



Research Article

Sealed surfaces limit bird diversity, whereas tall structures may support abundance of some species, while both filter traits in urban landscapes

Tamás Lakatos^{a,*}, José Javier Jiménez-Albarral^b, Teodor J. Purger^c, Jenő J. Purger^c,
Krisztina Sándor^d, Gábor Seress^{e,f}, Péter Batáry^a

^a "Lendület" Landscape and Conservation Ecology, Institute of Ecology and Botany, MTA–HUN–REN Centre for Ecological Research, Vácrátót, Hungary

^b Servicio Regional de Investigación y Desarrollo Agroalimentario (SERIDA), Ctra. AS-267, PK 19, Villaviciosa, Asturias E-33300, Spain

^c Department of Ecology, Faculty of Sciences, University of Pécs, Pécs, Hungary

^d Balaton Uplands National Park Directorate, Csopak, Hungary

^e HUN–REN–PE Evolutionary Ecology Research Group, Veszprém, Hungary

^f Behavioural Ecology Research Group, University of Pannonia, Veszprém, Hungary

ARTICLE INFO

Keywords:

Body mass
Community-weighted means
East-Central Europe
Foraging strategy
Habitat heterogeneity
Insectivory
Nesting sites
Species richness
Urban densification
Urban verticality

ABSTRACT

The use of vertical space by avian species remains a relatively unexplored area in urban ecology. Although the impacts of horizontal urban structures, such as sealed surfaces, are well understood, the influence of building height on bird communities is less clear, especially in Central Eastern Europe. We explored how three-dimensional urbanisation influences species richness, abundance, and key functional traits. We selected five cities in western Hungary, with 20 sites per city, using a 2×2 factorial design that combined two structural variables: building height (low vs. high) and sealed surface cover (low vs. high). We conducted point counts at 100 sites and assigned functional traits to each bird species, including adult and nestling diet, foraging technique, nesting site, migration status, and body mass. Species richness decreased with higher sealed surface, but was not affected by building height, while bird abundance increased with building height, but remained unaffected by sealed surface. Community-weighted means (CWMs) of nestling diet indicated a decline in insectivores with increased sealing. Foraging strategy shifted towards high-level foragers in areas with taller buildings. Nesting site CWM increased vertically with both building height and sealing. CWM body mass also increased with building height, with larger-bodied birds dominating tall structures. Our findings highlight that urban verticality, alongside surface sealing, filters bird communities both taxonomically and functionally. Therefore, incorporating three-dimensional habitat structure is essential for understanding urban biodiversity loss. These results suggest that vertical densification may support bird communities only if combined with low surface sealing and sufficient habitat heterogeneity including a diversity of native trees and bushes.

Introduction

While the majority of the world's population is now living in urban areas, natural landscapes are increasingly disturbed or even vanished (Aronson et al., 2014). This dramatic alteration is contributing to the global decline in terrestrial biodiversity, with avian populations being particularly vulnerable to the impacts of anthropogenic change (Tscharntke & Batáry, 2023). As the global conversion of land use continues, more people are settling in or near urban areas (Pellissier et al., 2012). Therefore, it is crucial to focus on maintaining ecosystem services within cities (McDonald et al., 2013).

Birds are widely recognised as ideal ecological indicators in urban environments because their diverse ecological roles and high sensitivity to habitat alterations allow them to reflect the impacts of urbanisation on local biodiversity (Pena et al., 2023; Taylor et al., 2013). Additionally, their relative abundance, detectability, and ease of monitoring make them practical for assessing how urban structural changes affect species composition and community functioning (Morelli et al., 2021). Urbanisation typically reduces species richness and results in a compositional shift toward generalist and urban tolerant species, often leading to biotic homogenisation (Sorace & Gustin, 2008; Tryjanowski et al., 2020). However, abundance may increase or remain stable across the

* Corresponding author.

E-mail address: lakatos.tamas@ecolres.hu (T. Lakatos).

<https://doi.org/10.1016/j.baae.2026.03.002>

Received 31 July 2025; Accepted 4 March 2026

Available online 5 March 2026

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increasing urban gradients due to a few adaptable species thriving in modified environments (Batáry et al., 2018). These phenomena is often accompanied by the loss of functionally specialised taxa, as urban environments act as ecological filters that favour species with specific trait syndromes suited for disturbed and fragmented conditions (Crocì et al., 2008; Lakatos et al., 2022; Meffert & Dziock, 2013).

Birds not only vary taxonomically across urban gradients but also functionally, through different traits such as diet, foraging techniques or nesting location (Evans et al., 2011; Grilo et al., 2022). To better understand the urbanisation induced ecological shifts, functional trait-based approaches may act as a powerful tool to complement traditional taxonomic metrics. Traits provide mechanistic insight into how different species respond to environmental filtering and, more importantly, how these changes affect ecosystem functioning in total (Gallé & Batáry, 2019). While general patterns of urban filtering are known (e.g., dietary specialist are more vulnerable than generalists (Lakatos et al., 2022)), less is understood about the trait-specific and landscape-specific mechanisms behind these patterns, particularly in Central and Eastern Europe.

Most urban studies have focused on green space quantity or connectivity, while finer-scale features of urban form (e.g., vegetation structure and building height) remain underexplored. Recent studies show that incorporating variables like vegetation height and volume, and building height, can better explain urban bird diversity and community composition, as tall or dense buildings often reduce habitat quality, while complex vegetation promotes diversity (Arévalo et al., 2022; Fairbairn et al., 2025; Yu et al., 2025). Thus, urban verticality and three-dimensional structure likely play key but often overlooked roles in shaping bird communities (Re et al., 2025). A study in Brisbane, Australia, found that birds generally mostly flew at heights that reflected the urban structural gradient, and species' ability to utilise vertical profiles varied based on their urban tolerance and foraging traits (Re et al., 2025). Similarly, research from Hakodate, Japan, showed that bird species used urban vertical zones differently depending on structural height, season, and behavioural context, with mid-level zones (e.g. electric poles and wires) often used not just for perching but also for breeding-related activities (Mikami et al., 2022). These findings indicate that vertical space use is species-specific and can act as a filter for urban biodiversity. Nevertheless, similar studies are still scarce, and the role of vertical structure in shaping urban bird communities is still poorly understood. Moreover, studies from Central and Eastern Europe are highly underrepresented in the literature, despite the region's distinct post-socialist urbanisation patterns which could yield unique results (Batáry et al., 2025; Csákvári et al., 2021; Neugebauer & Kovács, 2015).

Urban areas differ greatly in their built structural characteristics, and these differences can strongly influence biodiversity patterns (Faeth et al., 2011). Low-rise, low-sealed urban surfaces typically contain more embedded green infrastructure, e.g., trees, parks, gardens, and other permeable spaces which provide a greater diversity of microhabitats and resource types for wildlife (Beninde et al., 2015). In contrast, high-rise and highly sealed urban sites represent more densely built environments with reduced horizontal green space and a higher share of impervious surfaces. This contrast in vertical and horizontal urban form creates distinct ecological opportunities and constraints, shaping how species access resources, and interact with their environment (Werner, 2011).

In this study, we investigated how increasing urban infrastructure, specifically building height and the proportion of sealed surfaces, affects birds' species richness, abundance, and key functional traits. Our research focused on five medium-sized cities in the western part of Hungary and was guided by the following hypotheses:

- 1) Urban vertical structure (building height) has an independent influence on bird species richness, abundance, and community composition, beyond the effects of horizontal surface sealing (Re et al., 2025).

- 2) Urban structural configurations with low-rise buildings and low sealed surface support higher bird species richness, abundance, and various functional traits than highly sealed or uniformly high-rise areas (Soga et al., 2014).
- 3) Avian community composition will significantly differ among the urban structural categories, with each supporting distinct assemblages and characteristic indicator species, reflecting specific filtering characteristics (Evans et al., 2011; Lakatos et al., 2022).

Material and Methods

Study area and design

We conducted the study in Transdanubia, i.e. Western Hungary, using extensive spatial replication (Fig. 1). In each of the five study cities, we have preselected 157 potential sites based on a 2×2 factorial design that combined two key urban landscape structural variables: building height (low vs. high) and sealed surface cover (low vs. high). During ground truthing, we selected 20 sampling sites per city, with five replicates per urban structural type, resulting in a total of 100 sites (4 structural type $\times 5$ replicates $\times 5$ cities) (for a map, see Appendix 1; for photos, see Fig. S1). Potential study sites were selected by collecting data about building height and built-up area cover from the Urban Atlas Land Cover/Land Use database (CLMS, 2018). To identify potential sampling sites, we first created 100×100 m grid zones within the administrative boundaries of each city. For each grid, we calculated the average building height and percentage of sealed surface. Although each grid cell was 100×100 m (1 ha), the sealed-surface values used for classification were used from the Urban Atlas land-cover polygons intersecting the cell. These polygons often extend beyond the boundaries of a single grid cell, so the sealed-area values reflect the total sealed extent of the larger polygon, not only the 1-ha grid. Based on these values, we selected sites that best represented all four combinations of urban structural characteristics with high contrasts, but enabling a high number of potential sites for local selection: (1) sites with low buildings and low sealed surface (height < 17 m, sealed surface < 1.5 ha); (2) low buildings and high sealed surface (height < 17 m, sealed surface > 2.5 ha); (3) tall buildings and low sealed surface (height > 30 m, sealed surface < 1.5 ha), and (4) tall buildings and high sealed surface (height > 30 m, sealed surface > 2.5 ha). For a schematic graphical overview, see Fig. 2. Low sealing and low buildings are typically found in suburban neighbourhoods with garden-like settings, offering a mix of residential spaces and green areas. Areas with low buildings and high sealing might comprise older residential zones with extensive paving for roads and parking, resulting in less green space compared to their suburban counterparts. High building and low sealing surfaces were predominantly developed during the 1960s and 1970s and consist of communist-era block houses now characterized by relatively large trees and mature vegetation. High sealing with high buildings often corresponds to city centre areas where dense construction is common. Furthermore, industrial and commercial areas were excluded from the sampling design because most were recently constructed, lacking established vegetation and avian communities, which could possibly bias the ecological comparisons. To avoid the risk of double-counting bird individuals, we ensured that the edges of selected 100 m buffer zones were at least 250 m apart, based on the assumption that individual birds are unlikely to be recorded at multiple points (Morrison & Peitz, 2021). Furthermore, when selecting the final sites, we avoided concentrating sites in the same category too close to each other or in the same areas of the city. Finally, we conducted field visits to verify site suitability and access, and we confirmed the final sampling sites based on these on-site assessments.

Bird survey and functional traits

We conducted bird surveys using the point count method in 100 sampling sites. We visited each survey point two times in 2025 during

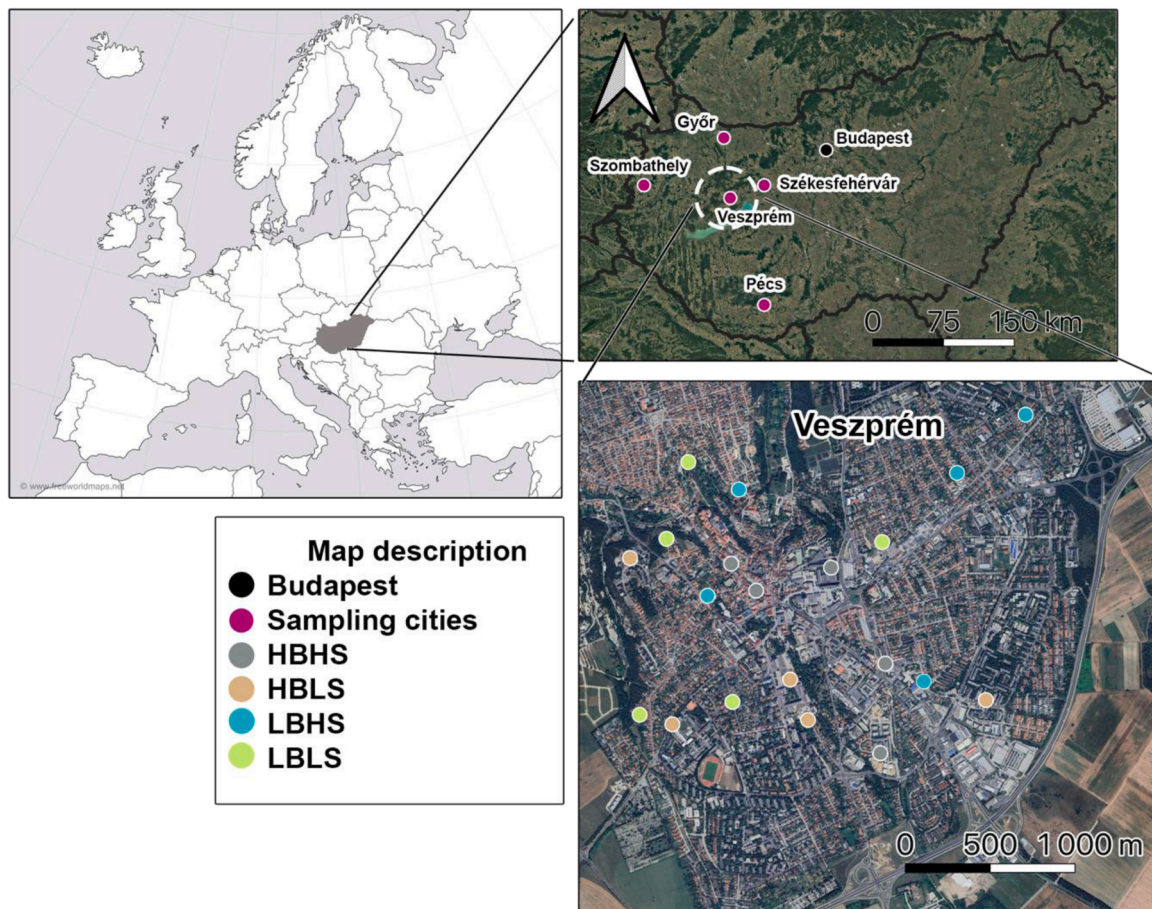


Fig. 1. Map showing Hungary within Europe and the five sampled cities, with sampling sites illustrated for the example of Veszprém ($n = 20$). Abbreviations of urban structural categories are as follows: ‘HBHS’ = high buildings and high sealed surface cover; ‘HBLS’ = high buildings and low sealed surface cover; ‘LBHS’ = low buildings and high sealed surface cover; and ‘LBLS’ = low buildings and low sealed surface cover. Source of base Europe map: <https://www.freeworldmaps.net>. The satellite image of Veszprém, Hungary, was acquired from Google (Google Maps. Accessed July 20, 2025. <https://maps.google.com>).

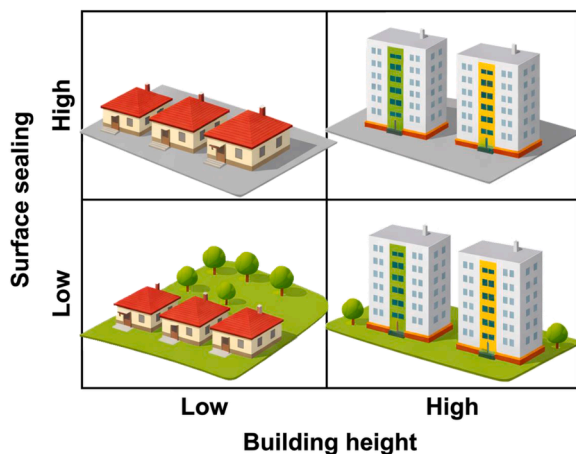


Fig. 2. Conceptual illustration of the 2×2 urban structural design defined by building height and sealed surface cover. Study sites were categorized as: (1) low buildings and low sealed surface (height < 17 m; sealed surface < 1.5 ha), (2) low buildings and high sealed surface (height < 17 m; sealed surface > 2.5 ha), (3) tall buildings and low sealed surface (height > 30 m; sealed surface < 1.5 ha), and (4) tall buildings and high sealed surface (height > 30 m; sealed surface > 2.5 ha). Illustrations were generated using artificial intelligence-generated content based on user-provided prompts and self-made photographs in ChatGPT (OpenAI, 2026).

early morning (within four hours after sunrise), once in each period (late April to early May and late May to early June) under calm and dry weather conditions (between 0–4 Beaufort wind scale). To account for temporal variation in bird activity, the second survey was conducted in the opposite order of the first one.

We recorded all birds contacted, visually and acoustically, within a radius of 100 m from the centre of survey points. We counted birds while standing still for 10 minutes (Bibby, 2000). We excluded species for which local site use was not evident, such as aquatic birds (i.e., *Laridae*, *Anseriformes*), whose presence typically reflected distant flyovers rather than habitat use (Ralph et al., 1995). Flyover species were only recorded if they were within close proximity to the observers (e.g., less than 15 m altitude), while high-flying individuals were excluded.

To classify the observed bird species, we selected a set of six functional traits and collected information about them from the available literature (Barbaro & van Halder, 2009; Cramp, 1993; Keller et al., 2020; Korányi et al., 2021): (i) diet (granivore, mixed diet or insectivore (including some carnivorous species, but hereafter referred to together as insectivores)); (ii) nestling diet (granivore, mixed diet, insectivore); (iii) body mass (expressed in grams as a continuous variable); (iv) nesting site (ground, reed/shrub, open in tree or cavity nesters); (v) foraging technique (ground prober, ground gleaner, understory gleaner, bark forager or canopy foliage gleaner/hawker); and (vi) migration status (resident, temperate/partial migrant or tropical migrant species) (Table S1). Data regarding the trait attributes were collected from Cramp et al. (1993). Trait-level categories for each functional trait were based on Barbaro and van Halder (2009).

Table 1

Summary table of the GLMM significant results on species richness, abundance and functional traits of birds. The following traits were considered: diet (granivore, mixed diet, insectivore), nestling diet (granivore, mixed diet, insectivore), foraging technique (ground prober, ground gleaner, understory gleaner, bark forager, canopy foliage gleaner/perch hunter, hawk [continuous aerial feeder]), nesting place (ground, shrub, open in tree, cavity, building), migration status (resident, temperate/partial migrant, tropical migrant) and body mass (in grams). Estimates are shown with 95 % CI.

Response variables ^a	Predictors	Estimate ± CI	df	t-value	p-value
Species richness (0.085, 0.138)	Sealed surface	1.260 ± 0.997	93	2.509	0.0134
Abundance (0.053, 0.623)	Building height	-0.247 ± 0.131	94	-3.743	<0.001
CWM Nestling diet (0.112, 0.129)	Sealed surface	0.114 ± 0.074	95.3	3.052	0.0029
CWM Foraging technique (0.124, 0.124)	Building height	-0.082 ± 0.029	96	-2.829	0.0057
CWM Nesting place (0.269, 0.326)	Sealed surface	-0.086 ± 0.025	92	-3.393	0.001
	Building height	-0.098 ± 0.025	92	-3.856	<0.001
CWM Body mass (0.082, 0.103)	Building height	-0.214 ± 0.141	96.1	-3.004	0.00339

^a Values in brackets: marginal/conditional R²

Statistical analysis

We pooled data from the two survey periods, retaining the higher abundance per species at a given site across visits. For categorical traits that represented clear ecological gradients (e.g., foraging technique, nesting location, migration status), we assigned ordinal numeric codes reflecting increasing levels along each gradient (e.g., foraging technique: ground prober – 1, ground gleaner – 2, understory gleaner – 3, bark forager – 4, canopy foliage gleaner/perch hunter – 5, hawk [continuous aerial feeder] – 6). These were used to calculate community-weighted means (CWMs), which represent community positions along each ecological axis (e.g., from ground to canopy/building for nesting). This approach allows interpretation of CWMs as functional gradients rather than as strictly categorical variables (Barbaro et al., 2017; Barbaro & Van Halder, 2009; Götzemberger et al., 2020; Ricotta & Moretti, 2011). For each trait categorisation, see Table S1. Then, we ranged all trait categories between 0 and 1. Thereafter, we calculated community-weighted means (CWM), which are averages of trait values weighted by the relative abundances of each bird species at each observation point for all functional traits using the BAT package's 'cwm' function (Cardoso et al., 2015). To eliminate any violation against the normal distribution of model residuals (Kéry & Hatfield, 2003), abundance, the CWM nestling diet and the CWM body mass data were log-transformed ('log10' function), then ranged between 0 and 1 before the analyses to remove skewness in data distribution (Lee & McLachlan, 2020). Prior to modelling, we assessed correlations among trait values using Spearman correlation, using 'cors' function of 'corrplot' package (Wei et al., 2017). Most traits were weakly correlated ($|r| < 0.45$), with the exception of diet and nestling diet ($r = 0.65$), justifying the use of separate models for each trait (Fig. S2). We used the species richness, abundance and CWM values as response variables against the urban structural types, which we treated as a fixed factor with two levels of each (building height: low vs. high and sealed surface: low vs. high) in general linear mixed-effects models using the 'lmer' function of 'lme4' package (Bates et al., 2015). In the models, we treated the observers (name of ornithologists, $n = 6$), the cities ($n = 5$) as nested random factors. In accordance with the syntax employed by the R function, the model would be constituted as follows: `lmer(Response_variable ~ Sealed_surface * Building_height + (1 | Observer/City))`, where response variables in the separate models were the species

richness, abundance, and CWM trait values. For model diagnostics, we examined the normal distribution of model residuals by creating normal quantile-quantile plots to visualise the error distribution. Additionally, we plotted the model residuals against the fitted values to assess the possibility of heteroscedasticity.

We additionally conducted a redundancy analysis (RDA) to examine the effects of urban structural variables on the species composition of the bird communities. As constrained variables, we used the urban structural types (building height: low vs. high and sealed surface: low vs. high), whereas for conditional variables we included the observers ($n = 6$), and the cities ($n = 5$). Before to RDA analysis, we ran a Hellinger transformation on the community data matrices to reduce the weight of species with high abundances (Legendre & Gallagher, 2001). We performed a permutation test based on 4999 permutations to reveal the significant effects of the predictor variables (building height vs. sealed surface) on community composition of bird species using the 'permutest' function of the 'vegan' package for R (Oksanen et al., 2023). We also conducted an indicator species analysis (Dufrene & Legendre, 1997) to identify indicator species for each variable by using the 'multipatt' function of 'indicspecies' package (Cáceres & Legendre, 2009). All analyses were carried out in R version 4.4.0 (R Core Team, 2024) and RStudio version 2024.09.0+375 (RStudio Team, 2024). Figures and maps were created using QGIS 3.30.0 (QGIS Development Team, 2020) and 'ggplot2' package in R (Wickham, 2016).

Results

At the 100 bird count points across the five cities, we observed a total of 4282 bird individuals (after the exclusion of non-relevant species) belonging to 58 species (Table S1). The most common species were the feral pigeon (*Columba livia*, 13.7 %), the common blackbird (*Turdus merula*, 9.8 %), and the common wood pigeon (*Columba palumbus*, 7.8 %), whereas the rarest ones were the European honey buzzard (*Pernis apivorus*, 0.02 %), common redstart (*Phoenicurus phoenicurus*, 0.04 %), and the white wagtail (*Motacilla alba*, 0.07 %).

Species richness was significantly influenced by sealed surface, with higher richness observed in areas with low sealed surface, regardless of building height (Fig. 3a, Table 1). The observed abundance of birds, on the other hand, was significantly affected by building height, with higher abundance in areas with tall buildings, regardless of sealed surface (Fig. 3b, Table 1).

The CWM of nestling's diet differed significantly between the distinct sealed surface cover. Number of insectivores decreased with increasing sealed cover, but building height did not affect the nestling's diet (Fig. 3b, Table 1). In contrast, the CWM of foraging technique showed a significant response to building heights with species typically foraging at higher elevations (e.g., aerial hunters) being more common near tall buildings (Fig. 4c, Table 1). However, we did not find significant sealed surface effect. Both building height and sealed surface significantly affected CWM nest location trait (Fig. 4d, Table 1), with urban areas featuring taller buildings and higher sealed surfaces being associated with communities dominated by species nesting at higher strata (e.g., particularly in tree canopies and cavities). Conversely, communities in low-rise and less sealed environments were rather characterised by species nesting in shrubs or on the ground. We found a significant effect of building height on the body mass of urban bird communities, with sites featuring taller buildings hosting communities composed of larger bodies species, while low-rise environments were associated with birds of lower body mass (Fig. 4f, Table 1). Sealed surface did not significantly affect CWM body mass. Finally, the CWM migration status and adult's diet was not affected by either of the urban structural variables (Fig. 4e), furthermore, we did not find any interaction effect between the two variables.

The redundancy analysis (RDA) revealed significant differences for the bird communities across the four distinct urban structural types (Fig. 5). These variables explained a significant part of the variation in

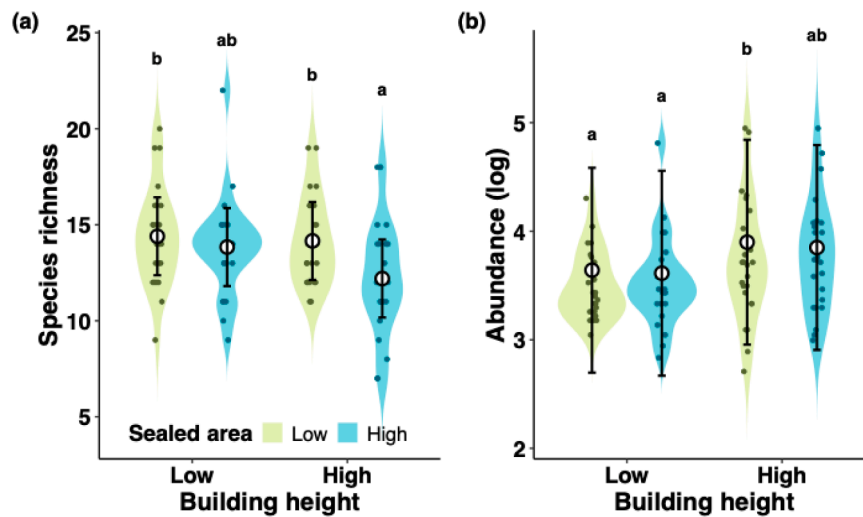


Fig. 3. Variation of (a) species richness and (b) abundance of birds across combinations of building height and sealed surface cover. Violin plots show observed values with jittered points (raw data), while white points and error bars represent model-derived estimated marginal means (EMMs) and 95 % CIs. Letters indicate significant pairwise differences based on compact letter displays (CLDs).

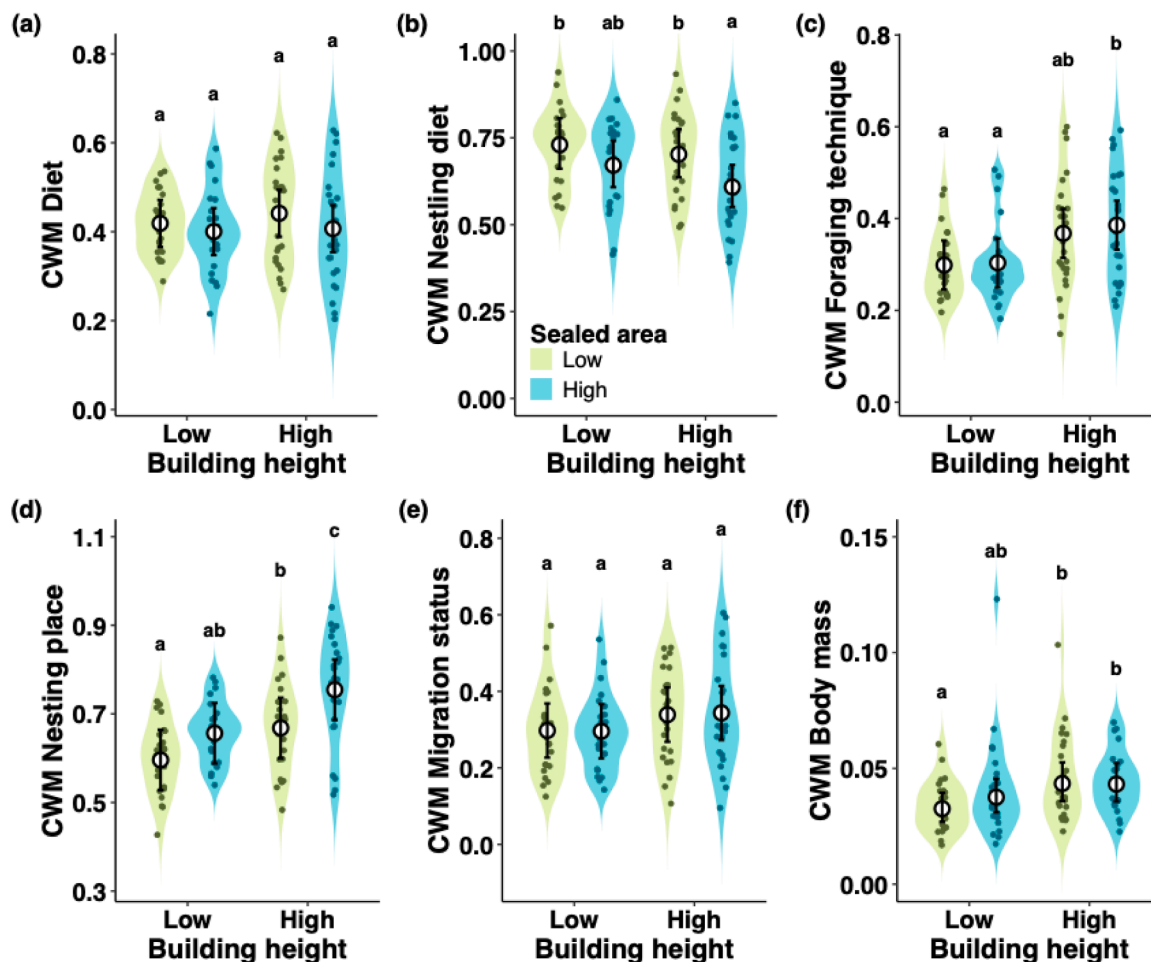


Fig. 4. Variation of community-weighted mean (CWM) of functional traits across combinations of building height and sealed surface cover. Violin plots show observed values with jittered points (raw data), while white points and error bars represent model-derived estimated marginal means (EMMs) and 95 % CIs, back-transformed from the log scale. Letters indicate significant pairwise differences based on compact letter displays (CLDs). The following traits were plotted: (a) diet (granivore, mixed diet, insectivore); (b) nestling diet (granivore, mixed diet, insectivore); (c) foraging technique (ground prober, ground gleaner, understory gleaner, bark forager, canopy foliage gleaner/perch hunter, hawk [continuous aerial feeder]); (d) nesting site (ground, shrub, open in tree, cavity, building); (e) migration status (resident, temperate/partial migrant, tropical migrant); (f) body mass (in grams).

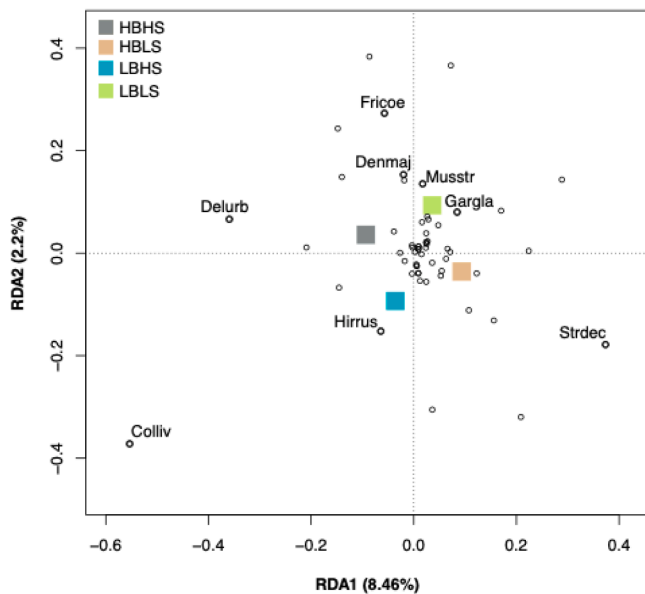


Fig. 5. Redundancy analysis biplots for all species (open circles) representing the effects of building height (HB – high buildings vs. LB – low buildings) and sealed surface cover (HS – high sealed surface vs. LS – low sealed surface) on bird communities. For better visibility, only species with significant indicator values are shown with bolded circles. Explained variance of RDA axes shown as percentage in parentheses. For species name abbreviations, see Table S1.

community composition, with RDA1 and RDA2 explaining 8.5 % and 2.2 % of the variance, respectively ($F = 6.46$, $p < 0.001$). The indicator value analysis (IndVal) identified several indicator species for each urban structural category (Table S1). Three species were indicators of high-rise buildings with a high share of sealed surface: the common house martin (*Delichon urbicum*), the barn swallow (*Hirundo rustica*), and the feral pigeon (*Columba livia*). Three species were associated with low-rise buildings and high sealed surface, namely the spotted flycatcher (*Muscicapa striata*), the common chaffinch (*Fringilla coelebs*), and the great spotted woodpecker (*Dendrocopos major*). Two species were indicators of sites with low buildings and low sealed surface: the Eurasian collared dove (*Streptopelia decaocto*) and the Eurasian jay (*Garrulus glandarius*).

Discussion

In this research, we examined how three-dimensional urban structural categories affect bird species diversity and their functional traits. Tall buildings were associated with higher abundances of species characterised by high-level foraging strategies, supported communities composed of larger-bodied species, and favoured species that select higher nesting sites. In contrast, high sealed surface reduced species richness, affected the dietary traits of nestlings by disadvantaging insectivores, and impacted nesting behaviour by discouraging low-level nesters. Bird community compositions differed among the urban structural categories (high buildings and high sealed surface cover; high buildings and low sealed surface cover; low buildings and high sealed surface cover; low buildings and low sealed surface cover), with each category harbouring distinct indicator species.

Species richness responded negatively to higher amounts of sealed surface, which well aligns with previous research on the negative impacts of urbanisation (Batáry et al., 2018; Sol et al., 2020). Increasing impervious surface area (due to urban infrastructure, roads, pavements, buildings) reduces habitat availability, structural complexity, and resource diversity for several bird species (Hastedt & Tietze, 2023). Highly sealed surfaces often have less vegetation, which results in poor nesting and foraging opportunities (Ding et al., 2023). As a result, more sensitive specialist species are often disadvantaged, leading to lower

overall richness. Consequently, permeable surfaces with well-maintained and connected green areas are crucial for sustaining diverse avian communities within cities (Beaugéard et al., 2021; Korányi et al., 2021).

Sites with taller vertical structures supported higher observed bird abundances than areas with lower buildings heights and this was consistent across both low and high sealed surface cover categories, suggesting that vertical features alone can provide habitat opportunities for certain urbanised species. The availability of diverse vertical foraging substrates, tall perching or nesting structures (which offer increased protection from predators), and the microclimatic buffering effects of taller buildings, i.e., the potential to modify temperature, wind exposure, and rainfall in the immediate surroundings of the structure, could all be contributing factors (James Reynolds et al., 2019; Wu et al., 2019). Despite the inconsistent findings about the "density-diversity" paradox, a meta-analysis conducted by Saari et al. (2016) revealed that urbanisation is generally associated with decreased overall animal abundance, challenging the idea that cities support higher densities despite lower species richness. Their meta-analysis also revealed strong geographic variation, with negative associations between urbanisation and both abundance and richness primarily found in Europe. In contrast, a bird-focused meta-analysis by Batáry et al. (2018) found increasing abundances along urban gradients toward city centres. Our findings further refine this pattern by showing that, despite strong urban pressures, taller buildings act as environmental filters that favour species adapted to high-level foraging and nesting sites. These species were primarily the common house martin, the barn swallow, and the feral pigeon (indicators of tall buildings). These urban-tolerant species also contribute to ecosystem functioning, e.g., through insectivory or food-web support, e.g., pigeons serving as prey for urban raptors. (Buenoño et al., 2023; Mak et al., 2023). Overall, our analyses show that tall buildings, not sealed surfaces, select for species adapted to high-elevation nesting and foraging (common house martin, common swift), while barn swallow remained rare and showed no structural associations, and its indicator status reflects only distributional clustering rather than true ecological preference or breeding on tall buildings. As detailed in the trait analysis below, the higher abundance in tall-building urban areas is mainly associated with communal, cavity-nesting and aerial-foraging species that are already well-adapted to vertical urban structures. Particularly, highly abundant urban exploiters such as the feral pigeon, contribute substantially to this pattern. Because these species usually occur at higher local densities, their presence can increase total abundance once suitable structures are available. Thus, the pattern likely reflects both the suitability of tall buildings and the aggregative nature of the species they harbour.

With decreasing sealed surface cover, the bird community composition shifted towards species whose nestlings are insectivorous. This suggests that during a sensitive life stage, high sealed surface cover can pose a major threat to these species. The lack of green areas with diverse native vegetation (e.g., trees, shrubs, and understory plants) reduces arthropod abundance, thereby limiting critical high quality food resources for insectivorous birds and their nestlings, which may hinder the reproductive success in urban environments (Lakatos et al., 2025; Seress et al., 2025). We acknowledge, however, that the dietary trait coding may simplify trophic relationships and does not reflect the potentially uneven ecological distances among diet categories; thus, the observed variation should be interpreted as broad directional patterns rather than precise quantitative differences.

Nest site selection of birds is a critical trait, that largely determines their survival (James Reynolds et al., 2019). According to our findings, ground-nesting bird species were more prevalent in areas with lower sealed surface cover. This corresponds to previous findings, about above ground nesters generally had higher urban densities than ground-nesting species (Lakatos et al., 2022), due to both increased predation risk and reduced availability of suitable ground-level habitats in urban settings (Evans et al., 2011). Nesting strategy is a more spatially

integrated functional trait, making it uniquely sensitive to changes in both dimensions of urbanisation, which shows why both of our variables affected it. While tall buildings may hinder low-level nesters, at the same time, they create opportunities for higher-place nesters, especially cavity nesters, which can utilise multi-storey apartment blocks, that are characteristic of Hungarian cities. As a result, urban built structures act as environmental filters that not only exclude species unable to tolerate high levels of sealed surfaces, but also favour nesting strategies that are compatible with the novel structural conditions of cities. Thus, the urban environment both limits which species can persist and selectively promotes those whose nesting requirements align with its altered habitats (Evans et al., 2018; Lakatos, Báldi, Gallé, et al., 2025).

Vertical structures also shaped the foraging composition of the community: areas with taller buildings were dominated by species that forage at higher elevations. Aerial foragers, e.g., hawkers, were more frequent in these areas, suggesting that vertical urbanisation may create novel ecological niches for species able to exploit elevated airspace. This adaptation possibly reflects the higher availability of artificial perching sites, altered wind patterns, and flying insect presence around and above tall buildings, which together support aerial hunting strategies (Beatley, 2020; Buenaño-Marino et al., 2025). Thus, urban verticality may not only constrain but also benefit certain foraging behaviours, favouring functionally distinct species.

Around taller buildings, larger-bodied birds were more common, indicating that urban verticality may selectively filter for species with larger body mass. These birds might have traits that can help them navigate and exploit the complex three-dimensional structure of high-rise urban environments (e.g., stronger flight capabilities and greater mobility). Additionally, these species (e.g., *Corvidae*, *Columbidae*) are generally better equipped to cope with the high levels of anthropogenic disturbance and reduced vegetation cover that characterise densely built urban centres. Several traits may explain these abilities: behavioural flexibility, high tolerance to humans, generalist diets, and the ability to exploit artificial food resources and nesting substrates (Evans et al., 2011). These traits are well-known driver of urban tolerance in birds and are typical of many corvids and columbids (Benmazouz et al., 2021; Kark et al., 2007). Our findings therefore suggest that vertical urban sprawl can act as a functional filter, favouring species whose behavioural and ecological traits align with the physical constraints and disturbance regime of heavily built-up, high-rise environments.

Our findings also demonstrate that the two major axes of urban structural development filter bird communities in distinctive but complementary ways, influencing not only which species can thrive in cities, but also which traits may support their persistence. Sealed surfaces were consistently associated with lower species richness and some loss of functionally specialised traits (e.g., insectivores and ground-level nesters), while vertical urbanisation benefited abundance and traits such as aerial foraging, elevated nesting, and larger body mass. This is particularly relevant for Central and Eastern European cities, where highly sealed historical centres coexist with socialist-era multi-storey housing blocks often surrounded by substantial green spaces. Sustaining vertical structural diversity within greener environments may help integrate urban density with biodiversity conservation. Therefore, urban planning should account for both horizontal and vertical dimensions of development, while mitigating potential risks (e.g., reducing reflective surfaces to minimise bird collisions with buildings). Combining permeable, green surfaces with diverse vertical structures offers a novel approach to support species richness and ecological functioning in an increasingly urbanised world (Grass et al., 2021).

Conclusions

Our findings emphasise the growing argument that vertical structures should be considered during urban planning. Tall buildings, when embedded within low-sealed surfaces, may represent a form of vertical densification that reduces horizontal habitat loss while still providing

opportunities for native and functionally diverse wildlife. At the same time, sealed surface cover acts as a strong ecological filter, reducing habitat heterogeneity and disrupting key ecological functions. Understanding how different organisms respond to the vertical dimension of cities can help identify specific habitat features that enhance urban biodiversity through better conservation strategies.

Funding

This work is a result of the project “Biodiversity under agricultural and urbanisation constraints” (NKFIH KKP 133839) and supported by the Sustainable Development and Technologies National Programme of the Hungarian Academy of Sciences (FFT NP FTA). G. Seress was supported by the National Research, Development and Innovation Office (FK-137743) and the János Bolyai Research Scholarship of the Hungarian Academy of Sciences.

Code and data availability

All code and data are available from the corresponding author upon reasonable request.

CRediT authorship contribution statement

Tamás Lakatos: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **José Javier Jiménez-Albarral:** Writing – original draft, Investigation. **Teodor J. Purger:** Writing – original draft, Investigation. **Jenő J. Purger:** Writing – original draft, Investigation. **Krisztina Sándor:** Investigation. **Gábor Seress:** Writing – original draft, Investigation. **Péter Batáry:** Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to thank Brigitta Palotás for her contribution to the site selection GIS work.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.baae.2026.03.002](https://doi.org/10.1016/j.baae.2026.03.002).

References

- Arévalo, C., Amaya-Espinel, J. D., Henríquez, C., Ibarra, J. T., & Bonacic, C. (2022). Urban noise and surrounding city morphology influence green space occupancy by native birds in a Mediterranean-type South American metropolis. *Scientific Reports*, 12(1), 4471. <https://doi.org/10.1038/s41598-022-08654-7>
- Aronson, M. F. J., La Sorte, F. A., Nilon, C. H., Katti, M., Goddard, M. A., Lepczyk, C. A., Warren, P. S., Williams, N. S. G., Cilliers, S., Clarkson, B., Dobbs, C., Dolan, R., Hedblom, M., Klotz, S., Kooijmans, J. L., Kühn, I., Macgregor-Fors, I., McDonnell, M., Mörtberg, U., ... Winter, M. (2014). A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings. Biological Sciences*, 281(1780), Article 20133330. <https://doi.org/10.1098/rspb.2013.3330>
- Barbaro, L., Rusch, A., Muiruri, E. W., Gravelier, B., Thiery, D., & Castagnérol, B. (2017). Avian pest control in vineyards is driven by interactions between bird functional diversity and landscape heterogeneity. *Journal of Applied Ecology*, 54(2), 500–508. <https://doi.org/10.1111/1365-2664.12740>
- Barbaro, L., & van Halder, I. (2009). Linking bird, carabid beetle and butterfly life-history traits to habitat fragmentation in mosaic landscapes. *Ecography*, 32(2), 321–333. <https://doi.org/10.1111/j.1600-0587.2008.05546.x>

- Batáry, P., Gallé, R., Korányi, D., et al. (2025). Biodiversity and human well-being trade-offs and synergies in villages. *Nature Sustainability*, 8, 894–904. <https://doi.org/10.1038/s41893-025-01592-y>
- Batáry, P., Kurucz, K., Suarez-Rubio, M., & Chamberlain, D. E. (2018). Non-linearities in bird responses across urbanization gradients: A meta-analysis. *Global Change Biology*, 24(3), 1046–1054. <https://doi.org/10.1111/gcb.13964>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Beatley, T. (2020). *The bird-friendly city: Creating safe urban habitats*. Island Press.
- Beaugueard, E., Brischoux, F., & Angelier, F. (2021). Green infrastructures and ecological corridors shape avian biodiversity in a small French city. *Urban Ecosystems*, 24(3), 549–560. <https://doi.org/10.1007/s11252-020-01062-7>
- Beninde, J., Veith, M., & Hochkirch, A. (2015). Biodiversity in cities needs space: A meta-analysis of factors determining intra-urban biodiversity variation. *Ecology Letters*, 18(6), 581–592. <https://doi.org/10.1111/ele.12427>
- Benmazouz, I., Jokimäki, J., Lengyel, S., Juhász, L., Kaisanlahti-Jokimäki, M.-L., Kardos, G., Paládi, P., & Kövér, L. (2021). Corvids in urban environments: A systematic global literature review. *Animals*, 11(11), 3226. <https://doi.org/10.3390/ani11113226>
- Bibby, C. J. (2000). *Bird census techniques*. Elsevier.
- Buenano, C. P., García-Esparza, J. A., Castelló, A. J., Altaba, P., & Valentín, A. (2023). Assessment of the ecological role of historic centres based on the relationship between biodiversity and urban composition. *Heliyon*, 9(9). <https://doi.org/10.1016/j.heliyon.2023.e20135>
- Buenano-Mariño, C., del, P., Sabán, J., Barba, E., & García-Esparza, J. A. (2025). Urban form shapes bird niches: Insights from the European green capital 2024. *Biodiversity and Conservation*, 34(5), 1857–1879. <https://doi.org/10.1007/s10531-025-03050-9>
- Cáceres, M. D., & Legendre, P. (2009). Associations between species and groups of sites: Indices and statistical inference. *Ecology*, 90(12), 3566–3574. <https://doi.org/10.1890/08-1823.1>
- CLMS (2018) - European Environment Agency (EEA). 2018. *Urban Atlas Land Cover/Land Use 2018 (vector), Europe, 3-yearly*. Copernicus Land Monitoring Service. <https://doi.org/10.2909/fb4df1a1-6ceb-4cc0-8372-1ed354c285e6> (accessed 2025).
- Cardoso, P., Rigal, F., & Carvalho, J. C. (2015). BAT – Biodiversity assessment tools, an R package for the measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. *Methods in Ecology and Evolution*, 6(2), 232–236. <https://doi.org/10.1111/2041-210X.12310>
- Cramp, S. (1993). *Handbook of the birds of Europe, the Middle East and North Africa: The birds of the Western Palearctic*. Oxford University Press.
- Croci, S., Butet, A., & Clergeau, P. (2008). Does urbanization filter birds on the basis of their biological traits. *The Condor*, 110(2), 223–240. <https://doi.org/10.1525/cond.2008.8409>
- Csákvári, E., Fabók, V., Bartha, S., Barta, Z., Batáry, P., Borics, G., Botta-Dukát, Z., Erős, T., Gáspár, J., Hideg, É., Kovács-Hostyánszki, A., Sramkó, G., Standovár, T., Lengyel, S., Líker, A., Magura, T., Márton, V. A., Molnár, V. A., Molnár, Z., ... Báldi, A. (2021). Conservation biology research priorities for 2050: A Central-Eastern European perspective. *Biological Conservation*, 264, Article 109396. <https://doi.org/10.1016/j.biocon.2021.109396>
- Ding, Z., Guo, A., Lian, M., Wang, Y., Ying, W., Jiang, H., Zhou, X., Qian, C., Lai, J., & Cao, J. (2023). Landscape factors influencing bird nest site selection in urban green spaces. *Frontiers in Ecology and Evolution*, 11. <https://doi.org/10.3389/fevo.2023.1258185>
- Dufrene, M., & Legendre, P. (1997). Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs*, 67(3), 345–366. <https://doi.org/10.2307/2963459>
- Evans, B. S., Reitsma, R., Hurlbert, A. H., & Marra, P. P. (2018). Environmental filtering of avian communities along a rural-to-urban gradient in Greater Washington, D.C., USA. *Ecosphere*, 9(11), Article e02402. <https://doi.org/10.1002/ecs2.2402>
- Evans, K. L., Chamberlain, D. E., Hatchwell, B. J., Gregory, R. D., & Gaston, K. J. (2011). What makes an urban bird? *Global Change Biology*, 17(1), 32–44. <https://doi.org/10.1111/j.1365-2486.2010.02247.x>
- Faeth, S. H., Bang, C., & Saari, S. (2011). Urban biodiversity: Patterns and mechanisms. *Annals of the New York Academy of Sciences*, 1223(1), 69–81. <https://doi.org/10.1111/j.1749-6632.2010.05925.x>
- Fairbairn, A. J., Katholnigg, S., Leitch, T., Merckens, L., Schroll, L., Weissner, W. W., & Meyer, S. T. (2025). NDVI and vegetation volume as predictors of urban bird diversity. *Scientific Reports*, 15(1), Article 12863. <https://doi.org/10.1038/s41598-025-96098-0>
- Gallé, R., & Batáry, P. (2019). Trait-based paradise—about the importance of real functionality. *Community Ecology*, 20(3), 314–316. <https://doi.org/10.1556/168.2019.20.3.11>
- Götzenberger, L., de Bello, F., Dias, A. T. C., Moretti, M., Berg, M. P., & Carmona, C. P. (2020). *Trait-based ecology tools in R [Data set]*. CSIC-GV-UV- Centro de Investigaciones sobre Desertificación (CIDE). <https://doi.org/10.1039/501100008331>
- Grass, I., Batáry, P., & Tschamntke, T. (2021). Chapter six—Combining land-sparing and land-sharing in European landscapes. In D. A. Bohan, & A. J. Vanbergen (Eds.), *Advances in Ecological Research: 64. Advances in Ecological Research* (pp. 251–303). Academic Press. <https://doi.org/10.1016/b.s.aacr.2020.09.002>
- Grilo, F., McPhearson, T., Santos-Reis, M., & Branquinho, C. (2022). A trait-based conceptual framework to examine urban biodiversity, socio-ecological filters, and ecosystem services linkages. *Npj Urban Sustainability*, 2(1), 32. <https://doi.org/10.1038/s42949-022-00077-7>
- Hastedt, A., & Tietze, D. T. (2023). The importance of unsealed areas in the urban core and periphery for bird diversity in a large central European city. *Urban Ecosystems*, 26(4), 1015–1028. <https://doi.org/10.1007/s11252-023-01361-9>
- James Reynolds, S., Ibáñez-Álamo, J. D., Sumasgutner, P., & Mainwaring, M. C. (2019). Urbanisation and nest building in birds: A review of threats and opportunities. *Journal of Ornithology*, 160(3), 841–860. <https://doi.org/10.1007/s10336-019-01657-8>
- Kark, S., Iwaniuk, A., Schalimtzek, A., & Banker, E. (2007). Living in the city: Can anyone become an 'urban exploiter'? *Journal of Biogeography*, 34(4), 638–651. <https://doi.org/10.1111/j.1365-2699.2006.01638.x>
- Keller, V., Herrando, S., & Voríšek, P. (2020). *European breeding bird atlas2: Distribution, abundance and change (Issue v. 2)*. Lynx Edicions. <https://books.google.hu/books?id=4YVzgEACAAJ>
- Kéry, M., & Hatfield, J. S. (2003). Normality of raw data in general linear models: The most widespread myth in statistics. *The Bulletin of the Ecological Society of America*, 84(2), 92–94. [https://doi.org/10.1890/0012-9623\(2003\)84%255B92:NORDIG%255D2.0.CO;2](https://doi.org/10.1890/0012-9623(2003)84%255B92:NORDIG%255D2.0.CO;2)
- Korányi, D., Gallé, R., Donkó, B., Chamberlain, D. E., & Batáry, P. (2021). Urbanization does not affect green space bird species richness in a mid-sized city. *Urban Ecosystems*, 24(4), 789–800. <https://doi.org/10.1007/s11252-020-01083-2>
- Lakatos, T., Báldi, A., Benkő, Z., Gallé, R., Korányi, D., Kovács, I., László, Z., Purger, J. J., Sándor, K., Seress, G., Urák, I., & Batáry, P. (2025). Landscape complexity and edge effects shape bird community composition and filter functional traits in villages. *Ecological Indicators*, 176, Article 113644. <https://doi.org/10.1016/j.ecolind.2025.113644>
- Lakatos, T., Chamberlain, D. E., Garamszegi, L. Z., & Batáry, P. (2022). No place for ground-dwellers in cities: A meta-analysis on bird functional traits. *Global Ecology and Conservation*, 38, Article e02217. <https://doi.org/10.1016/j.gecco.2022.e02217>
- Lee, S. X., & McLachlan, G. J. (2020). *On mean and/or variance mixtures of normal distributions* (arXiv:2005.06883). arXiv. <https://arxiv.org/abs/2005.06883>
- Legendre, P., & Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, 129(2), 271–280. <https://doi.org/10.1007/s004420100716>
- Mak, B., Drewitt, E. J. A., Francis, R. A., & Chadwick, M. A. (2023). The raptor lockdown menu—Shifts in prey composition suggest urban peregrine diets are linked to human activities. *People and Nature*, 5(2), 795–807. <https://doi.org/10.1002/pan3.10445>
- McDonald, R. I., Marcotullio, P. J., & Güneralp, B. (2013). Urbanization and global trends in biodiversity and ecosystem services. In T. Elmqvist, M. Fragkias, J. Goodness, B. Güneralp, P. J. Marcotullio, R. I. McDonald, S. Parnell, M. Schewenius, M. Sendstad, K. C. Seto, & C. Wilkinson (Eds.), *Urbanization, biodiversity and ecosystem services: Challenges and opportunities: A global assessment* (pp. 31–52). Netherlands: Springer. https://doi.org/10.1007/978-94-007-7088-1_3
- Meffert, P. J., & Dziock, F. (2013). The influence of urbanisation on diversity and trait composition of birds. *Landscape Ecology*, 28(5), 943–957. <https://doi.org/10.1007/s10980-013-9867-z>
- Mikami, K., Morimoto, G., Ueno, Y., & Mikami, O. K. (2022). Vertical space utilization by urban birds and their relationship to electric poles and wires. *Landscape and Ecological Engineering*, 18(1), 19–30. <https://doi.org/10.1007/s11355-021-00479-2>
- Morelli, F., Benedetti, Y., Ibáñez-Álamo, J. D., Tryjanowski, P., Jokimäki, J., Kaisanlahti-Jokimäki, M.-L., Suhonen, J., Díaz, M., Möller, A. P., Moravec, D., Prosek, J., Bussière, R., Mägi, M., Kominos, T., Galanaki, A., Bukas, N., Marko, G., Prusini, F., Tonelli, M., ... Reif, J. (2021). Effects of urbanization on taxonomic, functional and phylogenetic avian diversity in Europe. *Science of The Total Environment*, 795, Article 148874. <https://doi.org/10.1016/j.scitotenv.2021.148874>
- Morrison, L. W., & Peitz, D. G. (2021). Spacing of point counts for grassland bird surveys in small geographical areas: Biases and tradeoffs. *The Wilson Journal of Ornithology*, 132(4), 810–819. <https://doi.org/10.1676/19-00117>
- Neugebauer, C., & Kovács, Z. (2015). Paths of socio-spatial change in post-socialist cities—Insights from five city-regions in Central and Eastern Europe. In T. Lang, S. Henn, W. Sgibnev, & K. Ehrlich (Eds.), *Understanding geographies of polarization and peripheralization: perspectives from Central and Eastern Europe and beyond* (pp. 171–196). Palgrave Macmillan UK. https://doi.org/10.1057/9781137415080_10
- Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'hara, R., Solymos, P., Stevens, M., & Szoecs, E. (2023). *Vegan: Community ecology package. R package version 2.6-4*. 2022.
- Pellissier, V., Cohen, M., Boulay, A., & Clergeau, P. (2012). Birds are also sensitive to landscape composition and configuration within the city centre. *Landscape and Urban Planning*, 104(2), 181–188. <https://doi.org/10.1016/j.landurbplan.2011.10.011>
- Pena, J. C., Ovaskainen, O., MacGregor-Fors, I., Teixeira, C. P., & Ribeiro, M. C. (2023). The relationships between urbanization and bird functional traits across the streetscape. *Landscape and Urban Planning*, 232, Article 104685. <https://doi.org/10.1016/j.landurbplan.2023.104685>
- QGIS Development Team. (2020). Quantum GIS development team. *Quantum GIS geographic information system*. Open Source Geospatial Foundation Project [Computer software]. <http://qgis.osgeo.org>
- R Core Team. (2024). *R version 4.2.1: A language and environment for statistical computing* [Computer software]. <https://www.r-project.org/>
- Ralph, C. J., Sauer, J. R., & Droege, S. (1995). *Monitoring bird populations by point counts*, 187 p. 149). Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. <https://doi.org/10.2737/PSW-GTR-149>
- Re, A. J., Rogers, A. M., Possingham, H. P., & Kark, S. (2025). Bird utilisation of vertical space in urban environments. *Diversity*, 17(1), 1. <https://doi.org/10.3390/d17010016>. Article.

- Ricotta, C., & Moretti, M. (2011). CWM and Rao's quadratic diversity: A unified framework for functional ecology. *Oecologia*, 167(1), 181–188. <https://doi.org/10.1007/s00442-011-1965-5>
- RStudio Team. (2024). *R studio: Integrated development for R*. RStudio Team. Boston, MA: RStudio Inc (Version 2024.09.0+375) [Computer software] www.Rstudio.com.
- Saari, S., Richter, S., Higgins, M., Oberhofer, M., Jennings, A., & Faeth, S. H. (2016). Urbanization is not associated with increased abundance or decreased richness of terrestrial animals—Dissecting the literature through meta-analysis. *Urban Ecosystems*, 19(3), 1251–1264. <https://doi.org/10.1007/s11252-016-0549-x>
- Seress, G., Sándor, K., Bókony, V., Bukor, B., Hubai, K., & Liker, A. (2025). Radio-tracking urban breeding birds: The importance of native vegetation. *Ecological Applications*, 35(1), e3095. <https://doi.org/10.1002/eap.3095>
- Soga, M., Yamaura, Y., Koike, S., & Gaston, K. J. (2014). Land sharing vs. land sparing: Does the compact city reconcile urban development and biodiversity conservation? *Journal of Applied Ecology*, 51(5), 1378–1386. <https://doi.org/10.1111/1365-2664.12280>
- Sol, D., Trisos, C., Múrria, C., Jeliakov, A., González-Lagos, C., Pigot, A. L., Ricotta, C., Swan, C. M., Tobias, J. A., & Pavoine, S. (2020). The worldwide impact of urbanisation on avian functional diversity. *Ecology Letters*, 23(6), 962–972. <https://doi.org/10.1111/ele.13495>
- Sorace, A., & Gustin, M. (2008). Homogenisation processes and local effects on avifaunal composition in Italian towns. *Acta Oecologica*, 33(1), 15–26. <https://doi.org/10.1016/j.actao.2007.07.003>
- Taylor, L., Taylor, C., & Davis, A. (2013). The impact of urbanisation on avian species: The inextricable link between people and birds. *Urban Ecosystems*, 16(3), 481–498. <https://doi.org/10.1007/s11252-012-0283-y>
- Tryjanowski, P., Morelli, F., & Möller, A. P. (2020). Urban birds: Urban avoiders, urban adapters, and urban exploiters. *The routledge handbook of urban ecology* (2nd edn). Routledge.
- Tscharntke, T., & Batáry, P. (2023). Agriculture, urbanization, climate, and forest change drive bird declines. *Proceedings of the National Academy of Sciences*, 120(22), Article e2305216120. <https://doi.org/10.1073/pnas.2305216120>
- Wei, T., Simko, V., Levy, M., Xie, Y., Jin, Y., & Zemla, J. (2017). Package 'corrplot'. *Statistician*, 56(316), e24.
- Werner, P. (2011). The ecology of urban areas and their functions for species diversity. *Landscape and Ecological Engineering*, 7(2), 231–240. <https://doi.org/10.1007/s11355-011-0153-4>
- Wickham, H. (2016). *Ggplot2*. Springer International Publishing. <https://doi.org/10.1007/978-3-319-24277-4>
- Wu, Z., Dou, P., & Chen, L. (2019). Comparative and combinative cooling effects of different spatial arrangements of buildings and trees on microclimate. *Sustainable Cities and Society*, 51, Article 101711. <https://doi.org/10.1016/j.scs.2019.101711>
- Yu, H., Xiao, H., & Gu, X. (2025). Impact of urban environmental matrices on bird diversity: Mediating effects and ecological thresholds. *Applied Geography*, 174, Article 103476. <https://doi.org/10.1016/j.apgeog.2024.103476>

Supplementary Material of Sealed surfaces limit bird diversity, whereas tall structures may support abundance of some species, while both filter traits in urban landscapes

Table S1. Species names, codes, trait values, abundance (N), and indicator values (IndVal) of the observed bird species. The asterisks after indicator values show the significance levels: *P < 0.05, **P < 0.01, ***P < 0.001. Sources of trait categorisation: (Barbaro and van Halder, 2009; Cramp, 1993; Keller et al., 2020; Korányi et al., 2021; Lakatos et al., 2022; Remsen and Robinson, 1990; Sheard et al., 2024; Tobias et al., 2022).

Species	Species name codes	Diet ^a	Nestling diet ^b	Foraging technique ^c	Nest location ^d	Migration status ^e	Body mass (g)	N	IndVal	Habitat ^f
<i>Accipiter nisus</i> – Eurasian sparrowhawk	ACCNIS	Insectivore	Insectivore	Hawker	Open in tree canopy	Temperate/short term	220.79	5		
<i>Acrocephalus schoenobaenus</i> – Sedge warbler	ACRSCH	Insectivore	Insectivore	Understory gleaner	Shrub	Tropical	11.8	1		
<i>Aegithalos caudatus</i> – Long-tailed tit	AEGCAU	Insectivore	Insectivore	Understory gleaner	Shrub	Resident	8.6	13		
<i>Apus apus</i> – Common swift	APUAPU	Insectivore	Insectivore	Hawker	Building	Tropical	37.6	420		
<i>Buteo buteo</i> – Common buzzard	BUTBUT	Insectivore	Insectivore	Canopy foliage gleaner/perch hunter	Open in tree canopy	Resident	848.1	2		
<i>Carduelis carduelis</i> – European goldfinch	CARCAR	Granivore	Mixed diet	Understory gleaner	Open in tree canopy	Temperate/short term	16	186		
<i>Certhia familiaris</i> – Eurasian treecreeper	CERFAM	Insectivore	Insectivore	Bark forager	Cavity	Resident	9	1		
<i>Chloris chloris</i> – European greenfinch	CHLCHL	Granivore	Granivore	Understory gleaner	Shrub	Resident	26	53		
<i>Ciconia ciconia</i> – White stork	CICCIC	Insectivore	Insectivore	Ground gleaner	Open in tree canopy	Tropical	3445.8	2		
<i>Coccothraustes coccothraustes</i> – Hawfinch	COCCOC	Mixed diet	Mixed diet	Bark forager	Open in tree canopy	Temperate/short term	56.63	11		
<i>Columba livia</i> – Rock dove/Feral Pigeon	COLLIV	Granivore	Granivore	Ground gleaner	Building	Resident	297.1	588	0.357**	HBHS
<i>Coloeus monedula</i> – Eurasian jackdaw	COLMON	Mixed diet	Insectivore	Ground gleaner	Cavity	Temperate/short term	246	114		
<i>Columba palumbus</i> – Common wood pigeon	COLPAL	Granivore	Granivore	Ground gleaner	Open in tree canopy	Resident	487	334		

<i>Corvus frugilegus</i> – Rook	CORFRU	Mixed diet	Insectivore	Ground prober	Open in tree canopy	Resident	452.1	296		
<i>Corvus corone cornix</i> – hooded Crow	CORNIX	Mixed diet	Mixed diet	Ground prober	Open in tree canopy	Resident	499	58		
<i>Corvus corax</i> – Common raven	CORRAX	Mixed diet	Insectivore	Ground gleaner	Open in tree canopy	Temperate/short term	928	3		
<i>Cuculus canorus</i> – Common cuckoo	CUCCAN	Insectivore	Insectivore	Canopy foliage gleaner/perch hunter	Shrub	Tropical	111.4	2		
<i>Cyanistes caeruleus</i> – Eurasian blue tit	CYACAE	Mixed diet	Insectivore	Canopy foliage gleaner/perch hunter	Cavity	Resident	11.1	24		
<i>Delichon urbicum</i> – Common house martin	DELURB	Insectivore	Insectivore	Hawker	Building	Tropical	14.5	155	0.325*	HBHS
<i>Dendrocopos major</i> – Great spotted woodpecker	DENMAJ	Mixed diet	Insectivore	Bark forager	Cavity	Resident	74.9	22	0.332	LBHS
<i>Dendrocopos syriacus</i> – Syrian woodpecker	DENSYR	Mixed diet	Insectivore	Bark forager	Cavity	Resident	76.7	11		
<i>Erithacus rubecula</i> – European robin	ERIRUB	Insectivore	Insectivore	Ground gleaner	Shrub	Temperate/short term	17.7	12		
<i>Falco tinnunculus</i> – Common kestrel	FALTIN	Insectivore	Insectivore	Canopy foliage gleaner/perch hunter	Building	Temperate/short term	183.2	12		
<i>Fringilla coelebs</i> – Common chaffinch	FRICOE	Mixed diet	Insectivore	Understory gleaner	Open in tree canopy	Temperate/short term	23	75	0.273*	LBHS
<i>Garrulus glandarius</i> – Eurasian jay	GARGLA	Mixed diet	Insectivore	Understory gleaner	Open in tree canopy	Temperate/short term	159.5	21	0.325**	LBLS
<i>Hirundo rustica</i> – Barn swallow	HIRRUS	Insectivore	Insectivore	Hawker	Building	Tropical	20.5	26	0.286*	HBHS
<i>Lanius collurio</i> – Red-backed shrike	LANCOL	Insectivore	Insectivore	Understory gleaner	Shrub	Tropical	28.4	3		
<i>Linaria cannabina</i> – Common linnet	LINCAN	Granivore	Granivore	Ground gleaner	Shrub	Resident	19.5	13		
<i>Luscinia megarhynchos</i> – Common nightingale	LUSMEG	Insectivore	Insectivore	Ground gleaner	Ground	Tropical	19.6	13		
<i>Motacilla alba</i> – White wagtail	MOTALB	Insectivore	Insectivore	Ground gleaner	Building	Temperate/short term	23.9	3		

<i>Muscicapa striata</i> – Spotted flycatcher	MUSSTR	Insectivore	Insectivore	Canopy foliage gleaner/perch hunter	Cavity	Tropical	15.9	22	0.301*	LBHS
<i>Oriolus oriolus</i> – Eurasian golden oriole	ORIORI	Mixed diet	Insectivore	Canopy foliage gleaner/perch hunter	Open in tree canopy	Tropical	79	9		
<i>Parus major</i> – Great tit	PARMAJ	Mixed diet	Insectivore	Canopy foliage gleaner/perch hunter	Cavity	Resident	16.3	203		
<i>Parus palustris</i> – Marsh tit	PARPAL	Mixed diet	Insectivore	Understory gleaner	Cavity	Resident	11.1	8		
<i>Passer domesticus</i> – House sparrow	PASDOM	Mixed diet	Insectivore	Ground gleaner	Building	Resident	26.5	258		
<i>Passer montanus</i> – Eurasian tree sparrow	PASMON	Mixed diet	Insectivore	Understory gleaner	Building	Resident	21.4	47		
<i>Periparus ater</i> – Coal tit	PERATE	Mixed diet	Insectivore	Canopy foliage gleaner/perch hunter	Cavity	Resident	9.2	6		
<i>Phasianus colchicus</i> – Common pheasant	PHACOL	Mixed diet	Insectivore	Ground prober	Ground	Resident	1120.3	2		
<i>Phoenicurus ochruros</i> – Black redstart	PHOOCH	Mixed diet	Insectivore	Canopy foliage gleaner/perch hunter	Cavity	Temperate/short term	16.5	164		
<i>Phylloscopus collybita</i> – Common chiffchaff	PHYCOL	Insectivore	Insectivore	Canopy foliage gleaner/perch hunter	Ground	Tropical	8.3	15		
<i>Phylloscopus sibilatrix</i> – Wood warbler	PHYSIB	Insectivore	Insectivore	Canopy foliage gleaner/perch hunter	Ground	Tropical	9.2	4		
<i>Pica pica</i> – Eurasian magpie	PICPIC	Mixed diet	Insectivore	Ground prober	Open in tree canopy	Resident	217.5	14		
<i>Picus viridis</i> – European green woodpecker	PICVIR	Insectivore	Insectivore	Ground prober	Cavity	Resident	176	1		
<i>Saxicola rubicola</i> – European stonechat	SAXRUB	Insectivore	Insectivore	Ground gleaner	Ground	Tropical	16.6	1		
<i>Serinus serinus</i> – European serin	SERSER	Granivore	Granivore	Ground gleaner	Open in tree canopy	Temperate/short term	11.2	47		
<i>Sitta europaea</i> – Eurasian nuthatch	SITEUR	Insectivore	Insectivore	Bark forager	Cavity	Resident	20.4	5		

<i>Strix aluco</i> – Tawny owl	STRDEC	Granivore	Granivore	Ground gleaner	Open in tree canopy	Resident	149	231	0.309*
<i>Streptopelia turtur</i> – European turtle dove	STRTUR	Granivore	Granivore	Ground gleaner	Open in tree canopy	Tropical	132	6	
<i>Sturnus vulgaris</i> – Common starling	STUVUL	Mixed diet	Insectivore	Ground prober	Building	Temperate/short term	77.1	170	
<i>Sylvia atricapilla</i> – Eurasian blackcap	SYLATR	Mixed diet	Insectivore	Understory gleaner	Shrub	Temperate/short term	16.7	105	
<i>Curruca communis</i> – Common whitethroat	CURCOM	Mixed diet	Insectivore	Understory gleaner	Shrub	Tropical	15.1	2	
<i>Curruca curruca</i> – Lesser whitethroat	CURCUR	Mixed diet	Insectivore	Understory gleaner	Shrub	Tropical	11.4	24	
<i>Troglodytes troglodytes</i> – Eurasian wren	TROTRO	Insectivore	Insectivore	Ground gleaner	Shrub	Tropical	9.7	1	
<i>Turdus merula</i> – Common blackbird	TURMER	Mixed diet	Insectivore	Ground prober	Shrub	Temperate/short term	102.7	422	
<i>Turdus philomelos</i> – Song thrush	TURPHI	Mixed diet	Insectivore	Ground prober	Open in tree canopy	Temperate/short term	67.7	31	
<i>Otus scops</i> – Eurasian scops owl	OTUSCO	Insectivore	Insectivore	Canopy foliage gleaner/perch hunter	Building	Tropical	92	2	
<i>Pernis apivorus</i> – European honey buzzard	PERAPI	Insectivore	Insectivore	Ground prober	Open in tree canopy	Tropical	754.4	1	
<i>Phoenicurus phoenicurus</i> – Common redstart	PHOPHO	Insectivore	Insectivore	Canopy foliage gleaner/hawker	Cavity	Tropical	14.6	2	

^aDiet category codes: Granivore – 1, Mixed diet – 2, Carnivore – 3

^bNestling diet category codes: Granivore – 1, Mixed diet – 2, Carnivore – 3

^cForaging technique category codes: Ground prober – 1, Ground gleaner – 2, Understory gleaner – 3, Bark forager – 4, Canopy foliage gleaner/perch hunter – 5, Hawker (continuous aerial feeder) – 6

^dNest location category codes: Ground – 1, Shrub – 2, Open in tree canopy – 3, Cavity – 4, Building – 5^eMigration status category codes: Resident – 1, Temperate/short term – 2, Tropical – 3

^fCodes representing the habitats: HBHS – high buildings and high sealed area, HBLS – high buildings and low sealed area, LBHS – low buildings and high sealed area, LBLs – low buildings and low sealed area

Fig. S1. Photos of the studied urban structural types: (a) site with tall buildings and high sealed cover; (b) site with tall buildings and low sealed cover; (c) site with low buildings and high sealed cover; site with low building and low sealed cover (d).

a



b



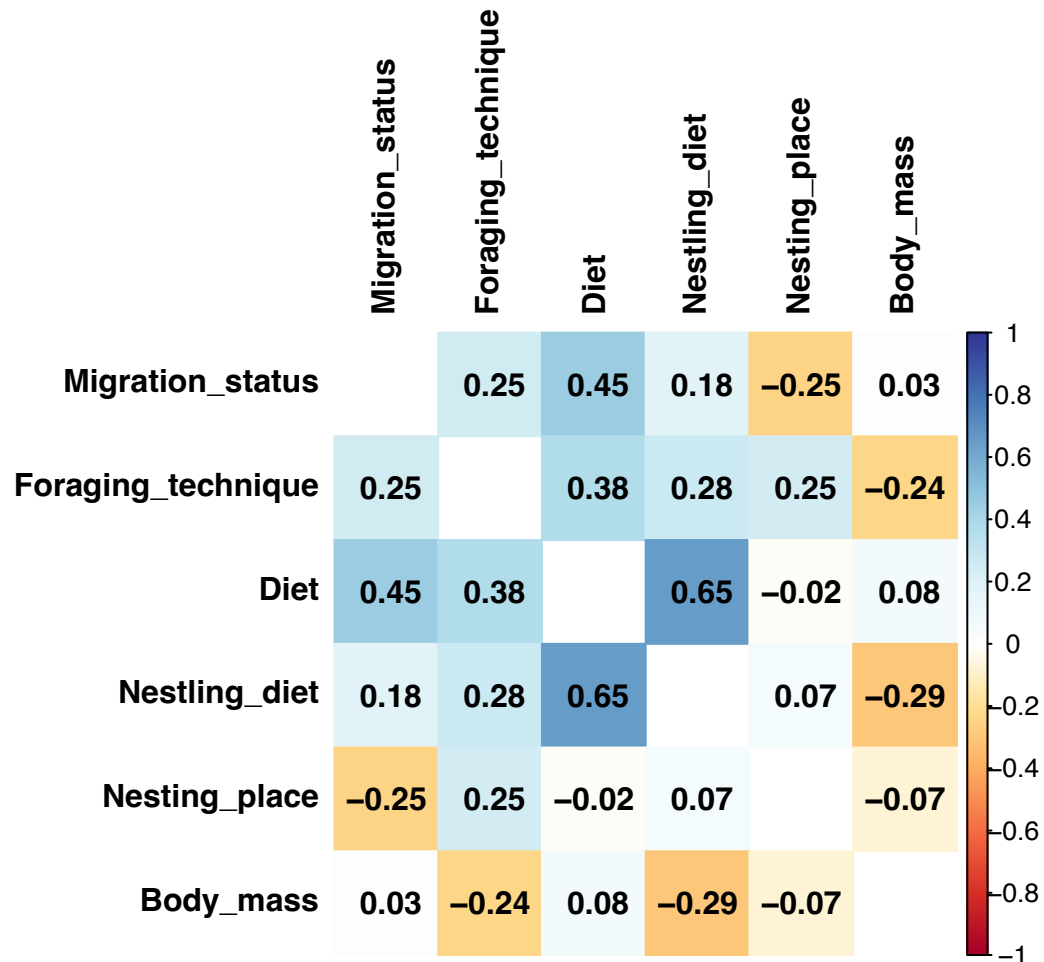
c



d



Fig. S2. Correlation matrix of bird functional trait values across all sampling sites. Numbers indicate Spearman correlation coefficients between pairs of traits. Darker yellow (red) indicates stronger positive correlations, darker blue indicates stronger negative correlations. Most traits were weakly correlated ($|r| < 0.4$), except for diet and nestling diet ($r = 0.65$), reflecting the ecological similarity of adult and nestling diets.



Appendix 1. Lakatos_sampling_sites.kmz

Location of the 100 sampling sites in Western Hungary. Sites are categorised based on urban structural variables: ‘HBHS’ indicates areas with high buildings and high sealed surface cover; ‘HBLS’ indicates high buildings and low sealing; ‘LBHS’ indicates low buildings and high sealing; and ‘LBLS’ indicates low buildings and low sealing. Numbers represent replicate sites within each category.

References

- Barbaro, L., van Halder, I., 2009. Linking bird, carabid beetle and butterfly life-history traits to habitat fragmentation in mosaic landscapes. *Ecography* 32, 321–333.
<https://doi.org/10.1111/j.1600-0587.2008.05546.x>
- Cramp, S., 1993. *Handbook of the Birds of Europe, the Middle East and North Africa: The Birds of the Western Palearctic*. Oxford University Press.
- Keller, V., Herrando, S., Voříšek, P., 2020. *European Breeding Bird Atlas 2: Distribution, Abundance and Change*. Lynx Edicions.
- Korányi, D., Gallé, R., Donkó, B., Chamberlain, D.E., Batáry, P., 2021. Urbanization does not affect green space bird species richness in a mid-sized city. *Urban Ecosyst* 24, 789–800.
<https://doi.org/10.1007/s11252-020-01083-2>
- Lakatos, T., Chamberlain, D.E., Garamszegi, L.Z., Batáry, P., 2022. No place for ground-dwellers in cities: A meta-analysis on bird functional traits. *Global Ecology and Conservation* 38, e02217. <https://doi.org/10.1016/j.gecco.2022.e02217>
- Remsen, J., Robinson, S., 1990. A Classification Scheme for Foraging Behavior of Birds in Terrestrial Habitats. *Studies in Avian Biology* 13.
- Sheard, C., Street, S.E., Healy, S.D., Troisi, C.A., Clark, A.D., Yovcheva, A., Trébaol, A., Vanadzina, K., Lala, K.N., 2024. Nest traits for the world's birds. *Global Ecology and Biogeography* 33, 206–214. <https://doi.org/10.1111/geb.13783>
- Tobias, J.A., Sheard, C., Pigot, A.L., Devenish, A.J.M., Yang, J., Sayol, F., Neate-Clegg, M.H.C., Alioravainen, N., Weeks, T.L., Barber, R.A., Walkden, P.A., MacGregor, H.E.A., Jones, S.E.I., Vincent, C., Phillips, A.G., Marples, N.M., Montaña-Centellas, F.A., Leandro-Silva, V., Claramunt, S., Darski, B., Freeman, B.G., Bregman, T.P., Cooney, C.R., Hughes, E.C., Capp, E.J.R., Varley, Z.K., Friedman, N.R., Korntheuer, H., Corrales-Vargas, A., Trisos, C.H., Weeks, B.C., Hanz, D.M., Töpfer, T., Bravo, G.A., Remeš, V., Nowak, L., Carneiro, L.S., Moncada R., A.J., Matysioková, B., Baldassarre, D.T., Martínez-Salinas, A., Wolfe, J.D., Chapman, P.M., Daly, B.G., Sorensen, M.C., Neu, A., Ford, M.A., Mayhew, R.J., Fabio Silveira, L., Kelly, D.J., Annorbah, N.N.D., Pollock, H.S., Grabowska-Zhang, A.M., McEntee, J.P., Carlos T. Gonzalez, J., Meneses, C.G., Muñoz, M.C., Powell, L.L., Jamie, G.A., Matthews, T.J., Johnson, O., Brito, G.R.R., Zyskowski, K., Crates, R., Harvey, M.G., Jurado Zevallos, M., Hosner, P.A., Bradfer-Lawrence, T., Maley, J.M., Stiles, F.G., Lima, H.S., Provost, K.L., Chibesa, M., Mashao, M., Howard, J.T., Mlamba, E., Chua, M.A.H., Li, B., Gómez, M.I., García, N.C., Päckert, M., Fuchs, J., Ali, J.R., Derryberry, E.P., Carlson, M.L., Urriza, R.C., Brzeski, K.E., Prawiradilaga, D.M., Rayner, M.J., Miller, E.T., Bowie, R.C.K., Lafontaine, R.-M., Scofield, R.P., Lou, Y., Somarathna, L., Lepage, D., Illif, M., Neuschulz, E.L., Templin, M., Dehling, D.M., Cooper, J.C., Pauwels, O.S.G., Analuddin, K., Fjeldsø, J., Seddon, N., Sweet, P.R., DeClerck, F.A.J., Naka, L.N., Brawn, J.D., Aleixo, A., Böhning-Gaese, K., Rahbek, C., Fritz, S.A., Thomas, G.H., Schleuning, M., 2022. AVONET: morphological, ecological and geographical data for all birds. *Ecology Letters* 25, 581–597.
<https://doi.org/10.1111/ele.13898>