npj | urban sustainability

Article

Published in partnership with RMIT University

https://doi.org/10.1038/s42949-025-00322-9

Urban bird diversity and ecosystem services are shaped by fine-scale habitat features

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Biodiversity and ecosystem services are known to respond to large-scale urban planning, but the ecological role of fine-scale, designable habitat features remains poorly quantified We analysed bird communities across six Italian cities in relation to habitat and human-designed features measured at a 100-m scale, quantifying taxonomic diversity and trait-based proxies of cultural (e.g. aesthetic appeal) and regulating (e.g. seed dispersal, pest control) ecosystem services. Grass and water were key predictors: grass-rich areas supported more diverse bird communities, while aquatic features enhanced both diversity and regulating services. Impervious surfaces reduced diversity and cultural values, whereas intermediate vegetation height maximized diversity, highlighting the value of structural heterogeneity. Scenario modelling showed that expanding green areas improved avian diversity far more than increasing tree height, while green-area loss caused severe declines. Our findings emphasize that integrating blue-green infrastructures and habitat complexity into urban design is essential to foster biodiversity and ecosystem services, supporting the EU Biodiversity Strategy 2030 and UN Sustainable Development Goals.

Urbanization is one of the most significant drivers of ecosystem transformation worldwide, with profound impacts on biodiversity and ecosystem functioning[1–3]. Currently, more than half of the world's population lives in urban areas, and this proportion is expected to increase to around 70% by 2050[4]. This rapid urban expansion is driving the extensive transformation of natural habitats into developed landscapes[5,6], which alters ecological processes by increasing impervious surfaces, fragmenting habitats, and modifying resource availability, resulting in biodiversity loss and biotic homogenization[7,8]. At the same time, urban environments can host diverse animal and plant communities, with some taxa adapting to novel conditions, while others decline or disappear[9,10].

Birds are among the most widely studied urban taxa[11,12]. The expansion of impervious surfaces, habitat fragmentation, and the alteration of natural land cover shape urban bird communities by filtering species based on their ability to adapt to urban environments[13–15]. These responses to urbanization drive shifts in taxonomic, functional, and phylogenetic diversity, which in turn affect ecosystem stability and the provisioning of ecosystem services[16–18]. The response of bird communities to urbanization typically varies along an urbanization gradient, from highly impervious city centres with limited green space to suburban and peri-urban areas that retain remnant natural habitats[19]. Urban green spaces, such as parks and tree-lined streets, play a crucial role in supporting diverse avian communities by providing habitat, food resources, and breeding sites[20,21]. However, the structure of urban environments may also facilitate the establishment of non-native species, influencing the functional and phylogenetic structure of native communities[22,23]. Human activities within urban parks and green spaces can also shape bird community dynamics[24]. Supplementary food provision, either intentional (e.g., bird feeding) or unintentional (e.g., food waste), can influence species composition by favouring generalist and opportunistic species[25,26]. Artificial light at night (ALAN), which is pervasive in urbanized areas, has also been shown to disrupt natural behaviours, including vocal activity, foraging patterns, and migration timing[27–29], further modifying urban bird assemblages.

Studying taxonomic, functional, and phylogenetic diversity in synergy can provide a more comprehensive understanding of how urban landscapes shape bird communities[30,31]. Functional diversity is directly linked to

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ecosystem functioning and ecosystem service provisioning, as it reflects the range of ecological roles played by species in a community[32]. For instance, functional traits related to diet and foraging strategy are key indicators of regulating ecosystem services such as seed dispersal and pest control[33]. At the same time, traits associated with bird attractiveness, such as plumage colour and vocalizations, serve as proxies for cultural ecosystem services, including human psychological well-being and recreation through birdwatching[34,35].

Given these dynamics, assessing how fine-scale habitat characteristics, including human-designed features, influence urban bird communities is crucial for understanding biodiversity patterns and the influence of the human footprint across urban landscapes. Such insights are essential not only for advancing ecological knowledge, but also for informing urban planning strategies aimed at promoting sustainable, biodiversity-friendly cities, in line with both European-wide[36] and global[37] sustainable development strategies. By identifying the habitat features that support diverse bird communities, we can help guide the design and management of urban spaces that integrate ecological and human needs. While broad-scale urbanization effects are well-documented[38–41], most studies assessing the effects of local habitat features on biodiversity have focused on analysing vegetation structure in green spaces[42–45], whilst the influence of human-designed features remains understudied[46].

We evaluate the effects of both fine-scale environmental and anthropogenic variables on avian taxonomic and functional diversity, explicitly linking urban habitat structure, human disturbance, and ecosystem service provisioning. By integrating species traits related to both regulating (e.g., pest control, seed dispersal) and cultural ecosystem services (e.g., aesthetic and recreational value), we provide a novel perspective on how urban biodiversity contributes to human well-being. Additionally, by comparing different urban contexts along an impervious-to-green gradient, we aim to disentangle the relative roles of habitat heterogeneity and human influence in shaping urban bird communities. We hypothesize that heterogeneous landscapes combining green and blue infrastructures will support greater taxonomic and functional diversity, thereby enhancing ecosystem service provisioning. Furthermore, we expect that human-designed features linked to human presence and disturbance, such as recreational spaces and artificial lighting, will mediate bird community structure and service delivery, potentially favouring generalist species over disturbance-sensitive taxa. To assess the broader planning implications of our findings, we also explore future scenarios simulating the expansion or reduction of green areas, evaluating their potential effects on avian diversity across urban landscapes. Our study contributes to a deeper understanding of how urban planning and management can promote biodiversity and ecosystem services in highly urbanized areas.

Methods

Study area and sampling design

This study was conducted across six cities in the Italian peninsula, spanning a latitudinal gradient of approximately 550 km (Fig. 1a). We adopted a stratified sampling approach to select sites within each city along a green area size-fragmentation gradient. We overlaid a 1 × 1 km grid on each city, calculated green area size and fragmentation within each cell and classified

Fig. 1 | Map of the study area and details of the study design. Location of the six cities surveyed in the Italian peninsula (**a**), details of the study design within the city of Florence (**b**) and examples of bird sampling locations according to the stratified sampling design derived from Dondina et al. (2025) (**c**); from top to bottom: urban matrix, transition zone and core green area).

cells into four size and four fragmentation classes based on cumulative green area and an aggregation index[47]. To quantify green space distribution and fragmentation, we used an updated land-use map derived from remote sensing data[48]. From this, we randomly selected 1-km grid cells (Fig. 1b), potentially representing each of the 16 possible combinations of green space size and fragmentation. Within each selected grid cell, we conducted bird surveys at three distinct locations: one in the core green area (i.e. inside parks or large vegetated areas), one in the transition zone (i.e. at the boundary between green space and urban surfaces) and one in the urban matrix (i.e. in highly built-up areas with minimal vegetation, see Fig. 1c). We aimed to include an equal number of sampling locations per city, but due to constraints such as the availability of suitable grid cells (i.e. not all of the 16 combinations were available in every city) and restricted access in some areas, the final sample size varied as follows: 47 in Turin, 45 in Milan, 34 in Florence, 35 in Rome, 32 in Naples, and 27 in Campobasso, for a total of 220 bird sampling locations.

Bird data

At each location we sampled urban bird communities using 10 min point counts[49] within a 100 m fixed-radius, recording all birds contacted visually and acoustically. We visited each sampling location twice during the breeding season to account for seasonal variations in the bird community (i.e. most resident species breed in early spring, while others, such as migrant species, breed later). Surveys were performed in April–June 2023 in the early morning under calm and dry weather conditions. During the breeding season, to avoid possible bias due to variation in diurnal activity of birds, for a given day, we performed point counts in a different order during the second survey period, leaving at least three weeks between consecutive visits to the same location. We excluded from analyses aerial foraging species (e.g. swifts *Apodidae*, swallows and martins *Hirundinidae*) since they can travel long distances to forage and are not representative of habitat use at the sampling location. For abundance estimates of each species, we pooled the data using the maximum abundance recorded over the two repeated visits for each point count location.

Habitat data

We collected fine-scale habitat data within the 100 m buffer for each point count location, considering several natural and anthropogenic habitat variables that could influence bird communities. Habitat variables were quantified as percentage cover and included impervious surfaces (e.g., streets, residential, and industrial zones), grass (used here as a general category encompassing herbaceous vegetation more broadly, without distinction among lawns, meadows, or semi-natural grasslands), shrubs (height < 4 m), tree cover (height > 4 m, separately categorized into coniferous and broad-leaved trees) and water. Additional variables included mean shrub height (calculated as the average of all shrubs) and the number of old trees (diameter at breast height > 80 cm). To characterize vertical vegetation development and its heterogeneity within the point, we extracted canopy height mean and standard deviation (SD) for each buffer (i.e. 100 m radius) from a global canopy height database[50], based on Sentinel-2 imagery at 10 m spatial resolution. Mean canopy height provides an estimate of the average vertical stature of the canopy layer, while the SD captures the heterogeneity of canopy height within the buffer, reflecting variation in vertical vegetation complexity.

We also retrieved a fine-scale land-use land-cover (LULC) classification that represented the general landscape around each point, which was created by merging and harmonizing three data sources: Land Cover Piemonte (www.geoportale.piemonte.it) for the city of Turin, DUSAF 6.0 (www.dati.lombardia.it) for the city of Milan, and Urban Atlas Copernicus (https://land.copernicus.eu/local/urban-atlas) for the other 4 cities. The 22 LULC categories were then merged into six categories: residential, impervious non-residential, farmland, forest/shrubland, urban green and others (see Table S1). We used these six categories and their percentage cover within a buffer around each point to classify each according to the dominant LULC category, i.e., the one with the highest percentage cover within the buffer.

We recorded the presence or absence of human-designed features that could potentially affect birds through disturbance (from both humans and dogs), supplementary food sources, or environmental modifications, but that can be considered as valuable features for humans. These included benches, fountains (both decorative and drinking), trash bins, small lakes or ponds, kiosks or bars, playgrounds, dog areas (i.e. fenced designated areas where dogs can be off-leash), sports facilities and artificial lighting.

Before analyses, we constructed a correlation matrix with habitat features, human-designed features and cover of LULC categories to check for potential collinearity. We omitted impervious cover and broadleaf tree cover from subsequent statistical analyses because of high collinearity with other variables (Spearman's rho > 0.6; see Fig. S1).

Trait data

We categorized bird species based on 26 functional traits, grouped into ten categories sourced from the literature[35,51–53]. These included five traits linked to cultural ecosystem services and 22 associated with regulating services. Each selected trait was hypothesized to have a functional relationship with the ecosystem service provided by the species[54], whether cultural (e.g. colour diversity as a proxy for aesthetics[55]) or regulating (e.g. diet as an indicator of biological control or seed dispersal[33]). For cultural ecosystem services, we selected five traits hypothesized to influence aesthetic and experiential value: relative tail length, colour diversity, colour elaboration, crest length, and the inverse of body mass[35]. For regulating services, we included 22 traits related to breeding behaviour, nesting, diet, foraging technique, and body size. Continuous traits were scaled between 0 and 1[56], and highly correlated variables were excluded to avoid redundancy (see Table S2 for details).

Diversity metrics

For each community (i.e. each point count), we derived three diversity metrics from the raw count data: taxonomic diversity, regulating functional diversity and cultural functional diversity. For taxonomic diversity, we calculated species richness as the cumulative number of species recorded over the two visits. We also investigated alternative diversity indices such as Shannon and Simpson, which were highly correlated with species richness (Richness vs Shannon $r = 0.82$; Richness vs Simpson $r = 0.62$; Shannon vs Simpson $r = 0.94$). Given these strong correlations, species richness was retained as the primary metric for clarity and interpretability.

As a functional diversity metric, we calculated functional dispersion using the set of traits that drives regulating ecosystem service provision for regulating functional diversity (henceforth RFD) and the set of traits that drives cultural ecosystem service provisioning for cultural functional diversity (henceforth CFD). We first built the functional trees with our species and trait set, using the R package *BAT*[67], applying the neighbour-joining algorithm. Given that our trait matrices contained both continuous and binary traits, we calculated the species trait dissimilarity matrix using Gower's distance[58] with the *gawdis* R package[59]. This method assigns weights to traits with similar ecological functions, preventing certain traits from disproportionately influencing the Gower's distance calculation. Therefore, we grouped variables representing the same functional trait (e.g., the six 'diet' variables were treated as part of a single trait), optimizing the weighting across the trait groups[59]. To avoid biases in functional diversity estimates, we excluded communities with fewer than three species[60].

Statistical analyses

To understand how species richness, RFD and CFD varied in response to fine-scale habitat variables ($n = 9$), human-designed features ($n = 10$) and LULC (a 6-level factor) across the urban environment, we fitted Generalized Linear Mixed Models using the *glmmTMB* R package[61]. We fitted six models, two for each response variable (i.e. species richness, RFD, and CFD), with one model including habitat variables and LULC, and the other including human-designed features as predictors. For species richness, we specified a Poisson distribution, while for RFD and CFD, we specified a

Gaussian distribution, as their residuals were normally distributed. Human-designed features were treated as presence-absence variables, given there was very limited variation in their abundance within the 100 m point count buffer. Each model included city identity as a random intercept to account for differences in bird communities across cities along the latitudinal gradient. To account for potential non-linear relationships, we included quadratic terms for continuous habitat variables (e.g., bare ground, grass, shrubs, trees, etc.) and selected the best model based on the lowest AIC. We also tested interactions between habitat variables that significantly influenced species richness and LULC to inform predictions for future scenarios (see below).

Model fit was assessed using the *performance* package[62] in R, through visual inspection of residual normality and heteroskedasticity, which indicated an acceptable fit. We checked species richness models using the check_overdispersion function, where no overdispersion was detected ($p > 0.05$). Additionally, we tested all models for spatial autocorrelation using the check_autocorrelation function, with no evidence of spatial autocorrelation between sampling locations ($p > 0.05$).

Scenarios of future development

We simulated future urban development scenarios to assess how projected changes in green areas and vegetation structure may influence urban bird communities. Building on current trends in land take and population growth in Italy[63], an additional 3.8 million inhabitants may be present by 2050, accompanied by an increase of approximately 700,000 hectares of urbanized land. This would result in a rise in per capita urbanization from 350 to 435 m^2 per inhabitant. While these projections suggest a continued expansion of urbanized land, exploring scenarios that include the creation or restoration of green spaces, particularly in targeted areas, remains essential to understand the potential for biodiversity gains through proactive urban planning and nature-based solutions. Testing for interactions between the significant predictors identified in our species richness GLMM and LULC types allowed us to model scenarios only within those LULC types for which a specific predictor had a significant effect. Based on these results, we created six scenarios involving green space area and canopy height, simulating: (1) an increase in green space area, (2) an increase in canopy height, (3) an increase in both components, (4) a decrease in green space area, (5) a decrease in canopy height, and (6) a simultaneous decrease in both. For each scenario, the increase or decrease was simulated in 10% increments, up to a maximum of 100%. Changes in richness were expressed as ratios between predicted richness under each scenario and predictions from the baseline dataset. This allowed us to quantify the sensitivity of urban bird communities to both spatial and structural changes in urban green infrastructure, providing insights into the relative importance of area versus vegetation complexity for biodiversity conservation in expanding urban landscapes. All analyses were conducted in R version 4.4.1.

Results

We recorded a total of 8849 individual birds belonging to 67 species (Table S3). Grass cover was positively associated with species richness, suggesting that this habitat feature is critical in supporting biodiversity in cities. Shrub height, mean and SD canopy height showed significant quadratic relationships with species richness, meaning that high levels of biodiversity are supported by intermediate levels of these features (Fig. 2a). Species richness was significantly lower where trash bins occurred, and higher where dog areas were present (Fig. 2b). There were significant differences in species richness between LULC categories, with impervious non-residential and residential areas harbouring the lowest levels of biodiversity (Fig. 2c). CFD was positively related to grass cover, water cover and mean canopy height, whilst SD canopy height showed a quadratic effect (Fig. 3a). The presence of trash bins and kiosks had a negative effect on CFD, whilst the presence of small lake/ponds and dog areas was related to higher CFD (Fig. 3b). Similar to species richness, CFD was significantly lower in impervious non-residential and residential areas (Fig. 3c). RFD was significantly and positively related to water cover and the presence of small lake/ponds (Fig. 4). Note that full outputs for all models are given in the Supplementary Information, Tables S4–S6).

There was a significant interaction between grass cover and LULC type ($\chi2 = 12.56$, $p = 0.013$): species richness increased significantly with increasing grass cover in residential ($\beta = 0.26$, SE = 0.10, $z = 2.58$, $p = 0.009$) and impervious non-residential areas ($\beta = 0.48$, SE = 0.12, $z = 3.90$, $p < 0.001$), but not in other LULC categories. Similarly, the interaction between quadratic mean canopy height and LULC type was significant ($\chi2 = 10.61$, $p = 0.031$), with significant effects in residential areas ($\beta = -0.17$, SE = 0.07, $z = -2.38$, $p = 0.017$, Fig. 5a), but no significant association among other LULC types. There were no significant interactions between LULC type and shrub height ($\chi2 = 3.37$, $p = 0.498$) or SD canopy height ($\chi2 = 1.50$, $p = 0.827$). Based on these results, we focused scenario modelling on residential and impervious non-residential areas, where grass cover and canopy height had the strongest and most consistent associations with species richness.

According to above models, a 50% increase in grass cover was predicted to result in a 7.8% increase in species richness in residential areas, and an 11% increase in species richness in impervious non-residential areas. At the same time, a decrease in grass cover led to steeper biodiversity losses in impervious non-residential contexts. A 10% increase in mean canopy height, which had a quadratic response, resulted in a small biodiversity gain (+0.06%), but sharp richness declines were predicted when canopy height decreased. Increasing canopy height beyond optimal levels led to a reduction in species richness, in accordance with the intermediate optimum detected in the models (Fig. 5b). When considering both variables together, the most beneficial scenario for urban biodiversity consisted of a combined strong increase in grass cover and a modest increase in canopy height (Fig. 5c). Expanding the extent of grass cover played a substantially greater role than changes in canopy height. The worst-case scenario involved concurrent reductions in both grass cover and canopy height, leading to pronounced losses in predicted species richness.

Discussion

Our study highlights the complex interplay between fine-scale habitat features, human-designed features, and land use in shaping urban bird communities across six Italian cities. By examining taxonomic diversity alongside cultural and regulating functional diversity, we provide a nuanced understanding of how urban habitats influence biodiversity patterns and ecosystem services provisioning. Our results emphasize the critical role of green and blue spaces in sustaining diverse urban bird communities, while also revealing the sometimes contrasting effects of human-made elements on biodiversity.

Grass cover emerged as a key driver of both taxonomic diversity and CFD, reinforcing the importance of open, vegetated areas in supporting diverse bird communities across the urban matrix[64,65]. These areas provide essential foraging grounds for many granivorous and insectivorous bird species[66], which may contribute to cultural ecosystem service provisioning in terms of birdwatching and aesthetic appreciation by people[67]. The positive association between CFD and water cover, as well as the presence of small lakes/ponds, underscores the multifunctionality of aquatic features. These elements not only have a high cultural value, but also contribute to fundamental ecological processes for ecosystem service provisioning[68], aligning with previous findings on the importance of access to water for urban biodiversity[69]. Water bodies often host waterfowl, which are aesthetically pleasing to people and enhance opportunities for birdwatching and recreational enjoyment such as bird feeding[70,71]. The presence of water may also attract insectivorous birds[72], as aquatic environments tend to support higher insect abundance, further reinforcing their ecological value in urban landscapes[73]. Water is especially important in urban habitats where free-standing water is generally scarce, and the large sources are limited to city centres (fountains) or are only short-lived (puddles after rain) and can thus be used for bathing or drinking by birds[74].

Canopy height, SD and shrub height had non-linear effects on taxonomic diversity and CFD, suggesting that intermediate structural

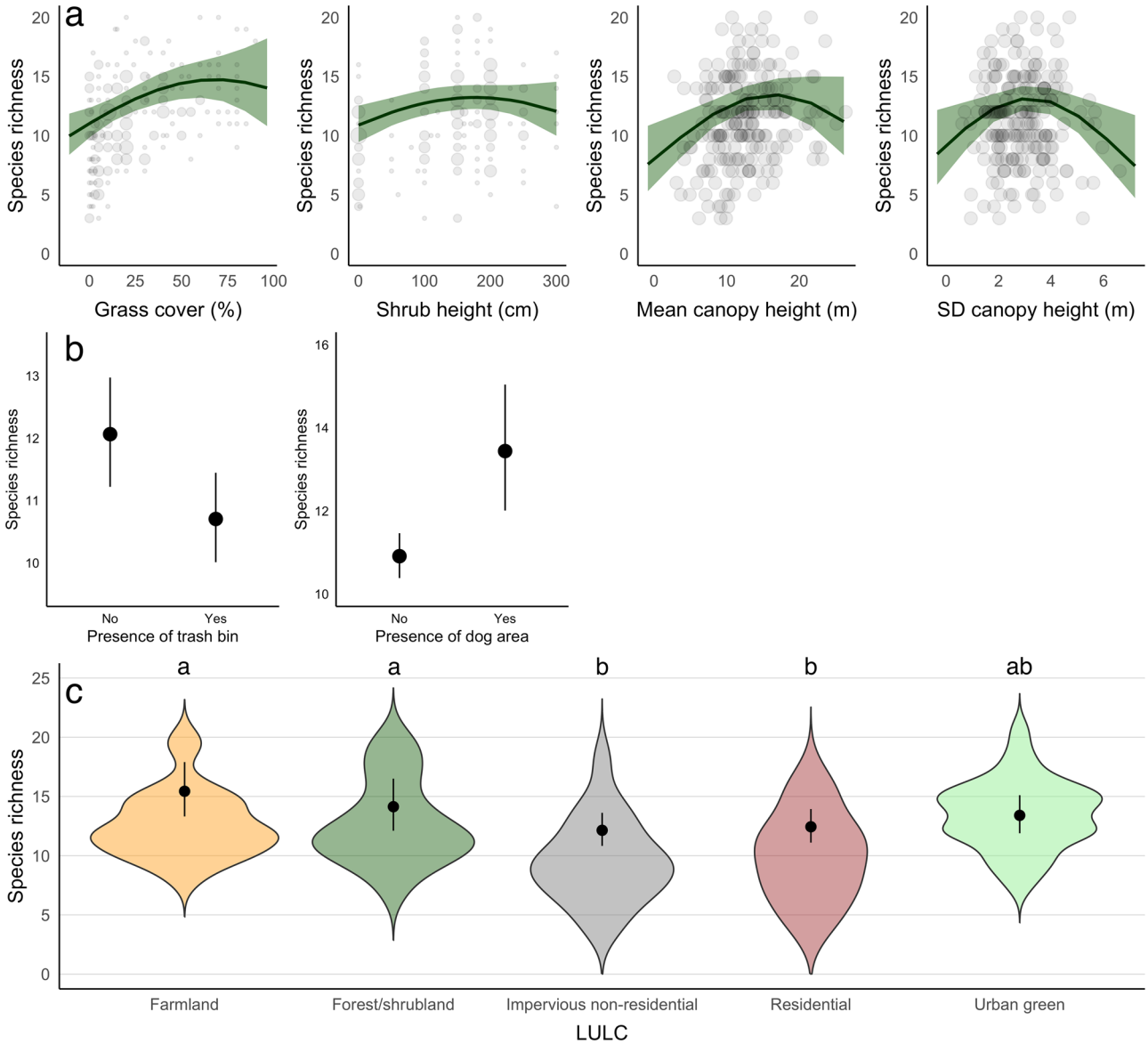


Fig. 2 | Environmental drivers of bird species richness (i.e. taxonomic diversity) across the six cities. Statistically significant effects of natural habitat (**a**), human-designed features (**b**) and land-use land-cover (LULC) (**c**) from model predictions are shown. Note that the "Others" LULC category is not shown to aid visual interpretation. Different lowercase letters represent significant differences in species richness across land-use types. See model outputs in Tab. S3.

complexity maximizes biodiversity[75]. This pattern likely reflects a balance between providing shelter and foraging opportunities without creating overly dense vegetation that may exclude open-habitat species. Such results highlight the need for thoughtful vegetation management, where heterogeneous vertical structures are needed to maintain high levels of biodiversity. Human-designed features played a complex role in shaping bird diversity. The negative impacts of trash bins on both taxonomic diversity and CFD suggest that waste accumulation and increased human activity may attract opportunistic generalists, such as corvids, at the expense of more sensitive taxa[76,77]. In contrast, the positive association between dog areas and taxonomic diversity and CFD may indicate that these spaces, often embedded within larger parks, coincide with extensive green areas that support richer and more diverse avian communities[78], despite potential disturbance from unleashed dogs. The negative effect of kiosks on CFD, similarly to trash bins, suggests that areas with high human activity and presence of generalist species may have detrimental effects on the entire bird community, with repercussions for cultural ecosystem services.

Our findings suggest that urban design should not only focus on habitat structure, but also consider how human interactions with the broader urban environment influence biodiversity and ecosystem services. The clear reduction in taxonomic diversity and CFD in impervious non-residential and residential areas underscores the detrimental impact of urbanization, as these environments lack the habitat complexity necessary to sustain diverse bird communities. However, the persistence of RFD in areas with water bodies suggests that even small-scale natural features can provide crucial refuges for species contributing to regulating ecosystem functions.

While our study provides valuable insights into the drivers of urban bird diversity across multiple cities, some limitations should be acknowledged. First, our sampling locations, although numerous and distributed across six cities, may not have captured the full heterogeneity of urban environments or seasonal dynamics in bird communities. Second, the relatively low number of sampling locations with water cover (6.8%) means that interpretations regarding the effects of aquatic features, though consistent with the literature, should be made cautiously. Moreover, functional diversity metrics are sensitive to trait data availability and trait selection; while we used ecologically relevant traits, additional dimensions (e.g., behavioural or other reproductive traits) might reveal further nuances.

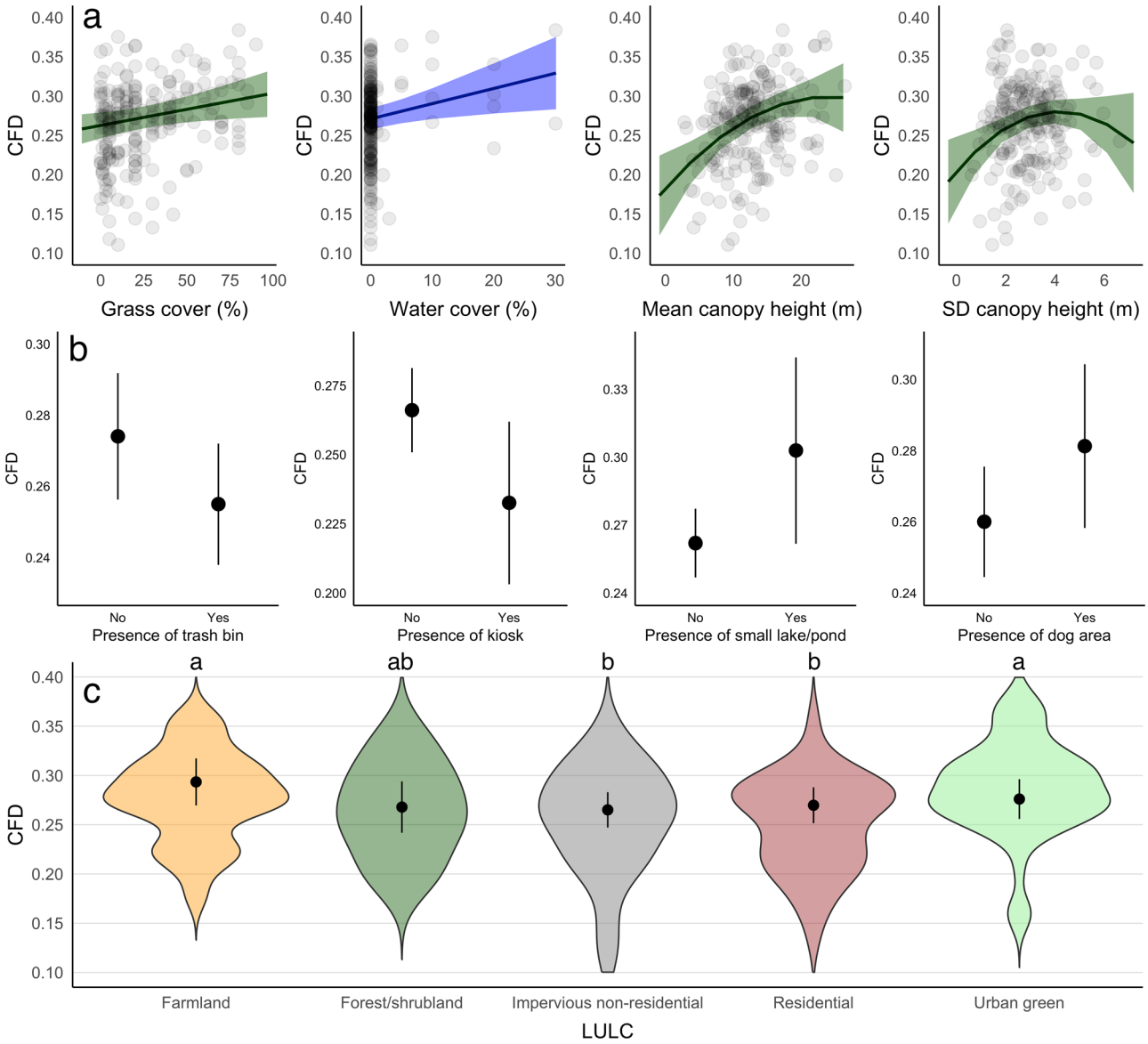
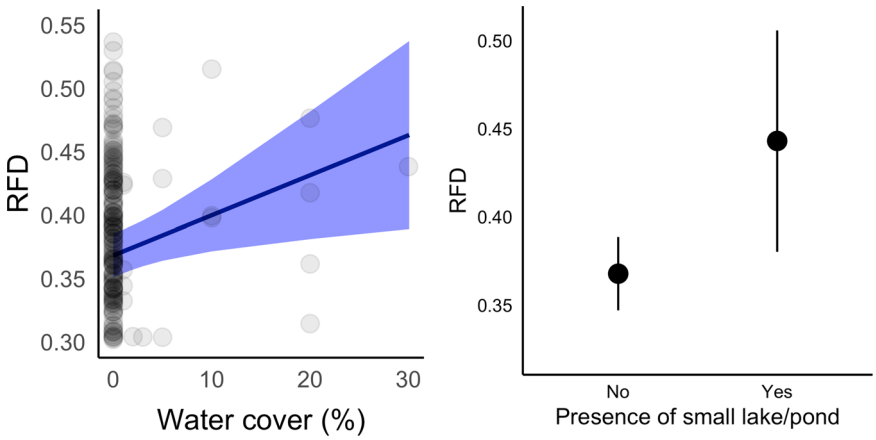


Fig. 3 | Environmental drivers of bird CFD (i.e. cultural functional diversity) across the six cities. Statistically significant effects of natural habitat (**a**), human-designed features (**b**) and land-use land-cover (LULC) (**c**) from model predictions are shown. Note that the "Others" LULC category is not shown to aid visual interpretation. Lowercase letters represent significant differences in CFD across land-use types. See model outputs in Tab S4.

Fig. 4 | Environmental drivers of bird RFD (i.e. regulating functional diversity) across the six cities. Statistically significant effects of natural habitat (left) and human-designed features (right) from model predictions are shown. See model outputs in Tab S5.



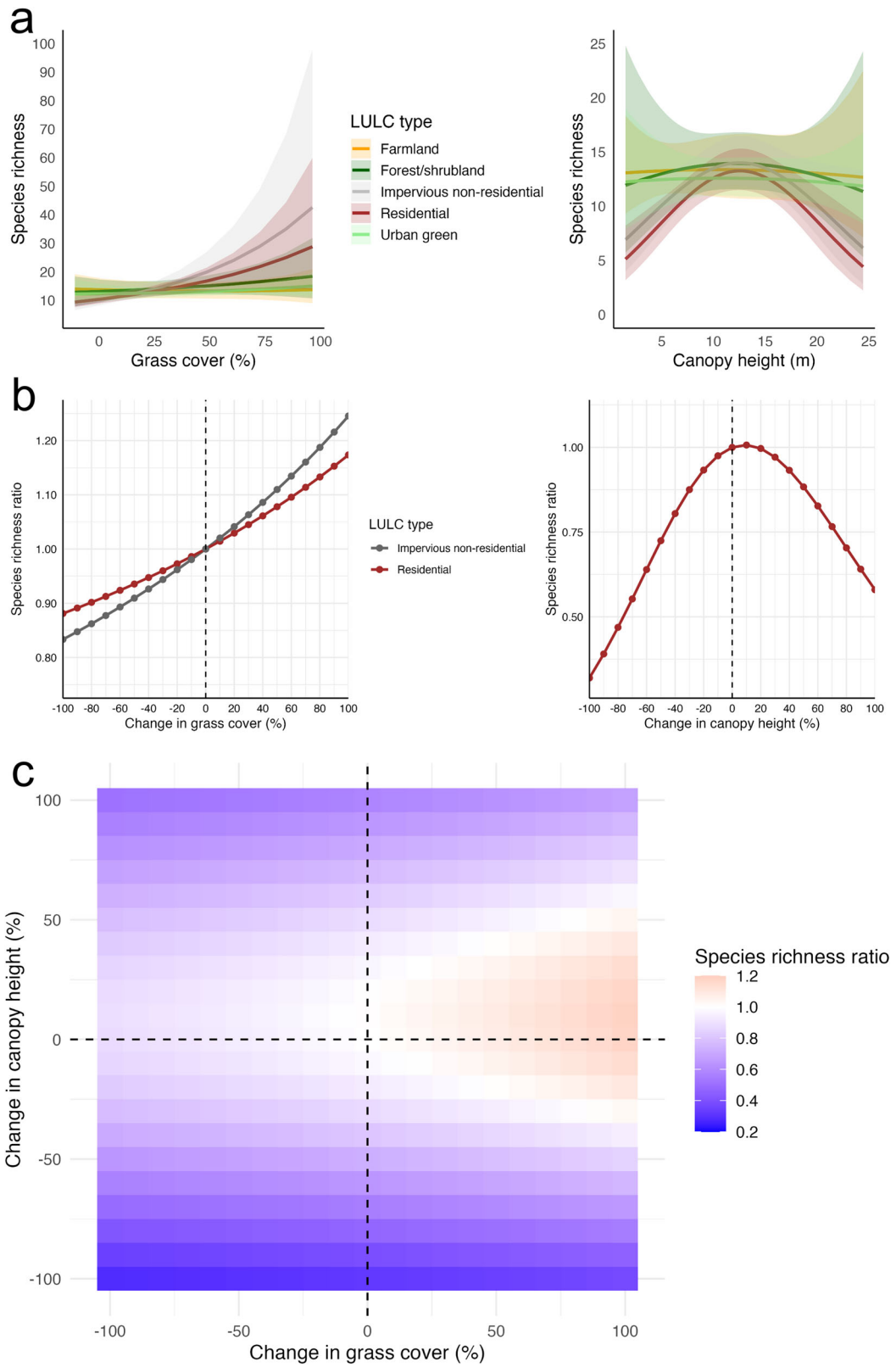


Fig. 5 | Interactive effects of grass cover and canopy height on bird species richness (i.e. taxonomic diversity) under current and simulated scenarios. Predicted effects of grass cover (left) and canopy height (right) scenarios from models including interactions with land-use/land-cover (LULC) type (**a**). Simulated future scenarios showing changes in species richness ratio (i.e. ratio between predicted richness under the scenario and predictions current dataset) in response to increases in grass cover (left) and canopy height (right), assuming other variables are held constant (**b**). Combined response surface showing the interactive effect of percentage change in grass cover and canopy height on species richness ratio (**c**). Dashed lines indicate no change (0%) in variables. Note that "Others" LULC category is not shown to aid visual interpretation.

Finally, urban features like trash bins or dog areas may co-occur with unmeasured variables such as human density or maintenance intensity, which could influence our results.

Future studies should address these limitations by expanding the analytical scope to new ecological and sensory dimensions, and by refining the classification of vegetation types. Integrating acoustic dimensions would provide a more complete understanding of how birds enhance human experiences in urban green spaces. While our study focused on the visual aspects of urban bird communities, we acknowledge that birdsong is an important component of cultural ecosystem services, contributing to psychological restoration and well-being in city dwellers[79,80]. Disentangling the effects of different forms of herbaceous cover, such as short-mown lawns, urban meadows, and semi-natural grasslands, would help clarify how vegetation structure and management intensity shape urban bird communities. Future analyses could explore whether bird diversity responds differently to the presence of true grasses (*Poaceae*) versus more complex herbaceous assemblages that include tall herbs and flowering species, which can support richer invertebrate prey bases and more diverse foraging opportunities[81]. Fine-scale approaches, such as that used here, are particularly valuable for informing on-the-ground management, complementing larger-scale studies that provide macroecological insights, but they often lack actionable guidance for urban planning interventions. Addressing remaining gaps will require targeted experimental manipulations, long-term monitoring, behavioural observations, and integration of citizen science data to link habitat features, management practices, and bird responses. Finally, although our study encompasses a range of urban contexts within Italy that are likely representative of many Southern European cities, caution is needed in generalizing the results to other regions. Replicated studies in diverse geographical and socio-ecological settings could provide a more dynamic and socially integrated understanding of urban biodiversity. Our scenario modelling supports the finding that increasing the extent of green areas, particularly grass cover, has a stronger and more consistent positive effect on urban bird diversity than modifying vertical vegetation. While canopy height exhibited a non-linear relationship with biodiversity, gains were modest and only occurred under slight increases, whereas reductions led to steep biodiversity losses. This highlights a potential vulnerability of bird communities to the removal or degradation of mature trees. However, increasing canopy height is a long-term and structurally constrained intervention, often dependent on tree species selection, growth rates, and urban design limitations. In contrast, expanding grass-covered areas presents a more direct and effective strategy for promoting biodiversity, particularly in residential and industrial areas where the potential for gains is highest. Yet, such interventions are also constrained by increasing urbanization and land-use pressures. Balancing the expansion of vegetated habitats with competing demands for infrastructure and housing will be a key challenge in urban planning[82]. Nevertheless, our results suggest that even modest increases in green area coverage can yield significant benefits for biodiversity and the ecosystem services birds provide.

Urban planning should therefore prioritize interventions that are both impactful and feasible: increasing the extent of grass and water cover (e.g. artificial ponds), maintaining intermediate vegetation complexity where possible, whilst incorporating elements for human leisure. Efforts should also focus on maximizing habitat quality within existing green spaces, ensuring that parks and open areas are not only accessible, but ecologically functional. While enhancing vertical vegetation structure may be constrained in the short term, preserving mature trees and ensuring structural diversity over time remain important complementary strategies. Taken together, these insights reinforce the need for multi-scalar, integrative planning approaches that incorporate biodiversity as a key component of urban resilience. Promoting vegetated surfaces, particularly in areas currently dominated by impervious land cover, represents one of the most effective ways to enhance taxonomic and functional diversity in cities, despite the competing pressures of densification and development. In this context, our findings contribute valuable knowledge to inform sustainable urban development and align with the goals of the EU Biodiversity Strategy 2030 to bring back nature to urban spaces[36], and more broadly to the objectives of the UN Agenda 2030, particularly Goal 11: Sustainable Cities and Communities[4], by highlighting actionable strategies to foster biodiversity and ecological functionality within urban landscapes.

Data availability

Breeding bird data used for the analyses are available in the Zenodo repository (https://doi.org/10.5281/zenodo.15343590). This data was originally collected and published in Alba et al. 2025[15] and was re-used here for additional analyses addressing different research questions.

Code availability

The underlying code for this study is not publicly available but may be made available to qualified researchers on reasonable request from the corresponding author.

Received: 2 September 2025; Accepted: 5 December 2025;
Published online: 22 December 2025

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Acknowledgements

We thank Luca Bajno for his help during fieldwork and land use analysis. R.A., V.F., G.A., F.C., I.R., E.C., and D.C. were funded by the National Recovery and Resilience Plan (NRRP), Mission 4 Component 2 Investment 1.4 - Call for tender No. 3138 of 16 December 2021, rectified by Decree n.3175 of 18 December 2021 of Italian Ministry of University and Research funded by the European Union – NextGenerationEU; Award Number: Project code CN_00000033, Concession Decree No. 1034 of 17 June 2022 adopted by the Italian Ministry of University and Research, CUP D13C22001350001, Project title "National Biodiversity Future Center - NBFC". L.I. and D.R. were partly supported by Ecosistema MUSA – Multilayered Urban Sustainability Action (funded by the European Union – NextGenerationEU under the NRRP M4C2 Investment Line 1.5: Strengthening of research structures and creation of R&D "innovation ecosystems", set up of "territorial leaders in R&D", project ECS_00000037). F.M. was supported by Foundation for Science and Technology (FCT) PhD fellowship 2020.06036.BD, DOI 10.54499/2020.06036.BD.

Author contributions

R.A. and D.C. devised the study and the main conceptual ideas. G.A. and L.I. collected the data in the field, and R.A. designed the statistical methodology, performed the computations, prepared the figures and wrote the original draft, with inputs from D.C. All authors (R.A., F.M., V.F., G.A., L.I., F.C., I.R., D.R., E.C. and D.C.) read, contributed and approved the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s42949-025-00322-9.

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