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Original article

Functional trait filtering and decline in species richness in urban parks hinder ground-breeding and insectivorous birds

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ABSTRACT

While urbanisation often leads to habitat degradation and biodiversity loss, some urban habitats, particularly city parks, can support high levels of diversity. However, their role in species conservation remains underexplored in Central Eastern Europe. In this study, we assessed bird species richness, abundance, and community and functional composition in nine cities across Hungary and Romania. In each city, we selected two parks in central and two in suburban areas, along with peri-urban reference sites (two forest edges and two agricultural margins per city), totalling 72 sampling sites. We conducted point counts and assigned functional traits to each bird species (adult and nestling diet, foraging technique, nesting site, migration status, and body mass). Species richness peaked at forest edges and decreased from peri-urban areas toward city parks, whereas overall bird abundance did not significantly differ among habitats. The number of insectivores decreased toward urban parks from forest edges, which was also evident in the case of nestlings' diet. Birds foraging at lower levels (i.e., closer to the ground) were more frequent at agricultural field margins, whereas those foraging at higher levels were more common at forest edges. The number of birds nesting at higher sites increased from peri-urban areas to urban parks, at the expense of species nesting on or close to the ground. Field margins hosted more large-bodied birds, whereas smaller-bodied birds were more common in city parks and forest edges. Our findings highlight that although intensively managed city parks can support relatively diverse bird communities, promoting nature friendly management and ecological connectivity is crucial for sustaining avian diversity and supporting associated ecosystem services in cities.

1. Introduction

Urbanisation takes areas away from nature at an increasing pace and is widely recognized as a major ecological threat (Elmqvist et al., 2016). As a result, many species face the overall negative consequences of land-use and land cover change, including habitat loss, fragmentation,

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and degradation (Elmqvist et al., 2013).

Nonetheless, a variety of urban green spaces, such as parks, gardens and roadside trees, can play important roles in maintaining wildlife populations within cities (Lakatos et al., 2025; Sandström et al., 2006; Threlfall et al., 2017). Urban parks and peri-urban areas, for example, may function as critical refuge habitats that mitigate the negative impact of urbanisation (Nielsen et al., 2014). Although these green areas are often fragmented, their capacity to preserve biodiversity increases considerably when they offer high-quality habitats (Lepczyk et al., 2017). Despite the importance of these peri-urban areas, studies incorporating multiple reference habitats are still scarce in urban ecology (LaPoint et al., 2015; Rivkin et al., 2019). Such approach, however, would improve the generalisability of findings, help disentangle local and global drivers of biodiversity, and account for the inherent heterogeneity of urban landscapes (Grimm et al., 2008).

Even though urbanisation often significantly alters bird communities, the exact pattern can vary depending on city structure and the age of the city (Humphrey et al., 2023; Møller et al., 2012). Previous studies showed that the relationship between urbanisation and species diversity, and abundance is not strictly linear, as avian species richness often peaks in moderately urbanised areas (Batáry et al., 2018). In some cases, city centres may even host more species than suburbs, highlighting the importance of considering the location of parks within the city when assessing urban biodiversity (Dong et al., 2024; Haas et al., 2020). Biodiversity patterns often vary significantly across regions due to differences in land-use history, climatic conditions, and ecological interactions, highlighting the importance of studying underrepresented regions like Central and Eastern Europe (Sutcliffe et al., 2015). While North America and Western Europe have several studies on these trends, Central Eastern Europe might present distinct conservation challenges that could impact the adoptability and applicability of the management strategies based on these studies (Csákvári et al., 2021). Conducting localised and context-specific research is necessary to design effective conservation actions that suit local needs.

Although urbanisation causes/results in a decline in overall species richness, certain bird species can flourish in cities. This indicates that urban areas act as ecological filters that favour species with traits suited for fragmented habitats, human disturbance, and limited availability of certain resources (e.g., arthropod prey or large trees as nesting sites) (Reis et al., 2012). This filtering process often leads to biotic homogenisation and the loss of functionally unique species, especially those with more specialist traits, such as ground-nesting or insectivory (Lakatos et al., 2022; Máthé and Batáry, 2015). Consequently, even if some species may remain (or become) abundant in urban areas, the reduction in overall functional diversity can undermine key ecosystem services like pest control, seed dispersal, or nutrient cycling (Heyman et al., 2017).

Understanding these processes requires moving beyond traditionally examined biodiversity metrics (e.g., species richness or abundance). A functional trait-based approach may offer a more mechanistic framework by focusing on species' characteristics that influence their fitness and ecological roles (Gallé and Batáry, 2019; Sol et al., 2014). Functional diversity (e.g., assessed as the range and value of functional traits within a community) is closely linked to the stability, resilience, and efficiency of ecosystem processes. Thus, urban filtering not only reduces the number of species but also the variety of ecological functions they fulfil, ultimately leading to impoverished ecosystem service provision in urban landscapes (Grilo et al., 2022).

Despite a growing body of research on how urbanisation affects bird communities and their functional traits, there is still no clear consensus on which species and traits are the most vulnerable. A recent study by Grünwald et al. (2024) found that in 18 Western and Northern European countries the more recently urbanised bird species had more positive population trends than pre-industrial urban dwellers, likely due to rapid environmental changes in cities that affect breeding and foraging opportunities. Urban habitats may also serve as refugia for open-landscape bird species facing declines due to agricultural intensification, as highly urbanised open-habitat species showed more positive trends than those in urban woodlands. A study from Ljubljana, Eastern Europe (de Groot et al., 2021), revealed that both green space quality and spatial configuration can significantly influence bird assemblages. Smaller patches unexpectedly supporting higher abundance and equal species richness compared to larger ones due to greater habitat heterogeneity, and parks hosting different, but not fewer, species than forests. Another large-scale European study by Morelli et al. (2021) found that city parks can support bird communities with lower phylogenetic relatedness and communities that are less phylogenetically clustered exhibit a greater variation in ecological strategies, such as resource use and competitive interactions. In Hungary, Seress et al. (2025) highlighted the importance of native vegetation and large, mature trees for foraging and nestling-rearing urban great tits.

While large-scale studies are increasingly common, many still primarily focus on single cities or large urban centres. However, multi-city comparisons can provide more nuanced insights into the effects of urbanisation on birds' responses, especially regarding their functional roles. Nevertheless, findings are not always consistent. Some studies, for instance, show no negative urbanisation effects on certain groups such as granivores or insectivores (Meffert and Dziock, 2013). In a previous meta-analysis, Lakatos et al. (2022) showed that the impact of urbanisation on bird species is modulated by certain functional traits, with short-distance migrants, ground nesters, ground gleaners, and granivores being the most negatively affected in urbanised areas. Although urbanisation tends to favour resident bird species over long-distance migrants (Evans et al., 2011; Jokimäki et al., 2013), the relationship between migratory behaviour and urbanisation is not always clear, indicating a need for further investigations (Meffert and Dziock, 2013). The type of green space, such as parks vs. gardens, also influence functional diversity (Korányi et al., 2021), which is crucial for maintaining key ecosystem processes (de Bello et al., 2010; Sol et al., 2020). For example, by providing stopovers during migration and serving as breeding habitats, urban parks play an important role in mitigating urbanisation effects and maintaining avian functional diversity across man-made landscapes.

In this study, we compared bird species richness, abundance, and functional traits, as well as community composition in urban and suburban parks, using peri-urban forest edges and agricultural field margins as reference habitats. The Carpathian Basin, with its distinct urbanisation patterns, historical land use legacies, and socio-political transitions, provides a unique context to test how generalisable functional responses of bird communities are across Europe. Our research focused on nine cities in the Carpathian Basin and was guided by the following hypotheses:

1) Species richness is expected to be highest in peri-urban reference sites, then lower in suburban parks, and lowest in urban parks, reflecting the overall impact of urbanisation, however, abundance may be higher in urban parks compared to other areas, likely due to the concentration of a few common species (Batáry et al., 2018);

2) Urban environments are expected to act as ecological filters, reducing the occurrence of species with sensitive or specialised traits (e.g., strict insectivory, ground-nesting) while favouring species with traits associated with urban tolerance (e.g., omnivory or granivory, elevated nesting) leading to a shift in functional composition and trait-based homogenisation along the urbanisation gradient (Callaghan et al., 2019; Evans et al., 2011; Møller, 2009);

3) Bird community composition will significantly differ among the four habitat types, with each supporting distinct assemblages and characteristic indicator species, reflecting habitat-specific filtering and preferences (Evans et al., 2011; Kark et al., 2007; Lakatos et al., 2022);

2. Material and methods

2.1. Study area and design

The study was performed in Hungary and Romania using extensive spatial replication (Fig. 1). For each city, we selected four parks (two in heavily urbanised centres and two in suburban areas) and four reference areas (two along agricultural field margins – hence after: field margins – and two along forest edges) (for a map, see Appendix 1; for photos, see Fig. S1). Potential study sites were selected by collecting data about cities, such as population size and built-up area, from publicly available databases (Humanitarian Data Exchange, 2024; OpenStreetMap, 2024). Outside city boundaries, we designated two spatially independent reference habitats with two replicates per city: two next to deciduous semi-natural forests and another two along arable field borders – both of these habitat types are typical in peri-urban areas in our study region. Parks that were too small (< 0.2 ha) or too large (> 3.4 ha) were excluded. Average park size was 1.01 ha ± 0.08 (mean ± SEM). Urban parks were the closest to the city centres (mean ± SEM = 0.76 km ± 0.08) and had a high proportion of sealed areas (75.0 % ± 1.5), whereas suburban parks were further (mean ± SEM = 2.15 km ± 0.22) and had a moderate proportion of sealed surfaces (43.7 % ± 1.7).

2.2. Bird survey and functional traits

We conducted bird surveys using the point count method in 72 sampling sites (n = 9 cities × 4 habitats × 2 replicates from each habitat = 72). We visited each survey point two times in 2023 during early morning (within three h 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 and 4 Beaufort wind scale). Experienced ornithologists carried out the surveys in each location.

We recorded all birds contacted, visually and acoustically, within a radius of 50 m from the survey points. We counted birds while standing still for 10 min (Bibby, 2000). We excluded species from the analyses whose use of a given habitat was not clearly evident, such as aquatic species (i.e., Ardeidae, Anseriformes) (Korányi et al., 2021).

To classify the observed bird species, we selected a set of six functional traits and collected information from the available literature (Barbaro and 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, carnivore (also including mostly insectivorous species)); (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). Data on 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).

2.3. Statistical analysis

Datasets from the two survey rounds were pooled, retaining the highest number of occurrences for each species. For the categorical traits, we employed the following coding system, for instance, diet trait with three distinct ordinal levels: 1 – granivore, 2 – omnivore, and 3 – carnivore. 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 (Table S1) using the FD package (Laliberté et al., 2014; Ricotta and Moretti, 2011). To eliminate any violation against the normal distribution of model residuals (Kéry and Hatfield, 2003), abundance 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 and McLachlan, 2020). We used the species richness, abundance and

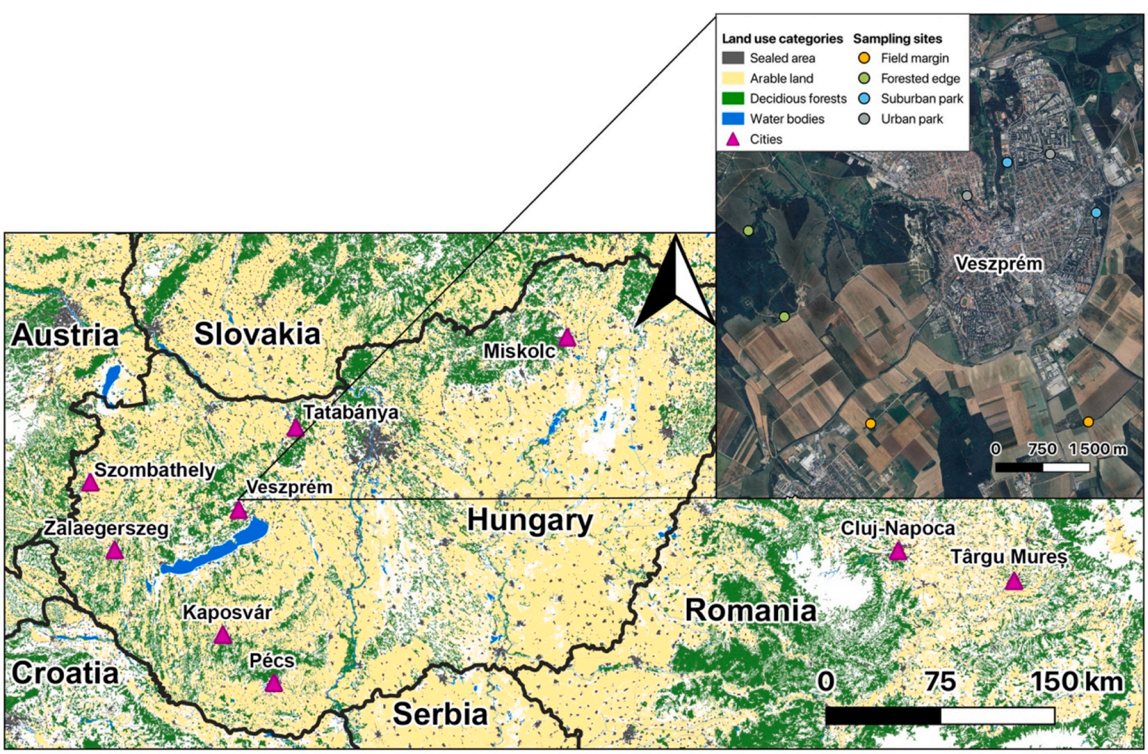

Fig. 1. Map showing the nine cities across the Carpathian Basin villages and the sampling sites within an example city (zoomed map). The map is based on the CORINE Land Cover 2018, which has some categories combined for simplicity; the satellite image of Veszprém, Hungary, was acquired from Google (CLMS, 2024; Google, 2024. "*Veszprém city map*." Google Maps. Accessed October 10, 2024. https://maps.google.com).

CWM values as response variables against the habitat types, which we treated as a fixed factor with four levels (urban park, suburban park, field margin, forest edge) 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 = 9), and the two major sampling site categories (city parks vs. reference habitats) as nested random factors. We used Tukey-type post hoc tests to conduct pairwise comparisons among the habitat types using the 'glht' function of 'multcomp' package (Hothorn et al., 2025). 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 conducted a redundancy analysis (RDA) to examine the effects of our four habitat types on the species composition of the bird communities. As constrained variables, we used the habitat types (urban and suburban parks, field margins and forest edges), whereas for conditioning variables we included the bird observers (initials of names, n = 6), cities (n = 9) and the two categories of the main habitats (parks or reference areas). Prior to RDA analysis, we ran a Hellinger transformation on the community data matrices to reduce the weight of species with high abundances (Legendre and Gallagher, 2001). We performed a permutation test based on 4999 permutations to reveal the significant effects of the predictor variables (habitat type) 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 and Legendre, 1997) to identify indicator species for each variable by using the 'indval' function of 'labdsv' package (Roberts, 2013). 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).

3. Results

At the 72 bird count points across the nine cities, we observed a total of 3021 bird individuals (after the exclusion of non-relevant species) belonging to 75 species (Table S1). The most common species were the rook (*Corvus frugilegus,* 12.7 %), the common wood pigeon (*Columba palumbus,* 8.4 %), and the common blackbird (*Turdus merula,* 7.9 %), whereas the rarest ones were the Eurasian goshawk (*Accipiter gentilis,* 0.03 %), fieldfare (*Turdus pilaris*, 0.07 %), and the garden warbler (*Sylvia borin*, 0.07 %).

Species richness was significantly lower in urban and suburban parks compared to the forest edges. There were no significant differences in the species richness between suburban and urban parks, whereas field margins did not differ significantly from both park types and forest edges (Fig. 2a, Table 1). The observed abundance of birds did not significantly vary among the four studied habitat types (Fig. 2b, Table S1).

The CWM of adult diet differed significantly between urban parks and forest edges with more granivores in urban parks and more insectivores in the forest edges, but it showed no significant differences for the other habitat type comparisons (Fig. 3a, Table 1). CWM of nestling diet showed a similar pattern to the adult's diet, with significant differences between urban parks and field margins, (urban parks showing more granivorous nestling diets), and between suburban parks and forest edges (forest edges had a higher proportion of insectivorous diets) (Fig. 2b, Table 1). The CWM values of foraging technique were higher at the forest edges compared to field margins, indicating that more species were feeding at higher elevations there, whereas there were no differences between the other habitat types (Fig. 3c, Table 1). Species nesting at higher sites were mainly found in city parks (with no significant differences between the urban and suburban parks), whereas the lower nesting sites were more common at the reference habitats outside the cities, (without significant differences between field margins and forest edges; Fig. 3d, Table 1). We observed a higher proportion of large birds in the community of field margins compared to that of suburban parks and forest edges (Fig. 3f, Table 1). We did not find any significant effect of the different habitats on the migration status of birds (Fig. 3e, Table 1).

The redundancy analysis (RDA) revealed significant differences for the bird communities across the four habitat types (Fig. 4). The four different habitat type explained a significant part of the variation in community composition, with RDA1 and RDA2 explaining 9.1 % and 1.2 % of the variance, respectively ($F = 3.56$, $p < 0.001$). The indicator value analysis (IndVal) identified several indicator species for each habitat type (Table S1). Five bird species were indicators for urban parks and one for suburban parks, six for field margins, and nine for forest edges. For example, the common blackbird (*Turdus merula*), the Eurasian collared dove (*Streptopelia decaocto*), and the black redstart (*Phoenicurus*

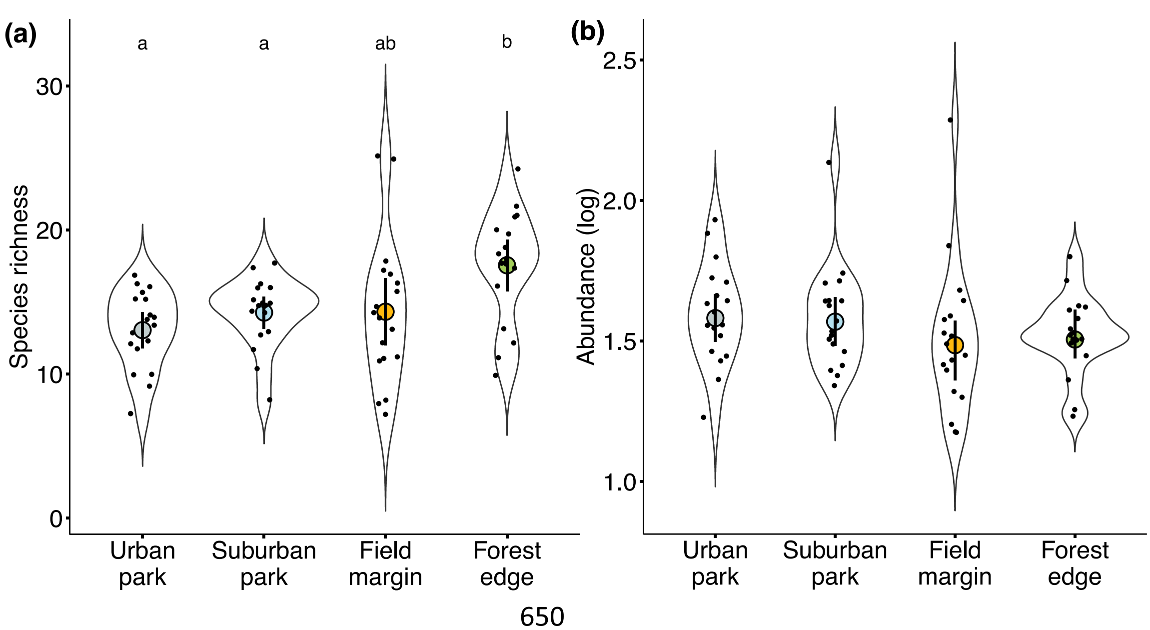

Fig. 2. Violin plots (mean ± 95 % CI; n = 72) showing the effects of habitat types on species richness (a) and abundance (b). Different letters indicate significant pairwise differences (Tukey-type post hoc tests, $p < 0.05$).

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, carnivore), nestling diet (granivore, mixed diet, carnivore), foraging technique (ground prober, ground gleaner, understory gleaner, bark forager, canopy foliage gleaner/hawker), nesting place (ground, shrub, open in tree, cavity), migration status (resident, temperate/partial migrant, tropical migrant) and body mass (in grams). Estimates are shown with 95 % CI.

Model[a]	Habitat comparison	Estimate ± CI	*df*	*t*-value	*p*-value
Species richness (0.184, 0.321)	Forest edge – Suburban park	−3.329 ± 2.507	41.3	−2.604	0.013
	Forest edge – Urban park	−4.551 ± 2.507	41.3	−3.56	< 0.001
CWM Diet (0.146, 0.404)	Field margin – Urban park	−0.080 ± 0.063	23.2	−2.51	0.02
	Forest edge – Suburban park	−0.074 ± 0.063	23.2	−2.331	0.029
	Forest edge – Urban park	−0.107 ± 0.063	23.2	−3.352	0.003
CWM Nestling diet (0.269, 0.329)	Field margin – Suburban park	−0.155 ± 0.112	63.7	−2.698	0.009
	Field margin – Urban park	−0.201 ± 0.112	63.7	−3.513	< 0.001
	Forest edge – Suburban park	−0.216 ± 0.112	63.7	−3.773	< 0.001
	Forest edge – Urban park	−0.263 ± 0.112	63.7	−4.588	< 0.001
CWM Foraging technique (0.087, 0.374)	Field margin – Forest edge	0.119 ± 0.074	53.7	3.143	0.003
CWM Nesting place (0.398, 0.549)	Field margin – Suburban park	0.134 ± 0.049	62.5	5.455	< 0.001
	Field margin – Urban park	0.169 ± 0.049	62.5	6.872	< 0.001
	Forest edge – Suburban park	0.095 ± 0.049	62.5	3.869	< 0.001
	Forest edge – Urban park	0.130 ± 0.049	62.5	5.286	< 0.001
CWM Body mass (0.098,0.237)	Field margin – Forest edge	−0.140 ± 0.121	54.1	−2.272	0.027
	Field margin – Suburban park	−0.172 ± 0.134	26.2	−2.516	0.018

[a] Values in brackets: marginal/conditional R^2

ochruros) were mainly present around the urban parks. In contrast, the house sparrow (*Passer domesticus*) was predominantly found in suburban parks. In the case of field margins, species like the Eurasian skylark (*Alauda* arvensis), common whitethroat (*Curruca communis*), and the barn swallow (*Hirundo rustica*) were present in high numbers. At forest edges, the common raven (*Corvus* corax), the great tit (*Parus major*), and the common chaffinch (*Fringilla coelebs*) were considered as indicators.

4. Discussion

In this study, we demonstrated that city parks across the Carpathian Basin exhibit lower bird species richness than forested peri-urban areas but maintain similar levels to agricultural areas. City parks primarily influenced bird nesting and foraging patterns, acting as ecological filters based on species' functional traits. Dietary traits of both adults and nestlings were particularly sensitive to urbanisation, with insectivorous species most negatively affected. Birds that forage at higher vegetation layers were more common in forest edges, while city parks served as intermediate habitats in this regard. However, city parks supported more birds nesting at higher elevations compared to reference sites, reflecting their vertical structure. Larger-bodied birds preferred agricultural field margins, likely due to their need for broader foraging areas. These findings suggest that urban parks, despite their reduced richness, play a distinct and structurally-mediated role in shaping urban bird communities. We also found region-specific patterns, such as the relatively high functional trait variance in some urban parks and the presence of species (e.g., black redstart) that respond uniquely to the historical and structural features of cities in the Carpathian Basin.

The decline in species richness in city parks compared to forest edges reflects the broader ecological consequences of urbanisation, especially in areas historically covered by forest vegetation (Fairbairn et al., 2024; Simkin et al., 2022). Interestingly, we observed no significant difference in species richness between urban and suburban parks, suggesting that city parks, in the Carpathian Basin context, can support similar numbers of species regardless of urban density (Korányi et al., 2021; Nielsen et al., 2014). This pattern may partly reflect historical urban development, as the timing of urbanisation has been shown to influence bird community composition, with long-established species often reaching higher densities (Møller et al., 2012). The observed similarity in bird abundance across habitat types may also result from the dominance of urban-tolerant species (e.g., common blackbird and house sparrow) within city parks. Furthermore, the structural heterogeneity of many parks, shaped by the legacy of socialist-era urban planning and regionally specific park management practices across Central and Eastern Europe, likely provides habitat conditions comparable to those in peri-urban areas (Haas et al., 2020).

Specialist birds are usually insectivorous species and are the most negatively affected guild by urbanisation (Máthé and Batáry, 2015; Wu et al., 2024). The main reason for the decline of this guild in urban environments is the absence of natural vegetation and the scarcity of suitable habitats for arthropods. Within each urban park, mowing was extremely frequent, with no refuge strips maintained. Nevertheless, this contrast was only visible when comparing city parks in highly urbanised environments with forest edges outside the cities. Suburban parks and agricultural field margins accounted for birds with similar dietary traits, indicating that these provide similar habitats in the sense that they support both granivorous and insectivorous species. The effects were similar for the nestlings' diet, but with a more pronounced difference between both city park types and the reference forest edge habitat, where the insectivores mostly occurred. These findings highlight the significance of diverse habitat structures in fostering higher arthropod diversity and abundance. Certain insectivores may overcome urban constraints due to their behavioural flexibility, life-history traits or specific microhabitat availability. The blackbird's urbanisation trajectory, involving distinct stages of arrival, adjustment, and spread, reflects these factors (Evans et al., 2010). Ecological conditions, human socio-economic factors, and adaptive traits influence these stages. The success of blackbird and black redstart in urban environments illustrates how urban colonisation is a gradual and spatially variable process, shaped by environmental filtering and species-specific behavioural and ecological adjustments. These differences likely reflect urban legacy effects, such as socialist-era park design, mowing regimes, tree retention, and socio-cultural use of green spaces (Møller et al., 2012). Therefore, urban conservation in Central and Eastern Europe should be tailored to regional habitat structure and management practices, rather than directly adopting Western European models.

Agricultural field margins mainly harboured ground foragers and gleaners, possibly due to the reduced structural and vertical diversity in these habitats, which limits species that forage at higher locations. Foraging techniques in both urban and suburban parks did not differ from those of the reference areas; thus, this trait was not affected by urbanisation. This finding contradicts the previous meta-analysis (studies were mainly from Western Europe), which concluded that ground gleaners are the most disadvantaged foragers within urban areas (Lakatos et al., 2022). The higher detectability of urban-tolerant ground gleaners in city parks vs. forest edges within the region, such as the common blackbird and the house sparrow (both species being the indicators of city parks), as well as the presence of trait syndromes within urban areas could be another explanation for this result. In urban areas, species with syndromes adapted to human-altered environments (e.g., tolerance to disturbance and generalist foraging behaviours) may prevail (Hahs et al., 2023). Contrastingly, at forest edges, the dominance of

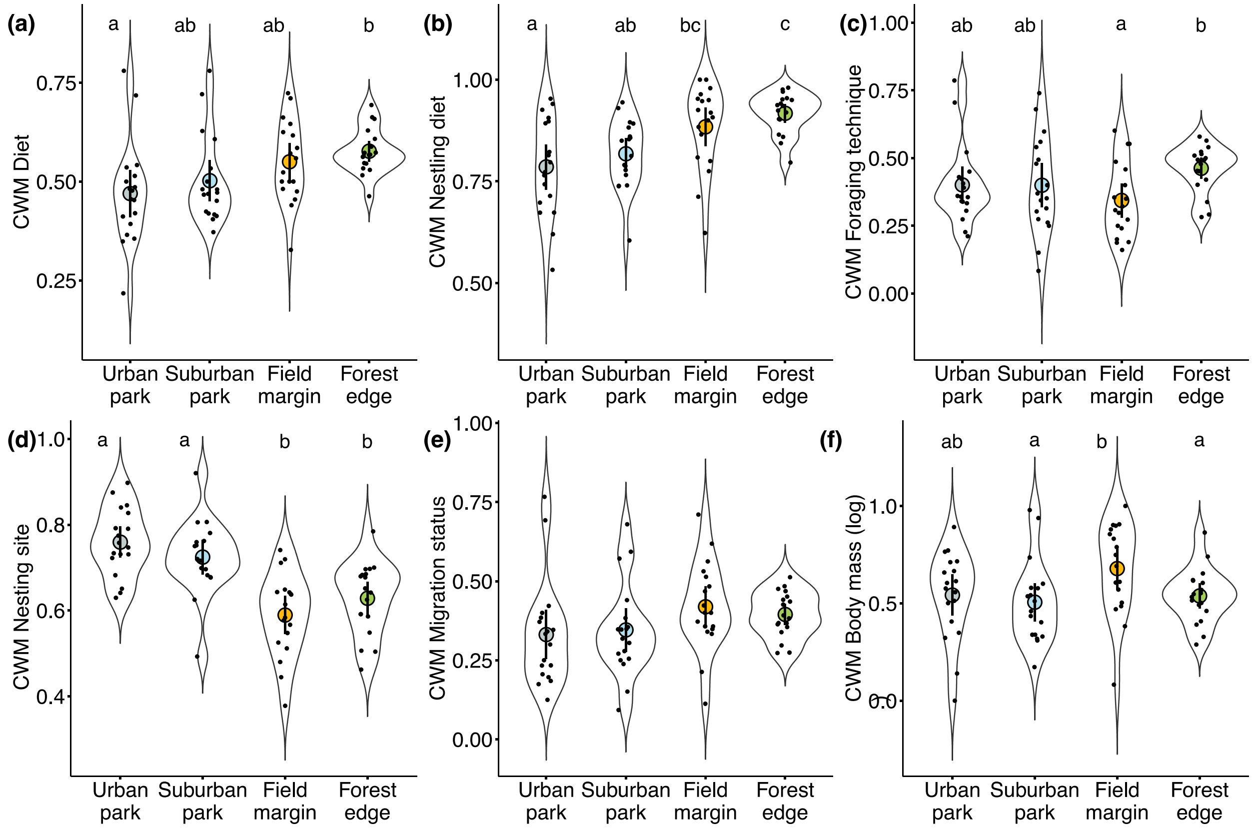

Fig. 3. Violin plots (mean ± 95 % CI; n = 72) showing the effects of habitat types on CWM trait values of bird species: (a) diet (granivore, mixed diet, carnivore); (b) nestling diet (granivore, mixed diet, carnivore); (c) foraging technique (ground prober, ground gleaner, understory gleaner, bark forager, canopy foliage gleaner/hawker); (d) nesting site (ground, shrub, open in tree, cavity); (e) migration status (resident, temperate/partial migrant, tropical migrant); (f) body mass (in grams). Different letters indicate significant pairwise differences (Tukey-type post hoc tests, p < 0.05).

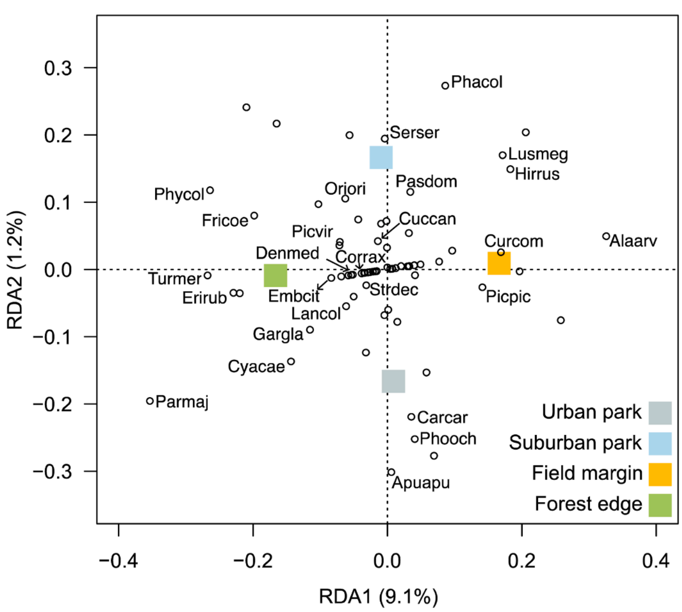

Fig. 4. Redundancy analysis biplots for all species (open dots) representing the effects of habitat types on bird communities. For better visibility, only species with significant indicator values are shown. Explained variance of RDA axes shown as percentage in parentheses. For species name abbreviations, see Table S2.

birds that forage at higher levels, highlights the importance of forested habitats in supporting birds that have specialised in vertical foraging. Management practices that support vertical vegetation complexity e.g., retaining old, tall trees, encouraging mid-storey shrub development and avoiding excessive understorey clearing can significantly support diverse foraging strategies. By structurally diversifying the vertical habitat profile, urban parks can accommodate a broader spectrum of foraging behaviours and enhance their functional role in biodiversity conservation.

Despite the diverse nesting behaviours of bird species, urban environments continue to pose substantial challenges to birds seeking suitable nesting sites. Within the highly altered urban setting, species that nest on elevated locations, e.g., tall trees and shrubs or buildings, tend to have higher survival rates compared to those species that nest closer to ground level due to elevated predation pressure by nest predators, increased human disturbance, and the frequent management of urban green infrastructures (Kurucz et al., 2021). Nest predation by corvids, red squirrels, domestic cats, and feral dogs is usually more common in highly urbanised areas, making ground- and close-to-ground nesting birds particularly susceptible (Jokimäki and Huhta, 2000; Lakatos et al., 2022). Our findings confirmed this widely detected phenomenon: among the examined nesting site categories, the most vulnerable were the ground nesters. In contrast, city parks offer better nesting opportunities for species that nest at higher sites (e.g., cavity nesters), due to the presence of buildings and other tall structures. Thus, some species can still utilise city parks, both in suburban and urban environments. To support a wider range of nesting strategies, urban park management should prioritise the retention of old trees with natural cavities, the installation of nest boxes at different heights, and the reduction of mowing intensity to preserve undisturbed nesting grounds. Restricting access for free-ranging pets, particularly cats, and minimising human disturbance near nesting areas during breeding season can further enhance breeding success.

The responses to urbanisation regarding the birds' body mass are often inconsistent. Body size may be related closely to other traits (feeding strategy or nesting behaviour), thus urbanisation's effect on body size could be more nuanced. An Australian study found that urban tolerance is positively associated with body mass, suggesting that larger-bodied birds are more prevalent in cities (Callaghan et al., 2019). In contrast, this association was negative in the case of raptors (Cooper et al., 2022). According to our study, field margins accounted for larger-bodied species (e.g., common pheasant and Eurasian magpie, which were indicator species of field margins), reflecting the suitability of these habitats for species with larger home ranges and more general dietary requirements. The patterns based on our results suggest that urbanisation favours smaller bird species, whereas semi-natural habitats like field margins provide some resources for larger-bodied birds.

We acknowledge that forest edges are subject to complex ecological processes, including edge effects as well as increased predation pressure, altered microclimates, and vegetation structure transitions (Batáry and Báldi, 2004). Disentangling these processes are integral to understanding how bird communities respond to urbanisation, given that both urban and peri-urban landscapes show strong edge characteristics, often with a mosaic of vegetation types and abrupt transitions. A possible limitation of our study is that our observations are based on a single year, which prevented examining long-term patterns. Another constraint is that we only counted birds during the breeding period, while some studies suggest that focusing on birds during the winter season can be crucial in urban ecological studies (Máthé and Batáry, 2015; Ramellini et al., 2024). Examining local parameters (e.g., park size and shape, vegetation cover and structure, surrounding land use types, etc.) could provide further insights into how city parks influence bird communities (Machar et al., 2022; Thompson et al., 2022). Focusing on species-specific responses and their phylogenetic relatedness (Morelli et al., 2021), and the potential effects of native and exotic tree species on bird species are also significant knowledge gaps (Seress et al., 2025).

5. Conclusions

City parks play an important role in conserving functionally rich bird communities; however, better park design and management with more natural features and undisturbed parts are crucial to reach their full conservation potential (Aronson et al., 2017). Nature-friendly management actions, such as reducing mowing frequency to support habitats for arthropods (prey for insectivorous birds), creating more diverse vegetation structures, and leaving old trees or dead wood on site for cavity-nesting species, could straightforwardly enhance the functional diversity of bird species in urban areas (Halecki et al., 2023; Heyman et al., 2017; Millward and Sabir, 2010; Rada et al., 2024; Threlfall et al., 2016).

Urban planners and managers should consider establishing park features that support diverse bird communities. Increasing vegetation complexity with native shrubs, groundcover, and old trees, along with creating near-natural zones, can benefit disturbance-sensitive species. Measures like artificial nest sites, predator control, and ecological corridors can further boost habitat quality and connectivity. Our findings highlight that even in green urban spaces, bird community composition reflects broader urbanisation pressure, underscoring the need for integrated, landscape-scale conservation strategies.

Our research provides novel evidence that the functional composition of urban bird communities reflects the intensity of surrounding urbanisation even within relatively green habitats like city parks. This finding suggests that local green space quality alone may not buffer the broader-scale effects of urbanisation. Combining functional trait-based approaches with large-scale landscape analysis, our work contributes a valuable perspective to the international discourse on urban biodiversity conservation.

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CRediT authorship contribution statement

Gábor Seress: Writing – review & editing. **Katalin Szitár:** Writing – review & editing. **Zoltán László:** Writing – review & editing. **Edgár Papp:** Writing – review & editing. **Jenő J. Purger:** Writing – review & editing. **Krisztina Sándor:** Writing – review & editing. **István Urák:** Writing – review & editing. **Tamás Lakatos:** Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Péter Batáry:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **András Báldi:** Writing – review & editing. **Róbert Gallé:** Investigation, Writing – original draft. **Dávid Korányi:** Writing – review & editing. **István Kovács:** Writing – review & editing. **Edina Török:** Writing – review & editing.

Declaration of Competing Interest

The authors declare no competing financial interests.

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Code and data availability

A detailed description of the models is provided in the Methods. All code and data are available from the corresponding author upon request.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ufug.2025.128988.

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Supplementary Material of "Functional trait filtering and decline in species richness in urban parks hinder ground-breeding and insectivorous birds"

Table S1. Species names, codes, trait values, abundance (N), and indicator values for habitats 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; 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	Indicator values	Habitat
Accipiter gentilis – Northern Goshawk	ACCGEN	Carnivore	Carnivore	Canopy foliage gleaner/hawker	Open in tree canopy	Temperate/short term	866	1		
Aegithalos caudatus – Long-tailed Tit	AEGCAU	Carnivore	Carnivore	Understory gleaner	Shrub	Resident	8.6	15		
Alauda arvensis – Eurasian Skylark	ALAARV	Mixed diet	Carnivore	Ground gleaner	Ground	Temperate/short term	37.3	40	0.602**	Field margin
Anthus trivialis – Tree Pipit	ANTTRI	Carnivore	Carnivore	Ground gleaner	Ground	Tropical	23.5	1		
Apus apus – Common Swift	APUAPU	Carnivore	Carnivore	Canopy foliage gleaner/hawker	Cavity	Tropical	37.6	109	0.289*	Urban park
Buteo buteo – Common Buzzard	BUTBUT	Carnivore	Carnivore	Canopy foliage gleaner/hawker	Open in tree canopy	Resident	742.3	10		
Carduelis carduelis – European Goldfinch	CARCAR	Granivore	Mixed diet	Understory gleaner	Open in tree canopy	Temperate/short term	16	79	0.385*	Urban park

Certhia brachydactyla – Short-toed Treecreeper	CERBRA	Carnivore	Carnivore	Bark forager	Cavity	Resident	8.2	3		
Certhia familiaris – Eurasian Treecreeper	CERFAM	Carnivore	Carnivore	Bark forager	Cavity	Resident	9	2		
Chloris chloris – European Greenfinch	CHLCHL	Granivore	Granivore	Understory gleaner	Shrub	Resident	26	28		
Ciconia ciconia – White Stork	CICCIC	Carnivore	Carnivore	Ground gleaner	Open in tree canopy	Tropical	3445.8	1		
Circus aeruginosus – Western Marsh Harrier	CIRAER	Carnivore	Carnivore	Canopy foliage gleaner/hawker	Ground	Temperate/short term	704.1	4		
Coccothraustes coccothraustes – Hawfinch	COCCOC	Mixed diet	Mixed diet	Bark forager	Open in tree canopy	Temperate/short term	56.63	13		
Coloeus monedula – Western Jackdaw	COLMON	Mixed diet	Granivore	Ground gleaner	Cavity	Temperate/short term	246	56		
Columba oenas – Stock Dove	COLOEN	Granivore	Granivore	Ground gleaner	Cavity	Resident	290.8	7		
Columba palumbus – Common Wood Pigeon	COLPAL	Granivore	Granivore	Ground gleaner	Open in tree canopy	Resident	487	255		
Corvus corax – Common Raven	CORRAX	Mixed diet	Mixed diet	Ground gleaner	Open in tree canopy	Temperate/short term	928	23	0.357*	Forest edge
Corvus corone cornix – Hooded Crow	CORNIX	Mixed diet	Mixed diet	Ground prober	Open in tree canopy	Resident	499	96		
Corvus frugilegus – Rook	CORFRU	Mixed diet	Carnivore	Ground prober	Open in tree canopy	Resident	452.1	383		

Coturnix coturnix – Common Quail	COTCOT	Mixed diet	Carnivore	Ground prober	Ground	Tropical	96.3	2		
Cuculus canorus – Common Cuckoo	CUCCAN	Carnivore	Carnivore	Canopy foliage gleaner/hawker	Shrub	Tropical	111.4	21		
Curruca communis – Common Whitethroat	SYLCOM	Mixed diet	Carnivore	Understory gleaner	Shrub	Tropical	15.1	20	0.566**	Field margin
Curruca curruca – Lesser Whitethroat	SYLCUR	Mixed diet	Carnivore	Understory gleaner	Shrub	Tropical	11.4	134		
Cyanistes caeruleus – Eurasian Blue Tit	CYACAE	Mixed diet	Carnivore	Canopy foliage gleaner/hawker	Cavity	Resident	11.1	40		
Delichon urbicum – Common House Martin	DELURB	Carnivore	Carnivore	Canopy foliage gleaner/hawker	Cavity	Tropical	14.5	3		
Dendrocopos major – Great Spotted Woodpecker	DENMAJ	Mixed diet	Carnivore	Bark forager	Cavity	Resident	74.9	5		
Dendrocopos syriacus – Syrian Woodpecker	DENSYR	Mixed diet	Carnivore	Bark forager	Cavity	Resident	76.7	3		
Dendrocoptes medius – Middle Spotted Woodpecker	DENMED	Carnivore	Carnivore	Bark forager	Cavity	Resident	59	6	0.361*	Forest edge
Dryocopus martius – Black Woodpecker	DRYMAR	Carnivore	Carnivore	Bark forager	Cavity	Resident	321	11		
Emberiza calandra – Corn Bunting	EMBCAL	Granivore	Carnivore	Ground gleaner	Ground	Temperate/short term	48.5	15		

Emberiza citrinella – Yellowhammer	EMBCIT	Granivore	Mixed diet	Ground gleaner	Ground	Temperate/short term	29.7	11	0.387**	Forest edge
Erithacus rubecula – European Robin	ERIRUB	Carnivore	Carnivore	Ground gleaner	Shrub	Temperate/short term	17.7	3	0.687**	Forest edge
Falco tinnunculus – Common Kestrel	FALTIN	Carnivore	Carnivore	Canopy foliage gleaner/hawker	Cavity	Temperate/short term	183.2	2		
Ficedula albicollis – Collared Flycatcher	FICALB	Carnivore	Carnivore	Canopy foliage gleaner/hawker	Cavity	Tropical	12.7	92		
Ficedula hypoleuca – European Pied Flycatcher	FICHYP	Carnivore	Carnivore	Canopy foliage gleaner/hawker	Cavity	Tropical	13.8	2		
Fringilla coelebs – Common Chaffinch	FRICOE	Mixed diet	Carnivore	Ground gleaner	Open in tree canopy	Temperate/short term	23	24	0.343*	Forest edge
Galerida cristata – Crested Lark	GALCRI	Mixed diet	Carnivore	Ground gleaner	Ground	Resident	42.7	111		
Garrulus glandarius – Eurasian Jay	GARGLA	Mixed diet	Carnivore	Understory gleaner	Open in tree canopy	Temperate/short term	159.5	3	0.328	
Hirundo rustica – Barn Swallow	HIRRUS	Carnivore	Carnivore	Canopy foliage gleaner/hawker	Cavity	Tropical	20.5	19	0.345*	Field margin
Jynx torquilla – Eurasian Wryneck	JYNTOR	Carnivore	Carnivore	Ground prober	Cavity	Tropical	35	9		
Lanius collurio – Red-backed Shrike	LANCOL	Carnivore	Carnivore	Understory gleaner	Shrub	Tropical	28.4	2	0.385*	Forest edge
Linaria cannabina – Common Linnet	LINCAN	Granivore	Granivore	Ground gleaner	Shrub	Resident	19.5	37		

Lullula arborea – Woodlark	LULARB	Carnivore	Carnivore	Canopy foliage gleaner/hawker	Cavity	Tropical	26.9	21		
Luscinia megarhynchos – Common Nightingale	LUSMEG	Carnivore	Carnivore	Ground gleaner	Ground	Tropical	19.6	5	0.491**	Field margin
Merops apiaster – European Bee-eater	MERAPI	Carnivore	Carnivore	Canopy foliage gleaner/hawker	Cavity	Tropical	56.5	9		
Motacilla alba – White Wagtail	MOTALB	Carnivore	Carnivore	Ground gleaner	Cavity	Temperate/short term	23.9	19		
Motacilla flava – Western Yellow Wagtail	MOTFLA	Carnivore	Carnivore	Ground gleaner	Ground	Tropical	17.7	38		
Muscicapa striata – Spotted Flycatcher	MUSSTR	Carnivore	Carnivore	Canopy foliage gleaner/hawker	Cavity	Tropical	15.9	166		
Oriolus oriolus – Eurasian Golden Oriole	ORIORI	Mixed diet	Carnivore	Canopy foliage gleaner/hawker	Open in tree canopy	Tropical	79	4	0.363**	Forest edge
Parus major – Great Tit	PARMAJ	Mixed diet	Carnivore	Canopy foliage gleaner/hawker	Cavity	Resident	16.3	88	0.324*	Forest edge
Passer domesticus – House Sparrow	PASDOM	Mixed diet	Carnivore	Ground gleaner	Cavity	Resident	26.5	74	0.328*	Suburban park
Passer montanus – Eurasian Tree Sparrow	PASMON	Mixed diet	Carnivore	Understory gleaner	Cavity	Resident	21.4	4		
Periparus ater – Coal Tit	PERATE	Mixed diet	Carnivore	Canopy foliage gleaner/hawker	Cavity	Resident	9.2	55		
Phasianus colchicus – Common Pheasant	PHACOL	Mixed diet	Carnivore	Ground prober	Ground	Resident	1120.3	47	0.449**	Field margin

Phoenicurus ochruros – Black Redstart	PHOOCH	Mixed diet	Carnivore	Understory gleaner	Cavity	Temperate/short term	16.5	34	0.458**	Urban park
Phylloscopus collybita – Common Chiffchaff	PHYCOL	Carnivore	Carnivore	Canopy foliage gleaner/hawker	Ground	Temperate/short term	8.3	4	0.633**	Forest edge
Phylloscopus sibilatrix – Wood Warbler	PHYSIB	Carnivore	Carnivore	Canopy foliage gleaner/hawker	Ground	Tropical	9.2	1		
Pica pica – Eurasian Magpie	PICPIC	Mixed diet	Carnivore	Ground prober	Open in tree canopy	Resident	217.5	23	0.432**	Field margin
Picus canus – Grey-headed Woodpecker	PICCAN	Carnivore	Carnivore	Ground prober	Cavity	Resident	137	5		
Picus viridis – European Green Woodpecker	PICVIR	Carnivore	Carnivore	Ground prober	Cavity	Resident	176	9		
Poecile palustris – Marsh Tit	PARPAL	Mixed diet	Carnivore	Understory gleaner	Cavity	Resident	11.1	5		
Riparia riparia – Sand Martin	RIPRIP	Carnivore	Carnivore	Canopy foliage gleaner/hawker	Cavity	Tropical	12.7	18		
Saxicola rubetra – Whinchat	SAXRUB	Carnivore	Carnivore	Ground gleaner	Ground	Tropical	16.6	31		
Serinus serinus – European Serin	SERSER	Granivore	Granivore	Ground gleaner	Open in tree canopy	Temperate/short term	11.2	75		
Sitta europaea – Eurasian Nuthatch	SITEUR	Carnivore	Carnivore	Bark forager	Cavity	Resident	20.4	6		
Streptopelia decaocto – Eurasian Collared Dove	STRDEC	Granivore	Granivore	Ground gleaner	Open in tree canopy	Resident	149	162	0.346*	Urban park

Streptopelia turtur – European Turtle Dove	STRTUR	Granivore	Granivore	Ground gleaner	Open in tree canopy	Tropical	132	88		
Sturnus vulgaris – Common Starling	STUVUL	Mixed diet	Carnivore	Ground prober	Cavity	Temperate/short term	77.1	2		
Sylvia atricapilla – Eurasian Blackcap	SYLATR	Mixed diet	Carnivore	Understory gleaner	Shrub	Temperate/short term	16.7	18		
Sylvia borin – Garden Warbler	SYLBOR	Mixed diet	Carnivore	Understory gleaner	Shrub	Tropical	18.2	18		
Troglodytes troglodytes – Eurasian Wren	TROTRO	Carnivore	Carnivore	Ground gleaner	Shrub	Temperate/short term	9.7	1		
Turdus merula – Common Blackbird	TURMER	Mixed diet	Carnivore	Ground prober	Shrub	Temperate/short term	102.7	240	0.362*	Urban park
Turdus philomelos – Song Thrush	TURPHI	Mixed diet	Carnivore	Ground prober	Open in tree canopy	Temperate/short term	67.7	39		
Turdus pilaris – Fieldfare	TURPIL	Carnivore	Carnivore	Ground prober	Open in tree canopy	Temperate/short term	106	2		
Upupa epops – Eurasian Hoopoe	UPUEPO	Carnivore	Carnivore	Ground prober	Cavity	Tropical	66.9	9		

[a]Diet category codes: Granivore – 1, Mixed diet – 2, Carnivore – 3

[b]Nestling diet category codes: Granivore – 1, Mixed diet – 2, Carnivore – 3

[c]Foraging technique category codes: Ground prober – 1, Ground gleaner – 2, Understory gleaner – 3, Bark forager – 4, Canopy foliage gleaner/hawker – 5

[d]Nest location category codes: Ground – 1, Shrub – 2, Open in tree canopy – 3, Cavity – 4

[e]Migration status category codes: Resident – 1, Temperate/short term – 2, Tropical – 3

Table S2. Summary table of the GLMM results on species richness, abundance and functional traits of birds. The following traits were considered: diet (granivore, mixed diet, carnivore), nestling diet (granivore, mixed diet, carnivore), foraging technique (ground prober, ground gleaner, understory gleaner, bark forager, canopy foliage gleaner/hawker), nesting place (ground, shrub, open in tree, cavity), migration status (resident, temperate/partial migrant, tropical migrant) and body mass (in grams). Bold estimates with 95% CI show significant effects at $p < 0.05$.

Variables[a]	Habitat comparison	Estimate ± CI	*df*	*t*-value	*p*-value
Species richness	Field margin – Forest edge	3.222 ± 2.129	53.3	2.968	0.004
(0.184, 0.321)	Field margin – Suburban park	-0.107 ± 2.507	41.3	-0.084	0.934
	Field margin – Urban park	-1.329 ± 2.507	41.3	-1.040	0.305
	Forest edge – Suburban park	**-3.329 ± 2.507**	**41.3**	**-2.604**	**0.013**
	Forest edge – Urban park	**-4.551 ± 2.507**	**41.3**	**-3.560**	**<0.001**
	Suburban park – Urban park	-1.222 ± 2.129	53.3	-1.126	0.265
Abundance	Field margin – Forest edge	0.018 ± 0.112	51.4	0.317	0.753
(0.046, 0.237)	Field margin – Suburban park	0.084 ± 0.116	37.6	1.428	0.162
	Field margin – Urban park	0.097 ± 0.116	37.6	1.640	0.109
	Forest edge – Suburban park	0.066 ± 0.116	37.6	1.121	0.269
	Forest edge – Urban park	0.078 ± 0.116	37.6	1.333	0.191
	Suburban park – Urban park	0.012 ± 0.112	51.4	0.219	0.828
CWM Diet	Field margin – Forest edge	0.027 ± 0.055	53.6	0.957	0.343
(0.146, 0.404)	Field margin – Suburban park	-0.047 ± 0.063	23.2	-1.490	0.150
	Field margin – Urban park	**-0.080 ± 0.063**	**23.2**	**-2.510**	**0.020**
	Forest edge – Suburban park	**-0.074 ± 0.063**	**23.2**	**-2.331**	**0.029**
	Forest edge – Urban park	**-0.107 ± 0.063**	**23.2**	**-3.352**	**0.003**

	Suburban park – Urban park	-0.032 ± 0.055	53.6	-1.160	0.251
CWM Nestling diet (0.269, 0.329)	Field margin – Forest edge	0.062 ± 0.112	62.9	1.077	0.286
	Field margin – Suburban park	**-0.155 ± 0.112**	**63.7**	**-2.698**	**0.009**
	Field margin – Urban park	**-0.201 ± 0.112**	**63.7**	**-3.513**	**<0.001**
	Forest edge – Suburban park	**-0.216 ± 0.112**	**63.7**	**-3.773**	**<0.001**
	Forest edge – Urban park	**-0.263 ± 0.112**	**63.7**	**-4.588**	**<0.001**
	Suburban park – Urban park	-0.047 ± 0.112	62.9	-0.816	0.418
CWM Foraging technique (0.087, 0.374)	Field margin – Forest edge	**0.119 ± 0.074**	**53.7**	**3.143**	**0.003**
	Field margin – Suburban park	0.054 ± 0.100	18.9	1.059	0.303
	Field margin – Urban park	0.055 ± 0.100	18.9	1.083	0.293
	Forest edge – Suburban park	-0.065 ± 0.100	18.9	-1.286	0.214
	Forest edge – Urban park	-0.064 ± 0.100	18.9	-1.262	0.222
	Suburban park – Urban park	0.001 ± 0.074	53.7	0.031	0.975
CWM Nesting place (0.398, 0.549)	Field margin – Forest edge	0.039 ± 0.047	61.7	1.594	0.116
	Field margin – Suburban park	**0.134 ± 0.049**	**62.5**	**5.455**	**<0.001**
	Field margin – Urban park	**0.169 ± 0.049**	**62.5**	**6.872**	**<0.001**
	Forest edge – Suburban park	**0.095 ± 0.049**	**62.5**	**3.869**	**<0.001**
	Forest edge – Urban park	**0.130 ± 0.049**	**62.5**	**5.286**	**<0.001**
	Suburban park – Urban park	0.035 ± 0.047	61.7	1.423	0.160
CWM Migration status (0.072, 0.300)	Field margin – Forest edge	-0.024 ± 0.076	53.3	-0.631	0.531
	Field margin – Suburban park	-0.076 ± 0.096	36.8	-1.539	0.132
	Field margin – Urban park	-0.091 ± 0.096	36.8	-1.837	0.074
	Forest edge – Suburban park	-0.052 ± 0.096	36.8	-1.044	0.303
	Forest edge – Urban park	-0.066 ± 0.096	36.8	-1.342	0.188
	Suburban park – Urban park	-0.015 ± 0.076	53.3	-0.380	0.706
CWM Body mass (0.098,0.237)	Field margin – Forest edge	**-0.140 ± 0.121**	**54.1**	**-2.272**	**0.027**
	Field margin – Suburban park	**-0.172 ± 0.134**	**26.2**	**-2.516**	**0.018**

	Field margin – Urban park	-0.136 ± 0.134	26.2	-1.981	0.058
	Forest edge – Suburban park	-0.032 ± 0.134	26.2	-0.464	0.647
	Forest edge – Urban park	0.005 ± 0.134	26.2	0.071	0.944
	Suburban park – Urban park	0.037 ± 0.121	54.1	0.592	0.556

[a]Values in brackets: marginal/conditional R^2

Fig. S1. Photos of the studied habitat types: (a) urban park; (b) suburban park; (c) field margin; forest edge (d).

Appendix 1. Lakatos_sampling_sites.kmz

Location of 72 sampling sites within Hungary and Romania. The name of the city is shortened to the first four letters. Urban parks are coded with ‘UP’, suburban parks with ‘SUP’, agricultural field margins with ‘AGE’, and forest edges with ‘FOE’. Numbers indicate the replicates.

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