey shrubs) with a higher tolerance to increased temperature. Specifically, many understorey or scavenger birds may become attracted to roadsides due to edge effects, if the availability of any relevant resource is markedly higher close to roads (Morelli et al., 2014).

Our results indicated that phylogenetic clustering directly increased in cities near rivers and coasts. This might be related to the historical establishment of cities in biodiversity-rich places near bodies of water (Bosker & Buringh, 2017; Carter, 1977). Several migratory flyways used by landbirds are closely linked to coastlines (Echeverría-Caro et al., 2022; Somveille et al., 2015). Resources such as lush vegetation and high arthropod abundance tend to be more available along coastlines (Lefebvre & Poulin, 1996), which could provide food for many overwintering birds. In our study, the

closest cities to the coasts presented the strongest clustering for species-poor assemblages. Therefore, coastlines represent suitable stopover sites during the non-breeding season, while rivers act as inland buffer zones for urban non-breeding species, allowing them to survive unsuitable regions. Proximity to water could similarly benefit resident species with small home ranges, with increasing distance from water acting as a soft geographic constraint. Thus, proximity to bodies of water appear to be positively affecting phylogenetic and functional divergence in these assemblages (Figures S6 and S7).

Elevation had a positive influence on taxonomic diversity and a negative influence on phylogenetic divergence. Urbanisation has historically extended on the plains and mostly occurred in the lowlands (Carter, 1977). If cities are mostly young, then there has been little time for urbanisation to impede the occurrence of clades with specific altitudinal tolerances. Aronson et al. (2014) identified a negative relationship between altitude and taxonomic diversity in breeding assemblages, which contrasted with our finding. This could be because the cities analysed in this study receive a large influx of both long-distance migrants and altitudinal migrants. It is possible that certain short-migrant species are already adapted to cities. On the contrary, urban-exploiters (House Sparrow) avoid high-altitude cities such as La Paz, Bolivia (Leveau, Leveau, et al., 2017). Thus, assemblages at higher elevations often represent a smaller subset of the overall species pool than lowland assemblages. Consequently, phylogenetic divergence decreased with elevation, a pattern expected by the gradual loss of lineages with increasing elevation (Montaño-Centellas et al., 2020).

GDP had a negative influence on phylogenetic diversity, which suggests that regardless of adequate landscape management, there will be a filtering against certain evolutionary lineages according to expectations (Asafu-Adjaye, 2003). If bird feeding (expected to be a relevant driver of avian taxonomic diversity) is related to socio-economic status, then number of bird feeders per city could be an alternative for human facilitation hypothesis testing (Aronson et al., 2016). Unfortunately, the lack of suitable data for each city does not allow us to delve into this topic.

Like all ecological studies, our study had some limitations. One of these shortcomings was that we did not incorporate artificial light, noise, and feeding, which could influence the outcomes (Aronson et al., 2016; Morelli et al., 2021). We were also unable to include estimates of bird abundances, which Suhonen and Jokimäki (2019) have proposed may be important. Furthermore, we did not incorporate the duration of monitoring effort as a predictor, as the implemented spatial regressions cannot consider categorical variables. Although these factors are interesting avenues for future urban ecology research, they are outside the scope of this study. In this spirit, future within-city level studies should feasibly address these limitations by incorporating data on species abundances other than only presence data per month and/or season so that they can be addressed in studies at broader scales. It is also necessary to have an up-to-date database of the number of bird feeders per city, as this variable could be influencing the

capture of multifaceted avian diversity in urban areas especially during the non-breeding season.

Another shortcoming of this study is the underrepresentation of urbanised ecosystems from the Global South. Certainly, regional biodiversity and urban features (city structure, the percentage of green spaces) differs between European cities and urban centres from Asia or Africa (Reynolds et al., 2021). So, it would be essential focus on mega- and highly populated cities located within biodiversity hotspots to a better understanding of macroecological patterns in urban environments.

5 | CONCLUSIONS

In broad terms, urban avian assemblages are at least partly independent from the regional species pool during the non-breeding season. We found significant environmental filtering of avian clades and functional traits during that season. Our hypothesis suggests that minimum temperature played a critical role in taxonomic diversity, while elevation, proximity to bodies of water, socio-economic and urban features, and productivity act under phylogenetic and functional contexts. Even when we modified the macroecological hypotheses to fit urban conditions, none of them performed better than our models for every biodiversity metric. All of these patterns are the joint result of historical and contemporary processes that have contributed to a high diversity of ecological assemblages within cities. It is important to improve the management of urban growth to improve urban habitat for birds, and mitigate the detrimental impact of urbanisation on the ever-smaller remaining area of pristine natural ecosystems.

AUTHOR CONTRIBUTIONS

Israel Moreno-Contreras: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; resources; visualization; writing – original draft; writing – review and editing. **Jukka Jokimäki:** Conceptualization; data curation; investigation; methodology; project administration; resources; supervision; writing – review and editing. **Marja-Liisa Kaisanlahti-Jokimäki:** Data curation; writing – review and editing. **Lucas M. Leveau:** Conceptualization; data curation; writing – review and editing. **Jukka Suhonen:** Conceptualization; data curation; methodology; writing – review and editing. **Joseph A. Tobias:** Data curation; writing – review and editing. **Piotr Tryjanowski:** Data curation; writing – review and editing.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in fig-share at https://doi.org/10.6084/m9.figshare.26065606.v2.

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SUPPORTING INFORMATION

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