Biodiversity and Conservation (2026) 35:98
https://doi.org/10.1007/s10531-026-03294-z

ORIGINAL RESEARCH

Wings over the city: avian and butterfly diversity across a gradient of anthropogenic disturbance

Della Rocca F.[1] **· Musiani M.**[2] **· Taioli D.**[2] **· Nardelli E.**[2] **· Milanesi P.**[2]

Received: 17 July 2025 / Revised: 31 January 2026 / Accepted: 17 February 2026

Abstract

In the last decades, interest in monitoring and quantifying biodiversity in human-modified landscapes ha increased, as anthropogenic disturbance is recognized as a major driver of biodiversity loss. However, green spaces within disturbed environments can sometimes serve as critical refuges for wildlife. In this study, we collected and analyzed data on bird and butterfly communities across a gradient of anthropogenic disturbance in Bologna (Italy) encompassing urban, agricultural and semi-natural contexts. We found the highest species richness and diversity for both taxa in peri-urban areas with natural and semi-natural habitats, while the dense built-up areas supported fewer, mostly generalist species. Intermediate zones, including parks and gardens, acted as ecological filters, hosting both specialist and generalist species, while agricultural areas favoured birds likely due to their greater vagility, but not butterflies, whose communities showed sharper compositional shifts. Finally, we found that both continuous urban cover, discontinuous high-density urban areas, distance to streets, and wood coverage were the main drivers of α and β diversity in our target groups. Our findings highlighted the importance of habitat heterogeneity and continuity with the natural areas surrounding the city in sustaining biodiversity under anthropogenic disturbance. The integrated analysis of two bioindicator groups along a disturbance gradient produced original and transferable results, offering a replicable model for ecological studies and urban planning in similar contexts.

Keywords Bird diversity · Cluster analysis · Species composition · Species richness · Urban ecology

---

Communicated by Stephen Garnett

✉ Della Rocca F.
francesca.dellarocca@unipv.it

✉ Musiani M.
marco.musiani@unibo.it

[1] Department of Biology and Biotechnology, University of Pavia, Via Ferrata, 9, Pavia, Italy

[2] Department of Biological, Geological and Environmental Sciences, University of Bologna, via Selmi 3, Bologna, Italy

Introduction

Anthropogenic disturbance is one of the dominant drivers in the Anthropocene, resulting in an ongoing process that significantly impacts both landscape features and biodiversity through habitat degradation, fragmentation, and destruction, the facilitation of non-native species establishment, and the homogenization of faunal and floral composition (Simkin et al. 2022; Liu et al. 2025). These alterations can lead to diminished ecosystem functions and resilience, with dramatic consequences for biodiversity at both local and global scale (Faeth et al. 2011; Aronson et al. 2014). However, urban green spaces, such as parks, gardens, and remnant natural fragments in cities and human-dominated environments can also function as refugia for certain endangered and endemic species, supporting their survival and conservation by providing critical habitats (e.g., for breeding, foraging, and shelter opportunities) within disturbed environment (Pierce et al. 2021; Rega-Brodsky et al. 2023).

In recent years, several studies focused not only on analyzing the structure, dynamics, and processes characterizing urban ecosystems but also on the complex interactions between living organisms and humans across gradients ranging from highly urbanized to semi-natural (Zhou et al. 2022; Marcolin et al. 2024; Tong et al. 2024; Alba et al. 2025; Faustino et al. 2025). Thus, ecological research in human-dominated landscape is increasingly playing a central role informing policy decisions for the design of modernized cities and infrastructures, providing solutions aimed at reducing environmental impact and preserving the species that inhabit disturbed areas, for example enhancing green spaces to promote biodiversity (Sadler et al. 2010; Zhao et al. 2022).

Avian research has long been central in this field, given the ease of bird observation and identification, as well as the strong correlation between avian species richness and overall biodiversity in modified landscapes (Fraissinet et al. 2023; McCloy et al. 2024).

Moreover, the relationship between avian diversity and gradient of disturbance has revealed stark shifts in species composition and richness in response to increasing human pressure (Hedblom and Murgui 2017; Kopij 2025). In parallel, growing attention has been given to other animal groups, including mammals, reptiles, amphibians, and invertebrates (French et al. 2018; delBarco-Trillo and Putman 2023; Lewthwaite et al. 2024). Among invertebrates, pollinators have received particular focus (Silva et al. 2021), with butterflies emerging as key bioindicators of environmental conditions (Fang and Guan 2010; Liu et al. 2015). Butterflies share several ecological characteristics with birds. For example, they are relatively easy to observe and identify and they respond quickly to ecological changes. This makes them valuable bioindicators of disturbance (Ramírez-Restrepo and MacGregor-Fors 2017; Malireddi et al. 2025), even in urban and agricultural contexts where their occurrence and diversity reflect also the effectiveness of urban green infrastructure in sustaining ecological functions (Sharma and Sharma 2017; Süle et al. 2025), such as pollination.

Despite the growing interest in the ecological value of human-modified landscapes, understanding of how different taxa respond to varied disturbance contexts is limited. Several studies are geographically biased or focus on a narrow range of taxa, which constrains broader insights into urban biodiversity, especially in underrepresented regions. At the same time, many European countries are developing various initiatives in the field of urban ecological research, with cities increasingly integrating biodiversity into planning and policy (Mahmoud et al. 2025). In Italy the city of Bologna stands out for its greening strategies—such as tree belts and micro-interventions—that enhance ecological connectivity and climate resilience (Boeri et al. 2022). Its participatory governance model, based on co-design and collaborative management, fosters inclusive decision-making and adaptive capacity (Fontana et al. 2025).

Investigating multiple taxa simultaneously across a heterogeneous disturbance gradient offers critical insights into how ecosystems imbedded in human-modified landscapes can remain functional and resilient. Thus, considering the central role that cities may play as reservoirs of biodiversity – ranging from highly artificial to semi-natural patches – we consider the city of Bologna to be an ideal model for investigating how anthropogenic disturbance influences bird and butterfly communities. Situated within the Po Plain—recognized as one of the most intensively exploited and human-modified regions in Europe—Bologna provides an example of ecological communities embedded in a highly altered landscape (Montanari et al. 2022). At the same time, the city's ecological dynamics are potentially buffered by its proximity to the biodiversity-rich Apennines, which host semi-natural habitats, forests, and protected areas. This dual geographic positioning creates a unique interface between urbanization and natural ecosystems, making Bologna a natural laboratory for examining how species richness, diversity, and community composition respond to both the pressures of intensive human activity and the ecological spillover from nearby biodiversity reservoirs. Specifically, in this study we (1) investigated and quantified the differences in species richness, diversity, and community composition of birds and butterflies across urban areas of Bologna characterized by varying levels of anthropogenic disturbance, (2) examined which ecological and spatial parameters most strongly influenced the differentiation of the communities under investigation.

Methods

Study area

We carried out this study in the city of Bologna, a metropolitan area of c. 141 km^2 located in the Emilia-Romagna region, Northern Italy (Fig. 1), with a resident population of approximately 400,000 (https://inumeridibolognametropolitana.it/100grafici/territorio).

The norther part of this city, faces one of the most anthropogenically-modified areas of Europe, the Po Plain, characterized by extensive urbanization and intensive agriculture. In contrast, the southern part of the city extends into a hilly and natural area, where Northern Apennines rise. Several watercourses, including the Reno and Savena rivers and the Lamone stream, pass through the city. Additionally, several wetlands, derived by former caves, retting pits, or rainwater collection basins – such as Lago della Birra, located near Giovanni Marconi Airport – increase the ecological diversity of the city. Moreover, within the municipality of Bologna, two sites belonging to the Natura 2000 network of protected areas occur, the Golena San Vitale and Golena del Lippo site (IT4050018), and the Boschi di San Luca e Destra Reno site (IT4050029) both located along the Reno River. As a result, the entire area is characterized by high environmental heterogeneity, with a mosaic of habitats ranging from heavily urbanized and degraded areas to urban parks – including large ones such as Giardini Margherita – along with uncultivated areas, roadside tree plantations, woodlands, hedgerows and private gardens (Av 2003).

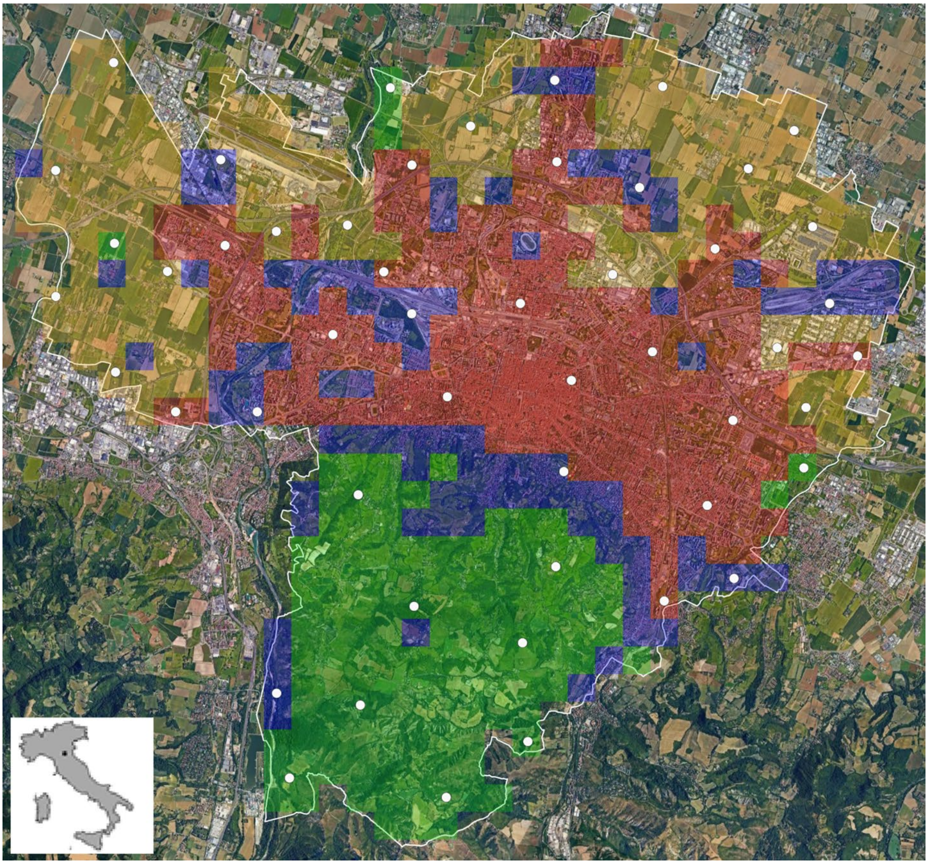

Fig. 1 Study area and spatial clusters. Municipal boundaries of the city of Bologna (Italy) in white and four distinct spatial clusters corresponding to "agricultural environment" in orange, "suburban environments with parks" in blue, "urban environment" in red, "hilly environment and preserved natural areas" in green, sampling sites in white dots

Sampling design

Given the heterogeneity of our study area, to reach our aims we first estimated an urban gradient of anthropic disturbance by performing a cluster analysis based on the spatial information available for the entire city of Bologna. Accordingly, we collected topographic information, i.e., mean elevation and slope together with their relative standard deviations (SD) in raster format from the TIN ITALY digital elevation model (DEM) with a 10 m spatial resolution (https://tinitaly.pi.ingv.it/Download_Area1_1.html, accessed on 15 February 2024). Moreover, we collected information regarding canopy height (mean ± SD) from the ETH Global Canopy Height 2020 dataset at 10 m spatial resolution (https://share.phys.ethz.ch/~pf/nlangdata/ETH_GlobalCanopyHeight_10m_2020_version1/3deg_cogs/, accessed on 10 February 2024), tree cover density (mean ± SD) from the Copernicus (C.) High Resolution Tree Cover Layer 2018, at 10 m spatial resolution (https://land.copernicus.eu/en/products/high-resolution-layer-tree-cover-density/tree-cover-density-2018, accessed on 10 February

2024), and the percentage of and distance to street trees, in vector format, from the C. Urban Atlas Street Tree Layer 2018 (https://land.copernicus.eu/en/products/urban-atlas/street-tree-layer-stl-2018, accessed on 10 February 2024). From the C. Urban Atlas Land Cover/Land Use 2018 vector dataset (https://land.copernicus.eu/en/products/urban-atlas/urban-atlas-2018), we derived the percentage of.

two urban vegetation, six proxies of urbanization and three land-use variables, as well as six distance metrics (Table 1), while from the C. Urban Atlas Building Height 2012, at 10 m spatial resolution (https://land.copernicus.eu/en/products/urban-atlas/building-height-2012, accessed on 10 February 2024), we derived the mean ± SD height of all the buildings in Bologna. Finally, we also derived mean ± SD of the human population density from Italy's High Resolution Population Density Maps + Demographic Estimates 2020 dataset at 20 m spatial resolution (https://data.humdata.org/dataset/italy-high-resolution-population-density-maps-demographic-estimates?, accessed on 10 February 2024).

Table 1 Spatial variables included in the analysis, their units, type and corresponding Variance Inflation Factor (VIF). Variables with VIF > 3 (those not in bold) were excluded from further analyses. Elevation is expressed in meters above sea level (m a.s.l.)

Variables	Unit	Type	VIF
Average elevation	m a.s.l.	Topography	>3
Elevation SD	m a.s.l.		>3
Average slope	°		>3
Slope SD	°		>3
Average canopy height	m	Vegetation structure	>3
Canopy height SD	**m**		**1.861**
Average tree cover density	n/m^2		>3
Tree cover density SD	n/m^2		>3
Street tree lines	**%**	Urban vegetation	**2.514**
Green urban areas	**%**		**1.933**
Streets	**%**	Proxy of urbanization	**1.755**
Continuous urban areas	**%**		**2.103**
Discontinuous high-density urban areas	**%**		**1.658**
Discontinuous medium-density urban areas	**%**		**1.573**
Discontinuous low-density urban areas	**%**		**2.004**
Sports and leisure facilities	**%**		**1.152**
Average building height	m		>3
Building height SD	m		>3
Average human population density	n/m^2		>3
Human population density SD	n/m^2		>3
Grasslands	**%**	Land-use	**1.541**
Woods	**%**		**1.976**
Croplands	%		>3
Distance to street tree lines	**m**	Distance to features	**2.353**
Distance to green urban areas	**m**		**2.256**
Distance to woods	**m**		**2.331**
Distance to highways	**m**		**2.108**
Distance to airports	**m**		**1.718**
Distance to waters	**m**		**1.835**
Distance to streets	**m**		**2.692**

We resampled all environmental predictors to a common 500-m grid by creating a template raster and then aggregating continuous rasters using the mean and standard deviation within each 500-m cell. Predictors originally at different resolutions were aligned to the same grid through resampling to the template. Land-use composition variables were computed as coverage fractions per grid cell, and distance-to-feature predictors were first computed as distance rasters and then aggregated to the same 500-m grid. Finally, we performed VIF analysis on the resulting predictor set to remove collinear variables (details and threshold now explicitly reported in the revised text). Then, we evaluated multicollinearity among predictors using the variance inflation factor (VIF). Predictors were removed iteratively when exceeding the selected VIF threshold (>3; Zuur et al. 2010) and thus we retained 18 variables with low multicollinearity for the further analyses (Table 1).

To characterize broad spatial patterns in landscape composition across the study area, we applied a descriptive clustering approach using the function Mclust in the R package *mclust* (Scrucca et al. 2016). This method fits finite Gaussian mixture models to multivariate data and identifies groups of grid cells that share similar combinations of landscape variables, without assuming any underlying ecological mechanism. We fitted models with 1–10 mixture components and used the Bayesian Information Criterion (BIC; Schwarz, 1978) to select the most parsimonious clustering structure. The best-supported model was an ellipsoidal, equal-shape (VEV) structure with four components (BIC = −17822.43; Fig. S1). These four clusters represent statistically defined groupings of grid squares with similar landscape characteristics. For ease of interpretation, we refer to them descriptively as: “agricultural environment” (CL1), “suburban environments with parks” (CL2), “urban environment” (CL3), and “hilly environment and preserved natural areas” (CL4), comprising 166, 95, 179, and 125 grid squares, respectively (Fig. 1). These labels are intended only as convenient summaries of the dominant features within each cluster, not as mechanistic habitat categories.

We then allocated sampling sites proportionally to the number of grid squares in each cluster, resulting in 15 sites in CL1, nine in CL2, 15 in CL3, and 11 in CL4 (total = 50 sites, with a minimum pairwise distance between sites ranging between 912 and 2260 m; Fig. 1). This ensured that sampling effort reflected the relative representation of each landscape grouping in the study area.

Animal surveys

Bird surveys were conducted, adopting the widely used point counts method as census technique (Milanesi et al. 2017; Herrando et al. 2017, 2019; Lardelli et al. 2022a, b; Howard et al. 2023), between April and June 2024 representing the peak nesting season for most species in this temperate climate (Keller et al. 2020; Lardelli et al. 2022a, b). All bird sampling sites were visited twice, alternating between early and late morning sessions and with a minimum interval of one month between visits to account for the occurrence of juveniles and late-nesting individuals, using the point count method (Blondel et al. 1981; Bibby et al. 2000; Gregory et al. 2004). Each survey lasted 10 min and was preceded by an additional minute for preparing the sampling data sheet. Bird identification was based on both direct visual observation of individual animals (e.g., with 8 × 32 binoculars) and on the recognition of their songs and calls. All birds detected strictly within a 100-m radius of the observer were recorded (Knaus et al. 2018), including flying individuals that entered the survey area, such as aerial foragers like swifts, and soaring raptors.

Diurnal butterfly surveys were conducted from late May to early September 2024. All sampling sites were visited four times throughout the sampling season (approximately once a month), using the transect method count (Pollard walk; Pollard et al. 1994). At each site, adult butterfly species and the number of individuals of each species was recorded along a 400-meter transect, during daylight hours (10:00–16:00) coinciding with peak flight activity (Cormont et al. 2011). Individuals were captured using an entomological net, photographed and then released at the end of each sampling session. Common and easily recognizable butterfly species were quickly classified based on key morphological traits such as coloration, wing patterns, body size, and antennae shape. For species that proved more difficult to identify in the field the images were later examined in greater detail following Tolman and Lewington (2022) and Balletto et al. (2023). In this study, the term “butterflies” is used, for simplicity, to refer to all the Lepidoptera recorded, because the sampling was carried out during the day and the individuals were collected in a period corresponding to the typical flight season of butterflies.

Biodiversity analysis

We analyzed the collected data of both birds and butterflies to verify differences between the four clusters in terms of alpha (α-) and beta (β-)diversity (i.e. focusing on diversity within a single site, and on diversity between clusters, respectively) and the effect of the spatial variables on these differences. For butterflies, given that the average adult lifespan ranges from approximately 2.5 to 15 days (Niitepõld and Hansk 2013; Bubová et al. 2016), we assumed there was no likelihood of recapturing the same individual in two consecutive sessions. Therefore, species-specific abundances were estimated by summing the number of individuals recorded at each site throughout the entire sampling period.

For birds, to minimize the risk of double-counting individuals, we estimated species-specific abundances by selecting the highest count observed at each site during a single sampling session.

Species richness and diversity

As measures of α-diversity, we focused on three measures of Hill numbers (Hill 1973) of order Q: species richness (Q0), Hill-Shannon diversity (Q1) and Hill-Simpson diversity (Q2). These three forms of Hill diversity differ only in how they scale rarity (Roswell et al. 2021). Richness uses an arithmetic rarity scale, which gives high leverage to, and therefore remains very sensitive to, rare species; Hill–Simpson diversity uses a reciprocal scale, which shifts leverage towards, and is thus dominated by common species; Hill–Shannon uses a logarithmic scale, and falls between the two.

We graphically compared species richness and diversity among clusters (CL1, CL2, CL3, CL4) by means of rarefaction curves calculated by iNEXT package (interpolation/extrapolation) of the R programming language (Hsieh et al. 2016). For each diversity measure considered (Q0, Q1, Q2), iNEXT uses the observed sample of abundance data to compute diversity estimates (Chao and Jost 2012; Chao et al. 2016). The 95% confidence intervals associated with the estimates are also calculated and a sample-size-based rarefaction and extrapolation (R/E) curve is plotted. We verified significant differences in terms of species richness and diversity among the 50 plots grouped according to the cluster they belong to (i.e., CL1, CL2, CL3, CL4) using the Kruskal-Wallis test and subsequently the Mann-Whitney post hoc test for pairwise comparisons between the clusters.

We adopted the information-theoretic approach with multi-model inference (function "dredge" in the R package "MuMIn"; v.1.48.4. Barton 2009) to alternatively investigate the relationships between richness and diversity of birds and butterfly with the spatial variables. This approach involves generating as many models (generalized linear models, GLMs with Gaussian error distribution, in our case) as potential combinations of the spatial variables considered (Table 1), standardized (centered on its mean and divided by its standard deviation) using the 'scale' function in R, alternatively using Q0, Q1 and Q2 as response variable. The resulting models were then ranked using the corrected Akaike Information criterion (AICc; Akaike 1973). Specifically, we chose the model with the lowest AICc as the "best"' model and then ranked the remaining models as the difference (ΔAICc) between the AICc of the best model and those of the other models. Following the recommendations of Anderson and Burnham (2002), we considered only models with $\Delta\text{AICc} < 2$. These were tested for spatial autocorrelation in model residuals using Moran's I (function 'moran.test' in the 'spdep' R package; Bivand et al. 2017) resulting in no significant spatial autocorrelation was detected, indicating that spatial structure did not bias model inference.

Then, we computed the Akaike weight for each model, representing the relative likelihood that a given model is the best among those considered (Akaike 1981) and, to evaluate the contribution of individual spatial predictors, calculated variable importance (W_i) by summing the Akaike weights across all the best models in which each variable appeared (Anderson and Burnham 2002).

Communities assemblage

We assessed β-diversity by examining how similar species compositions were among sites grouped into four clusters (CL1–CL4). To test whether these clusters differed significantly, we used Permutational Analysis of Variance (Primer 6 + with PERMANOVA+). This non-parametric method partitions variance among groups based on a similarity matrix. Here, the matrix was built from species abundance data using the Bray–Curtis coefficient, a widely used measure for ecological data.

Because some comparisons involved few sites, we also reported Monte Carlo p-values, which provide more reliable significance estimates under limited replication. Abundance data were standardized by taking the square root of the proportion of individuals of each species relative to the total counted per site.

To explore differences between specific pairs of clusters, we ran Post-Hoc pairwise tests, which yield a t-value and associated probability. We then applied the SIMPER test to identify which species contributed most to the observed dissimilarities between clusters.

Next, we examined how spatial variables influenced community composition using DistLM (Distance-Based multivariate multiple regression). This method correlates environmental variables with biological similarity patterns. We ran Marginal tests (9,999 permutations) to evaluate the explanatory power of each variable individually. To find the best overall model, we applied the BEST selection procedure with the Akaike Information Criterion (AIC), which balances explanatory strength with model simplicity.

Finally, we used Distance-Based Redundancy Analysis (dbRDA) to visualize differences in species composition across all sites and to highlight the contribution of the most significant spatial variables.

Results

Butterfly and bird's species richness and diversity

During the whole sampling period, we recorded a total of 2462 birds belonging to 78 species (Table S2) and *Sturnus vulgaris* was the most abundant species with 521 detections, followed by *Apus apus/pallidus* ($N=237$), *Columba livia domestica* ($N=223$), *Columba palumbus* ($N=168$) and *Corvus cornix* ($N=106$). In the same period, we counted a total of 1554 individuals of *Lepidoptera* belonging to 40 species (Table S1) and *Pieris rapae* was the most abundant species, with a total of 413 individuals, followed by *Pieris brassicae* ($N=178$), *Coenonympha pamphilus* ($N=171$), *Plebejus argus* ($N=153$) and *Polymmatus icarus* ($N=150$).

Although less frequently, uncommon and threatened species were also sampled, such as the birds *Alauda arvensis*, *Chloris chloris*, *Riparia riparia*, *Lanius collurio* and *Passer italiae*, (all listed as "Vulnerable" as for the IUCN red list of Italian bird species) and the butterfly *Lycaena dispar* (listed in Annex II of the Habitats Directive − 92/43/EEC).

The part of the city of Bologna falling within CL4 "hilly environment and preserved natural areas" showed the highest values of species richness and diversity compared to the other clusters, both in the case of birds and butterflies (Fig. 2). However, only for butterflies we found a significant difference between clusters (Kruskal-Wallist test: Q0: chi-square = 15.686; $p<0.01$; Q1: chi-square = 15.207, $p<0.01$; Q2: chi-square = 14.787; $p<0.01$). In particular, we found differences between CL4 and CL1 "agricultural environment" (Post-hoc test: Q0: $p=0.01$, Q1: $p<0.01$, Q2: $p<0.01$) and between CL4 and CL3 "urban environment" (Post-hoc test: Q0: $p<0.01$, Q1: $p<0.01$, Q2: $p<0.01$).

Our results were further confirmed by species abundance data (Table S1, S2). Specifically, Cluster 1 hosted the highest number of birds with a total of 898 individuals belonging to 60 species (Table S2). However, most of the individuals sighted belonged to few species such as *Sturnus vulgaris* ($N=211$), *Columba livia domestica* ($N=110$), *Hirundo rustica* ($N=68$), *Phasianus colchicus* ($N=44$) and *Psittacula krameri* ($N=44$). On the contrary, CL4, with a total of 328 individuals, ranked last in terms of abundance (Table S2) but had the highest species diversity, as individuals were comparatively more evenly distributed among species (Fig. 2), while CL2 and CL3 had a number of individuals in between the two previous clusters (Table S1). However, CL 2 hosted a larger number and a greater diversity of species than CL3 (Fig. 2).

For butterflies, the cluster with the highest number of observed individuals was CL4 with a total of 493 individuals distributed rather evenly among all species (Fig. 2), followed by CL1 (Table S1). However, unlike CL4, most of the observed individuals in CL1 belong to only a few, abundant species including *Plebejus idas*, *Coenonympha pamphilus*, and *Vanessa atalanta* (Table S1) likely explaining the lower diversity indices (Fig. 2). Cluster 2 "suburban environments with parks" and CL3 had the lowest number of individuals. However, species were distributed much more evenly in CL2 compared to CL3, indicating

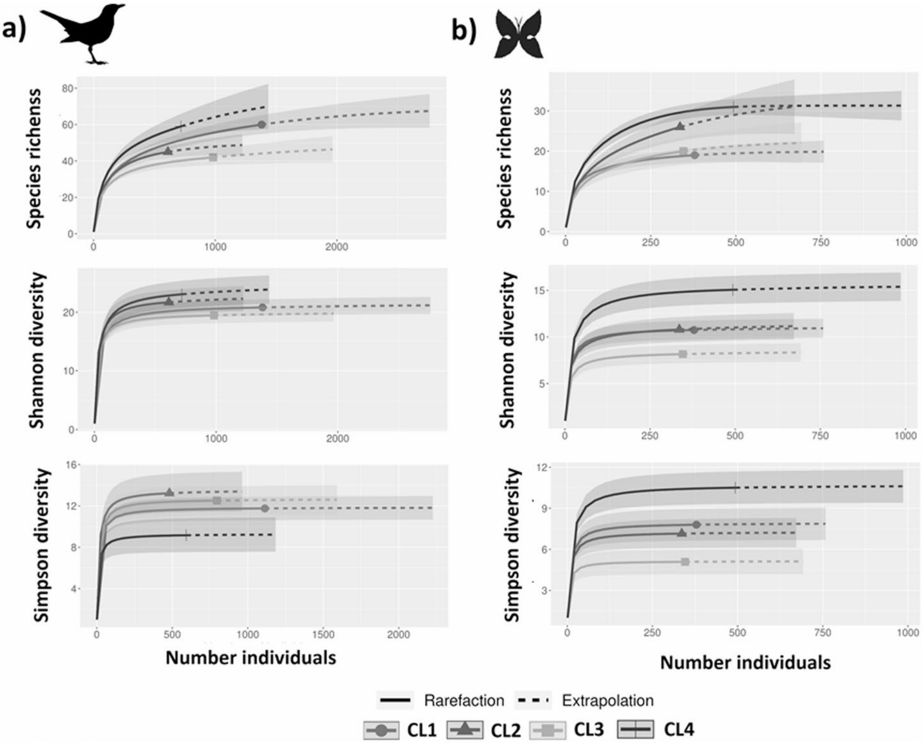

Fig. 2 Rarefaction curves showing the diversity of (**a**) birds and (**b**) butterflies, sampled from May to September 2024 in four distinct clusters within the municipal boundaries of the city of Bologna, Italy - clusters corresponded to “agricultural environment” (CL1), “suburban environments with parks” (CL2), “urban environment” (CL3), “hilly environment and preserved natural areas” (CL4)

higher diversity (Fig. 2). Additionally, we found that a single site within CL2 hosted five species that were not sampled in any other site or cluster: *Spiris slovenica*, *Leptotes pirithous*, *Zerynthia cassandra*, *Gonepteryx rhamni*, and *Leptidea sinapis*.

For birds, also through multi-model inference, we identified and then averaged a total of 12 GLMs with ΔAICc $<$ 2 for species richness (Q0), 10 for Shannon diversity (Q1) and 11 for Simpson diversity (Q2, Table 2). In this analysis, discontinuous low-density urban areas and the distance to roads significantly and positively related to species richness, accounting for 60.17% of the variable importance, while continuous urban areas significantly but negatively related to Shannon and Simpson diversity, accounting for 53.04% and 47.75% of the variable importance (Table 2).

For butterflies, through multi-model inference, we identified and then averaged a total of nine GLMs with ΔAICc $<$ 2 for species richness (Q1), 12 for Shannon diversity (Q0) and 20 for Simpson diversity (Q2, Table 2). Specifically, discontinuous high urban areas and the percentage of woods significantly related, negatively and positively respectively, to all the three measure of diversity considered, accounting for 59% of the variable importance (Table 2).

Table 2 Average estimates of the standardized coefficients (β), ± standard errors (SE), and relative importance from Akaike weights (W) of the covariates entered in the best models (N is the number of models with ΔAICc <2) to estimate birds and butterflies species richness, Shannon diversity, and Simpson diversity, through multi-model inference, using generalized linear models. *Significant variables ($p<0.001$) in bold

Response	Variable	🐦				🦋			
		N	***β***	**SE**	***Wi***	**N**	***β***	**SE**	***Wi***
Species richness	**(Intercept)***	**12**	**2.852**	**0.029**	**-**	**9**	**1.921**	**0.065**	**-**
	Discontinuous high-density urban areas*		**0.069**	**0.032**	**27.797**		**−0.171**	**0.071**	**33.026**
	Woods*		-	-	-		**0.176**	**0.078**	**26.247**
	Green urban areas		0.042	0.033	5.986		0.109	0.071	17.776
	Distance to woods		0.059	0.039	11.411		−0.142	0.084	13.701
	Street tree lines		0.053	0.036	6.786		0.086	0.072	6.414
	Distance to waters		−0.057	0.041	8.861		−0.061	0.066	2.836
	Distance to streets*		**0.071**	**0.032**	**32.379**		-	-	-
	Continuous urban areas		−0.032	0.033	2.431		-	-	-
	Distance to green urban areas		−0.031	0.032	2.377		-	-	-
	Distance to street tree line		−0.024	0.032	1.972		-	-	-
Shannon diversity	**(Intercept)***	**10**	**2.733**	**0.03**	**-**	**12**	**1.832**	**0.063**	**-**
	Discontinuous high-density urban areas*		-	-	-		**−0.17**	**0.069**	**31.784**
	Woods*		-	-	-		**0.173**	**0.074**	**26.152**
	Green urban areas		0.021	0.031	4.041		0.107	0.067	14.675
	Distance to woods		-	-	-		−0.141	0.083	11.034
	Street tree lines		0.036	0.031	9.999		0.101	0.081	6.756
	Distance to waters		−0.027	0.031	4.751		−0.059	0.065	3.927
	Canopy height SD		-	-	-		−0.064	0.066	2.066
	Discontinuous low-density urban areas		0.027	0.031	4.693		−0.099	0.082	1.847
	Sports and leisure facilities		-	-	-		−0.051	0.067	1.761
	Continuous urban areas*		**−0.072**	**0.031**	**53.046**		-	-	-
	Distance to airports		0.035	0.031	9.845		-	-	-
	Distance to green urban areas		−0.028	0.031	4.862		-	-	-
	Distance to street tree lines		−0.026	0.031	4.516		-	-	-
	Streets		−0.023	0.031	4.248		-	-	-

Table 2 (continued)

Response	Variable	🐦				🦋			
		N	*β*	SE	*Wi*	N	*β*	SE	*Wi*
Simpson diversity	**(Intercept)***	**11**	**2.601**	**0.034**	**-**	**20**	**1.751**	**0.062**	**-**
	Discontinuous high-density urban areas*		-	-	-		**−0.171**	**0.068**	**31.621**
	Woods*		0.034	0.037	3.475		**0.161**	**0.074**	**23.554**
	Green urban areas		0.032	0.035	3.437		0.089	0.067	10.121
	Distance to woods		−0.021	0.035	2.683		−0.136	0.078	14.084
	Street tree lines		-	-	-		0.089	0.074	6.786
	Canopy Height SD		0.031	0.035	3.278		−0.067	0.066	6.518
	Distance to waters		−0.047	0.035	10.755		−0.059	0.064	2.588
	Distance to airports		0.051	0.035	17.931		0.061	0.065	1.251
	Distance to highways		-	-	-		0.061	0.068	1.201
	Discontinuous low-density urban areas		-	-	-		−0.091	0.081	1.199
	Sports and leisure facilities		-	-	-		−0.051	0.066	1.081
	Continuous urban areas*		**−0.084**	**0.036**	**47.756**		-	-	-
	Distance to green urban areas		−0.041	0.036	7.876		-	-	-
	Distance to street tree lines		−0.033	0.036	2.809		-	-	-

Differences in species composition

Species composition of both birds and butterflies differed significantly among clusters (Birds PERMANOVA: pMC < 0.001; pseudo-F = 2.4201 df = 3; Butterflies PERMANOVA: pMC < 0.001; pseudo-F = 2.7214, df = 3). For birds, assemblages in CL4 differed significantly from those in CL1 and CL3 (Table 3; Fig. 3). *Emberiza cirlus* occurred exclusively in CL4. The species contributing most to the dissimilarity between CL4 and CL1 were *Sturnus vulgaris*, *Columba livia domestica* and *Psittacula krameri*, all more frequent in CL1 (Table S3). Differences between CL4 and CL3 were mainly driven by *Apus apus/pallidus*, *Carduelis carduelis*, *Streptopelia decaocto* and *Serinus serinus* (more common in CL3), and by *Phasianus colchicus* (more common in CL4).

Butterfly assemblages also differed significantly between CL4 and both CL1 and CL3 (Table 3; Fig. 3). In these comparisons, *Pieris rapae* and *Pieris brassicae* were the main contributors to dissimilarity and occurred mostly in CL3 (Table S3). CL4 further differed from CL1 due to the higher contribution of *Plebejus argus*, and from both CL1 and CL3 for the exclusive presence of *Melanargia galathea*.

Significant differences were also detected between CL1 and CL3 (Table 3; Fig. 3). Again, *P. rapae* and *P. brassicae* were the strongest contributors, being more abundant in CL3. Additional contributors included *Thymelicus acteon*, *Lasiommata megera*, *Plebejus idas* and *Aricia agestis* (higher in CL3), and *Iphiclides podalirius* (higher in CL1). *Polyommatus thersites* was also found predominantly in CL3.

For both birds and butterflies, multivariate analysis showed that four variables explained important amounts of the variability in community composition, i.e., 28.6% for birds and 22.1% for butterflies (Table 4; Fig. 3). The percentage of discontinuous high urban areas and

Table 3 Pairwise PERMANOVA comparisons indicating the average similarity within each cluster and between pairs of clusters in terms of species composition, coefficient t and Monte Carlo p-value (pMC) – significant p-values in bold

	Cluster (CL*)	🐦				🦋			
		1	2	3	4	1	2	3	4
t	**CL1*agricultural environment***	-	-	-	-	-	-	-	-
pMC		-	-	-	-	-	-	-	-
Similarity		42.685	-	-	-	43.601	-	-	-
t	**CL2*suburban environments with parks***	0.691	-	-	-	1.081	-	-	-
pMC		0.807	-	-	-	0.299	-	-	-
Similarity		44.425	42.074	-	-	41.741	40.801		
t	**CL3** ***urban environment***	1.471	1.441	-	-	1.982	0.997	-	-
pMC		0.056	0.059	-	-	**0.001**	0.435	-	-
Similarity		43.031	42.618	47.645	-	44.007	47.547	54.411	
t	**CL4** ***hilly environment and preserved natural areas***	1.762	1.299	2.668	-	1.579	1.161	2.097	-
pMC		**0.009**	0.122	**0.001**	-	**0.008**	0.201	**0.001**	-
Similarity		42.066	42.618	37.136	50.173	38.769	39.701	40.791	40.628

*Clusters: "agricultural environment" (CL1), "suburban environments with parks" (CL2), "urban environment" (CL3), "hilly environment and preserved natural areas" (CL4)

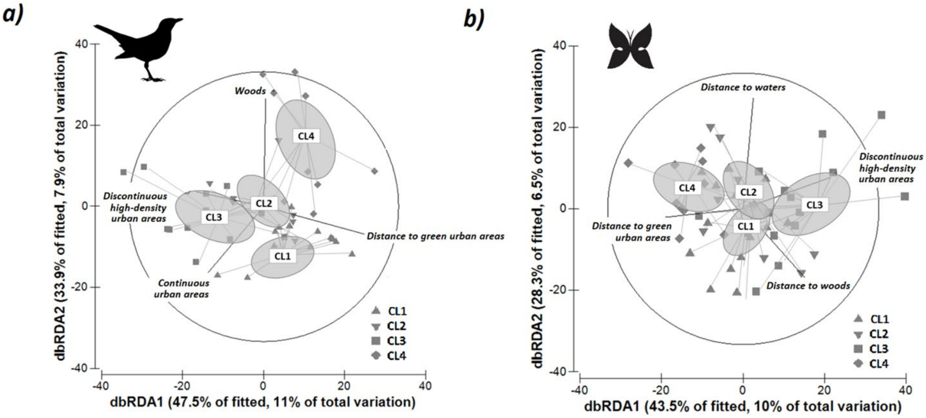

Fig. 3 Biplots of the distance-based redundancy analysis (dbRDA) of multiple variables (names as in Table 4) related to the structure of the bird (**a**) and butterfly (**b**) communities in the city of Bologna, Italy. Variables were superimposed onto the dbRDA plots vectors whose direction and length are related to their partial correlation with the dbRDA axes. Clusters: "agricultural environment" (CL1), "suburban environments with parks" (CL2), "urban environment" (CL3), "hilly environment and preserved natural areas" (CL4)

Table 4 Results of distance-based multivariate multiple regressions for birds and butterflies species composition analyses. The table shows the variables entered in the best models (ΔAICc < 2), listed in order of their contribution to percentage of variance explained (%)

Variables	🐦			🦋		
	pseudo-F	%	*p*	pseudo-F	%	*p*
Continuous urban areas	3.412	6.36	**<0.001**		-	-
Discontinuous high-density urban area	3.999	7.69	**<0.001**	3.707	7.16	**<0.01**
Woods	3.566	6.91	**<0.001**	-	-	-
Distance to green urban areas	3.971	7.64	**<0.001**	3.670	7.10	**<0.01**
Distance to woods	-	-	-	1.966	3.93	**<0.05**
Distance to waters	-	-	-	1.953	3.91	**<0.05**
AIC	**367.45**			**370.02**		
R^2	**0.219**			**0.231**		

the distance to green urban areas were two important variables explaining bird community structure, followed by the percentage of woods and continuous urban areas. The percentage of discontinuous high urban areas and the distance to green urban areas were strongly related to the butterfly community assemblage, followed by distance to forest and distance to water that however explained lower variability.

Discussion

Our cluster analysis proved to be a crucial methodological step for disentangling the effects of human-modified landscapes on birds and butterflies (as proxies of broader biodiversity patterns) within Bologna's heterogeneous territory. This approach moved beyond simplistic urban–rural dichotomies, instead capturing the nuanced gradients of anthropogenic disturbance, land use, and habitat structure that define contemporary ecosystems. Importantly, this clustering framework facilitated a more targeted examination of how landscape-level features interact with biological communities, providing insights that would likely be obscured in less spatially explicit designs.

In this study, we found a clear diversification of butterfly and bird communities along a gradient of human-modified landscapes within the city of Bologna, a densely urbanized metropolis located in a heavily transformed region.

The study area is predominantly situated at low elevations within the Po River Valley, and known to host a rich biodiversity due to its varied microhabitats and temperate climate (Bolpagni et al. 2020). However, for both taxa, the areas classified under Cluster 4 ("hilly environment and preserved natural areas") were shown to support more species-rich and diverse communities. These zones are predominantly composed of natural and semi-natural habitats, interspersed with low-density residential developments. Located in the southern part of the city, adjacent to the foothills of the Bolognese Apennines, these areas reflect the additional contribution of biodiversity-rich Apennine ecosystems (Ronchi and Brambilla 2025).

From an avian perspective, we observed the occurrence of species associated with woodland habitats, such as *Erithacus rubecula* and *Turdus philomelos*, as well as species typical of riparian environments, including *Microcarbo pygmaeus* and *Anas platyrhynchos*. Moreover, Cluster 4 hosted species that prefer sub-Mediterranean habitats and extensive agricultural landscapes—such as *Lanius collurio*, *Hippolais polyglotta*, and *Merops apiaster*—alongside cliff-nesting birds like *Tachymarptis melba* and *Falco peregrinus*. Notably, the latter species has also been observed nesting on tall buildings in the city center, highlighting its adaptability to urban settings (Tinarelli et al. 2002).

Butterfly communities similarly reflected this pattern. Indeed, we found *Hipparchia alcyone* and *Limenitis reducta*, whose habitat is mainly represented by open woodlands, which are abundant in the study's Cluster 4 (Lange et al. 2025; Hinneberg et al. 2023). *Brintesia circe* also requires environmental conditions characterized by cooler and more stable temperatures, resembling those of Apennine habitats, particularly during egg-laying (Birch et al. 2021).

Finally, *Zygaena loti* has a habitat consisting of species-rich grasslands (Bergman et al. 2020), which were also common in CL4.

Although the central urban areas (i.e. of Cluster 3) are located close to the more natural sites of Cluster 4, the urban core exhibited a pronounced decline in both species richness and diversity, especially among butterflies, whose communities were dominated by just a few highly abundant species such as *Pieris rapae* (above all) and *Pieris brassicae*. These are generalist species, and are unaffected by the loss and fragmentation of natural habitats in any specific environment (Callaghan et al. 2021; Deppe et al. 2023). Therefore, they are highly tolerant of anthropogenic disturbance (Kuussaari et al. 2021). While differences in richness and diversity of species were less stark among birds, species assemblages differ clearly. Urban bird communities were primarily composed of *Apus apus*, *Serinus serinus*, *Larus cachinnans*, and *Streptopelia decaocto*. All these species are closely associated with anthropogenic elements commonly found in urban areas, such as rooftops, building crevices, and ornamental or planted trees, which provide nesting sites and food resources (Reynolds et al. 2019; Pais et al. 2023; Eddajjani et al. 2024; Sandoz and de Margerie 2026).

The difference we found in species assemblages between the natural and semi-natural environments of the outskirts (CL4) and the city center (CL3) was likely due to the "filtering effect" of sub-urban zones categorized under CL2 ("suburban environments with parks") that indeed exhibited an intermediate species composition between cluster 4 and cluster 3 for both birds and butterflies. Several studies have shown that peri-urban areas act as ecological filters, allowing generalist species to colonize urban zones while limiting the spread of forest specialists (Canedoli et al. 2018; Liu et al. 2025; Piquet et al. 2025). In our study we also found that Cluster 2 exhibited greater site-level heterogeneity in both species' richness and community composition. Urban parks for instance, mostly located within cluster 2, hosted high species diversity. An exemplary case is Villa Ghigi Park, where 22 butterfly species were recorded, making it the most species-rich site in the city. Among these were *Zerynthia cassandra* (a protected Italian endemic species listed under Annex IV of the EU Habitats Directive 92/43/EEC), a sedentary butterfly with highly localized movement patterns (Vovlas et al. 2014), as well as *Gonepteryx rhamni* and *Leptidea sinapis*, both found exclusively in this location.

Similarly, parks and gardens in Bologna's sub-urban cluster have proven suitable for birds such as *Delichon urbicum*, *Picus viridis*, and *Sitta europaea*, which rely on essential resources such as for example shelter, and nesting sites—features largely absent from heavily urbanized areas (Sandström et al. 2006). For instance, *Delichon urbicum* commonly nests on buildings near open foraging grounds, whereas *Picus viridis* and *Sitta europaea* require mature trees for nesting and feeding (Hardersen et al. 2004).

Cluster 1, largely comprising agricultural land, appeared much more hospitable to birds than to butterflies. These fields dominate Bologna's northern sector and extend into the broader Po Valley agricultural zone, while bordering the urban core to the south. In this northern stretch, the peri-urban buffer of Cluster 2 is minimal, and agricultural zones often abut densely built-up areas directly. Despite this, bird communities in these areas remain relatively unaffected, likely due to their superior dispersal capacity, which enables species to move readily between rural and urban environments. Many of these species—*Columba palumbus*, *Sturnus vulgaris*, *Sylvia atricapilla*, *Corvus cornix*, and *Parus major*—are ecological generalists, whereas others, such as *Psittacula krameri*, *Phasianus colchicus*, and *Columba livia domestica*, are non-native. Overall, these are species well adapted to both urban and agricultural environments (Callaghan et al. 2019; Vorisek et al. 2008). Their occurrence reflects a common pattern in urban ecosystems, where artificial habitats, abundant resources, and reduced competition facilitate the establishment of adaptable taxa (Carlon and Dominoni 2024). For example, *P. krameri* readily exploits urban nesting cavities and may compete with native hole-nesting birds (Battisti and Fraticelli 2023), while *C. livia domestica* is widespread in cities due to its ability to nest on buildings (Rose et al. 2006). In contrast, butterfly communities are known to display sharp compositional differences between agricultural and urban contexts (Lin et al. 2023; Guariento et al. 2023; Pignataro et al. 2025). Some of the species we observed are highly specific to either cluster such as *Thymelicus acteon a*nd *Coenonympha pamphilus* (for agricultural context), while others with broader ecological tolerances were found in both types of environments (*Pieris rapae*, *Pieris brassicae* and *Vanessa atalanta*).

Our findings show that bird communities are primarily shaped by anthropogenic pressures, including urban area extent and road proximity. These factors drive habitat fragmentation, elevate noise and light pollution, and reduce the availability of suitable nesting and foraging sites (Mardiastuti et al., 2020; Merrall and Evans 2020), disproportionately impacting specialist and sensitive species. Similarly, human-driven landscape negatively affects butterfly communities, reducing richness and altering assemblages. However, lepidopterans are also influenced by natural factors occurring in some urban settings, including the extent and proximity of wooded areas and water bodies (de Brito et al. 2021).

We also found that proximity to urban green spaces (parks and gardens) plays a significant role in shaping community composition for both birds and butterflies. This aligns with previous studies (Fang et al. 2023; Lepratto and Zanotto 2024; Apfelbeck et al. 2025), which highlight the ecological value of mosaic environments offering structural vegetation diversity and resources like food and water, also within human-modified landscapes. These green spaces often represent the only viable habitat within cities for taxa such as Piciformes (including woodpeckers and relatives), which nest in tree cavities (Hastedt et al., 2023) or many species of Lycaenidae (i.e. a large family of butterflies), which during their larval stage are dependent on ants (Schär et al. 2018). The peri-urban areas of Bologna fulfill many of these requirements, offering vegetation heterogeneity and habitat complexity, key drivers of both species richness and community structure in birds and butterflies alike.

Conclusion

Our work has highlighted how even large, highly human-modified cities can serve as important refuges for bird and butterfly species, especially when equipped with parks and gardens that offer diverse natural habitats. The role of Bologna's landscape as quality wildlife habitat is certainly supported by the ecological continuity between the natural areas of the Apennines and the urban green spaces in the outskirts, which are extensive and well distributed throughout the city. For this reason, we can assert that the city of Bologna can undoubtedly be considered a virtuous model of land-use planning that promotes biodiversity, despite some critical issues—particularly in the highly urbanized areas of the historic center and in the peripheral zones subjected to intensive agriculture. As such pressures are common, our findings seem transferable to other urban, agricultural and suburban landscapes that encroach on comparatively more natural areas. Finally, we stress the need to develop statistically robust sampling design to collect robust data for community analyses.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10531-026-03294-z.

Acknowledgements We would like to thank Editor-in-Chief, associate editor, and reviewers for their effort in managing and revising our manuscript.

Author contributions FDR: conceptualization, methodology, data analysis, figure editing, writing the original draft, final revision; PM: conceptualization, supervision, methodology, data analysis, revision of drafts, final revision; MM: revision of drafts, final revision; DT: data collection, writing the original draft; EN: data collection, writing the original draft. All authors contributed critically to the drafts and gave final approval for publication. We confirm that the work is original and has not been submitted for publication elsewhere.

Funding Open access funding provided by Università degli Studi di Pavia within the CRUI-CARE Agreement. Project funded by the European Union—NextGenerationEU, under the National Recovery and Resilience Plan (NRRP), Project title “National Biodiversity Future Center—NBFC” (project code CN_00000033) and by the “Canziani Bequest” fund, University of Bologna (grant number A.31.CANZELSEW).

Data availability The dataset analyzed in this study is available from the corresponding author upon request.

Declarations

Competing interests The authors declare no competing interests.

References

Akaike H (1973) Maximum likelihood identification of Gaussian autoregressive moving average models. Biometrika 60(2):255–265

Akaike H (1981) Likelihood of a model and information criteria. J Econom 16(1):3–14

Alba R, Marcolin F, Assandri G et al (2025) Different traits shape winners and losers in urban bird assemblages across seasons. Sci Rep 15:16181

Anderson DR, Burnham KP (2002) Avoiding pit falls when using Information-theoretic methods. J Wildl Manage 66:912–918

Anderson MJ (2001) A new method for non-parametric multivariateanalysis of variance. Austral Ecol 26:32–46

Apfelbeck BA, Navalpotro Buscail M, Sommer A, Petermann JS (2025) Bird community responses to urbanization and vegetation parameters across the city of Salzburg, Austria. Urban Ecosyst 28:131

Aronson MF, La Sorte FA, Nilon CH, Katti M, Goddard MA, Lepczyk CA et al (2014) A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. Proc R Soc Lond B Biol Sci 281(1780):20133330

Av V (2003) Il sistema verde della città di Bologna. Fondazione Villa Ghigi. Available: http://informa.comune.bologna.it/iperbole/media/files/sistema_verde_bologna.pdf

Balletto E, Barbero F, Bonelli S, Casacci LP, Dapporto L (2023) Lepidoptera papilionoidea - butterflies. Fauna d'Italia, Bologna

Barton K (2009) MuMIn: multi-model inference. R package version http://r-forge.r-project. org/ proje cts/ mumin

Battisti C, Fraticelli F (2023) When 'bullies' come out of cities: mobbing among introduced Rose-Ringed Parakeets *Psittacula krameri* and native species of conservation concern in extra-urban habitats with suggestions for a framework of PSIR indicators. Biodiversity 24(1–2):96–101

Bergman KO, Burman J, Jonason D, Larsson MC, Ryrholm N, Westerberg L, Milberg P (2020) Clear-cuts are temporary habitats, not matrix, for endangered grassland burnet moths (*Zygaena spp*). J Insect Conserv 24:269–277

Bibby CJ, Burgess ND, Hill DA, Mustoe S (2000) Bird census techniques. Academic, London

Birch RJ, Markl G, Gottschalk TK (2021) Aestivation as a response to climate change: the Great Banded Grayling *Brintesia circe* in Central Europe. Ecol Entomol 46(6):1342–1352

Bivand R, Altman M, Anselin L, Assunção R, Berke O, Bernat A, Blanchet G (2017) Package 'spdep'. Spatial dependence: Weighting schemes, statistics, R package version, 1(5)

Blondel J, Ferry C, Frochot B (1981) Point Counts with Unlimited distance. In: Estimating Numbers of terrestrial birds. Stud Avian Ecol 6:414–420

Boeri A, Longo D, Orlandi S, Roversi R, Turci G (2022) Community engagement and greening strategies as enabling practices for inclusive and resilient cities. Int J Environ Impacts 5(1):1–14

Bolpagni R, Laini A, Buldrini F, Ziccardi G, Soana E, Pezzi G, Nascimbene J (2020) Habitat morphology and connectivity better predict hydrophyte and wetland plant richness than land-use intensity in overexploited watersheds: evidence from the Po plain (northern Italy). Landsc Ecol 35(8):1827–1839

Bubová T, Kulma M, Vrabec V et al (2016) Adult longevity and its relationship with conservation status in European butterflies. J Insect Conserv 20:1021–1032

Callaghan CT, Bowler DE, Pereira HM (2021) Thermal flexibility and a generalist life history promote urban affinity in butterflies. Glob Change Biol 27(15):3532–3546

Callaghan CT, Major RE, Wilshire JH, Martin JM, Kingsford RT, Cornwell WK (2019) Generalists are the most urban-tolerant of birds: a phylogenetically controlled analysis of ecological and life history traits using a novel continuous measure of bird responses to urbanization. Oikos 128:845–858

Canedoli C, Manenti R, Padoa-Schioppa E (2018) Birds biodiversity in urban and periurban forests: environmental determinants at local and landscape scales. Urban Ecosyst 21:779–793

Carlon E, Dominoni DM (2024) The role of urbanization in facilitating the introduction and establishment of non-native animal species: a comprehensive review. J Urban Ecol 10(1):juae015. https://doi.org/10.1093/jue/juae015

Chao A, Hsieh KH, Ma TC (2016) iNEXT (iNterpolation and EXTrapolation) Online:Software for Interpolation and Extrapolation of Species Diversity. Program and User's Guide published at http://chao.stat.nthu.edu.tw/wordpress/software_download/

Chao A, Jost L (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93:2533–2547

Cormont A, Malinowska AH, Kostenko O, Radchuk V, Hemerik L, WallisDeVries MF, Verboom J (2011) Effect of local weather on butterfly flight behaviour, movement, and colonization: significance for dispersal under climate change. Biodivers Conserv 20:483–503

de Brito MRM, Lion MB, Oliveira IF, Cardoso MZ (2021) Butterflies on the dry edge of the Atlantic Forest: water availability determines community structure at the Northern limit of Atlantic Forest. Insect Conserv Divers 14(4):476–491

delBarco-Trillo J, Putman BJ (2023) Not all cities are the same: variation in animal phenotypes across cities within urban ecology studies. Urban Ecosyst 26(6):1725–1737

De Pais J, Paiva VH, Verissimo SN, Lopes CS, Soares R, Oliveira J et al (2023) Plenty of rooftops with few neighbours occupied by young breeding Yellow-legged Gulls (*Larus michahellis*): Does this occur at the expense of their health condition? *Ibis 165*(1): 312–321

Deppe F, Achterberg C, Dittmar JM, Kunz S, Näckel L, Wittkamp L, Fischer K (2023) No impact of habitat fragmentation on condition and dispersal abilityin the highly mobile butterfly *Pieris rapae*. Ecosphere 14(10):e4679

Eddajjani A, Hanane S, Hamza F, Agharroud K, El Kandry A, Qninba A (2024) Assessing the importance of landscape, anthropogenic and spatial factors in predicting urban nesting sites: the Columbidae of the city of Rabat (Morocco) as a case study. J Urban Ecol 10(1):juae012. https://doi.org/10.1093/jue/juae012

Faeth SH, Bang C, Saari S (2011) Urban biodiversity: patterns and mechanisms. Ann N Y Acad Sci 1223(1):69–81

Fang L, Guan J (2010) Progress in the studies of butterflies in responding to global climate change. J Environ Entomol 32

Fang W, Lin X, Lin Y et al (2023) The impact of urbanization on taxonomic diversity and functional similarity among butterfly communities in waterfront green spaces. Insects 14(11):851

Faustino IAT, González-García F, Ramos-Robles M, Dáttilo W (2025) A macroscopic synthesis and future directions on the study of ecological interaction networks in urban areas. Urban Ecosyst 28(3):101

Fontana C, Testi A, Allegretti G, Zetti I, Rossi M (2025) Embedding justice into climate policies through participatory approaches: prospects and pitfalls toward community-based adaptation pathways in Bologna, Italy. Cities 163:105998

Fraissinet M, Ancillotto L, Migliozzi A, Capasso S, Bosso L, Chamberlain DE, Russo D (2023) Responses of avian assemblages to spatiotemporal landscape dynamics in urban ecosystems. Landsc Ecol 38(1):293–305

French SS, Alison CW, Spencer BH, Emily EV (2018) Town and country reptiles: a review of reptilian responses to urbanization. Integr Comp Biol 58(5):948–966

Gregory RD, Gibbons DW, Donald PF (2004) Bird Census and Survey Techniques. Bird Ecology and Conservation: A Handbook of Techniques. Oxford University Press, Oxford

Guariento E, Rüdisser J, Fiedler K, Paniccia C, Stifter S, Tappeiner U, Hilpold A (2023) From diverse to simple: butterfly communities erode from extensive grasslands to intensively used farmland and urban areas. Biodivers Conserv 32(3):867–882

Hardersen S, Cerretti S, Hardersen F, Mason G, Nardi M (2004) Habitat usage of woodpeckers and nuthatch. Ricerche naturalistiche a Boscodella Fontana. Quaderni Conservazione Habitat 3:49–59

Hastedt A, Tietze D T (2023) The importance of unsealed areas in the urban core and periphery for bird diversity in a large Central European city. Urban Ecosyst 26:1015–1028

Hedblom M, Murgui E (2017) Urban bird research in a global perspective. In: Murgui E, Hedblom M (eds) Ecology and conservation of birds in urban environments. Springer, Heidelberg

Herrando S, Franch M, Voříšek P, Kipson M, Milanesi P, Keller V (2017) EBBA2: Latest pilot maps, modelling work and planning ahead. Bird Census: 12

Herrando S, Keller V, Bauer HG, Brotons L, Eaton M, Kalyakin M et al (2019) Using the first European Breeding Bird Atlas for science and perspectives for the new Atlas. Bird Study 66(2):149–158

Hill M (1973) Diversity and evenness: a unifying notation and its consequences. Ecology 54:427–432

Hinneberg H, Kőrösi Á, Gottschalk T (2023) Providing evidence for the conservation of a rare forest butterfly: results from a three-year capture-mark- recapture study. Basic Appl Ecol 73:27–39

Howard C, Marjakangas EL, Morán-Ordóñez A, Milanesi P, Abuladze A, Aghababyan K et al (2023) Local colonisations and extinctions of European birds are poorly explained by changes in climate suitability. Nat Commun 14(1):4304

Hsieh TC, Ma KH, Chao A (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods Ecol Evol 7(12):1451–1456

Keller V (2020) European Breeding Bird Atlas 2. Distribution, Abundance and Change. European Bird Census Council & Lynx Edicions, Barcelona, p 967

Knaus P (2018) Swiss Breeding Bird Atlas 2013–2016. Distribution and population trends of birds in Switzerland and Liechtenstein. Swiss Ornithological Institute, Sempach

Kopij G (2025) The importance of urban greening spaces for avian communities in an urbanized landscape. Land 14(2):400

Kuussaari M, Toivonen M, Heliölä J, Pöyry J, Mellado J, Ekroos J et al (2021) Butterfly species' responses to urbanization: differing effects of human population density and built-up area. Urban Ecosyst 24:515–527

Lange M, Gelbrecht J, Wiemers M, Schmitt T (2025) What makes a habitatsuitable for the open-forest specialist rock grayling (*Hipparchia alcyone* [DenisSchiffermüller], 1775) An ecological comparison between current andhistorical habitats of a highly endangered butterfly species. J Insect Conserv 29(2):20

Lardelli R (2022b) Atlante degli uccelli nidificanti in Italia. Edizioni Belvedere

Lardelli R, Bogliani G, Brichetti P, Caprio E, Celada C, Conca G et al (2022a) Atlante degli uccelli nidificanti in Italia. Edizioni Belvedere, pp 1–703

Lepratto F, Zanotto F (2024) Towards biodiverse urban public spaces: a morphological study in Milan. J Contemp Urban Aff. https://doi.org/10.25034/ijcua.2024.v8n1-7

Lewthwaite JMM, Baiotto TM, Brown BV et al (2024) Drivers of arthropod biodiversity in an urban ecosystem. Sci Rep 14:390

Lin Y, Huang S, Fang W, Zhao Y, Huang Z, Zheng R, Huang J, Dong J, Fu W (2023) Butterfly communities vary under different urbanization types in city parks. Animals 13:1775. https://doi.org/10.3390/ani13111775

Liu L, Pan C, Liu J, He L (2015) Resources and fauna of butterflies in Jiulongshan Mountain National Nature Reserve. Chin J Ecol 34:3438–3442

Liu N, Liu Z, Wu Y (2025) Direct and indirect impacts of urbanization on biodiversity across the World's cities. Remote Sens 17(6):956

Mahmoud I, Dubois G, Liquete C, Robuchon M (2025) Understanding collaborative governance of biodiversity-inclusive urban planning: methodological approach and benchmarking results for urban nature plans in 10 European cities. Urban Ecosyst 28(2):17

Malireddi P, Jarpla M, Patel RD, Bandhavi HL, Desai HR (2025) Safeguarding insects as bio-indicators of environmental changes and pollution: a review. Plant Arch 25(1):1018–1032

Marcolin F, Segurado P, Chamberlain D, Reino L (2024) Testing the links between bird diversity, alien species and disturbance within a human-modified landscape. Ecography: e06886

Mardiastuti A et al (2020) Bird Diversity Patterns along Urbanization Gradients: Some Recommendations for Landscape Planner. IOP Conf Ser Earth Environ Sci 556:012012

McCloy MW, Andringa RK, Maness TJ, Smith JA, Grace JK (2024) Promoting urban ecological resilience through the lens of avian biodiversity. Front Ecol Evol 12:1302002

Merrall E S, Evans K L (2020) Anthropogenic noise reduces avian feeding efficiency and increases vigilance along an urban–rural gradient regardless of species' tolerances to urbanisation. J Avian Biol, e02341

Milanesi P, Herrando S, Pla M, Villero D, Keller V (2017) Towards continental bird distribution models: environmental variables for the second European breeding bird atlas and identification of priorities for further surveys. Vogelwelt 137:53–60

Montanari I, De Bernardini N, Gizzi G, Bolpagni R, Buldrini F, Campione L, Castellari I, Landi S, Spiezia L, Chiarucci A (2022) Flora and plant communities across a complex network of heavily modified water bodies: geographical patterns, land use and hydrochemical drivers in a temperate overexploited plain. Landsc Ecol Eng 18:367–380

Niitepõld K, Hanski IA (2013) Long life in the fast lane: positive association between peak metabolic rate and lifespan in a butterfly. J Exp Biol 216(8):1388–1397

Pierce JR, Drill S, Halder MD, Tan MMJ, Tiwari A, López Guijosa PA (2021) Scaling biodiversity conservation efforts: an examination of the relationship between global biodiversity targets and local plans. Front Conserv Sci 2:752387

Pignataro T, Lourenço GM, Cornelissen T (2025) Shot down in grays: an integrative review and meta-analysis of the negative effects of urbanization on butterfly communities. Urban Ecosyst 28:116

Piquet A, Piano E, Tolve M, Isaia M (2025) City as a filter: urban density affects taxonomic and functional diversity of foliage-dwelling spiders. Landsc Ecol 40:3

Pollard E, Yates TJ, Courtney SP (1994) Monitoring butterflies for ecology and conservation: the British butterfly monitoring scheme. Ecology 75(6):1851

Ramírez-Restrepo L, MacGregor-Fors I (2017) Butterflies in the city: a review of urban diurnal Lepidoptera. Urban Ecosyst 20:171–182

Rega-Brodsky CC, Weiss KC, Green AM, Iannarilli F, Tleimat J, Fritts S et al (2023) Mammalian functional diversity and trait responses to anthropogenic and environmental factors across the contiguous USA. Urban Ecosyst 26(2):309–322

Reynolds SJ, Ibáñez-Álamo JD, Sumasgutner P, Mainwaring MC (2019) Urbanisation and nest building in birds: a review of threats and opportunities. J Ornithol 160(3):841–860

Ronchi S, Brambilla M (2025) Scarce consideration of climate and land use changes impacts on ecosystem services and biodiversity in the Apennines Mountain system, Italy. Reg Environ Chang 25(2):1–15

Rose E, Nagel P, Haag-Wackernagel D (2006) Spatio-temporal use of the urban habitat by feral pigeons (*Columba livia*). Behav Ecol Sociobiol 60:242–254

Roswell M, Dushoff J, Winfree R (2021) A conceptual guide to measuring species diversity. Oikos 130:321–338

Sadler J, Bates ADAM, Hale J, James P (2010) Bringing Cities Alive: The Importance of Urban Green Spaces for People and Biodiversity. In: Gaston KJ (ed) Urban Ecology. Cambridge University Press, Cambridge, pp 230–260

Sandoz N, de Margerie E (2026) Conserving a urban habitat: Enhanced detection of common swift nests in buildings using a video fusion method. https://doi.org/10.1101/2025.08.25.671194-

Sandström UG, Angelstam P, Mikusiński G (2006) Ecological diversity of birds in relation to the structure of urban green space. Landsc Urban Plann 77(1–2):39–53

Schär S, Eastwood R, Arnaldi KG, Talavera G, Kaliszewska ZA, Boyle JH et al (2018) Ecological specialization is associated with genetic structure in the ant-associated butterfly family Lycaenidae. Proc R Soc Lond B Biol Sci 285(1886):20181158

Schwarz G (1978) Estimating the dimension of a model. Annal Stat 6:461–464

Scrucca L, Fop M, Murphy TB, Raftery AE (2016) Mclust 5: clustering, classification and density estimation using Gaussian finite mixture models. R J 8:289–317

Sharma M, Sharma N (2017) Suitability of butterflies as indicators of ecosystem condition: a comparison of butterfly diversity across four habitats in Gir Wildlife Sanctuary. Int J Adv Res Biol Sci 4(3):43–53

Silva JLS, de Oliveira MTP, Cruz-Neto O, Tabarelli M, Lopes AV (2021) Plant–pollinator interactions in urban ecosystems worldwide: a comprehensive review including research funding and policy actions. Ambio 50(4):884–900

Simkin RD, Seto KC, McDonald RI, Jetz W (2022) Biodiversity impacts and conservation implications of urban land expansion projected to 2050. Proc Natl Acad Sci USA 119(12):e2117297119

Süle GA, Báldi D, Kleijn et al (2025) Pollinator-Promoting Interventions in European Urban Habitats—A Synthesis. Ecol Lett 28(8):e70189

Tinarelli R, Bonora M, Balugani M (2002) Atlante degli Uccelli nidificanti nella Provincia di Bologna (1995–1999). Comitato per il Progetto Atlante Uccelli Nidificanti nella Provincia di Bologna

Tolman T, Lewington R (2022) Guida alle farfalle d'Europa, Ediz. a colori. Ricca Editore

Tong Y, Shi T, Zhang S, Cheng Y, Liang J, Lei J (2024) Study on the interaction mechanism between urbanization and ecological resilience—the case of urban agglomeration on the North Slope of Tianshan Mountain. Appl Sci 14(24):12066

Vorisek P, Gregory RD, Van Strien AJ, Meyling AG (2008) Population trends of 48 common terrestrial bird species in Europe: results from the pan-European common bird monitoring scheme. Rev. Catalana Ornitol 24:4–14

Vovlas A, Balletto E, Altini E, Clemente D, Bonelli S (2014) Mobility and oviposition site-selection in *Zerynthia cassandra* (Lepidoptera, Papilionidae): implications for its conservation. J Insect Conserv 18:587–597

Zhao X, Li F, Yan Y, Zhang Q (2022) Biodiversity in urban green space: a bibliometric review on the current research field and its prospects. Int J Environ Res Public Health 19(19):12544

Zhou Y, Chen G, Zhou W (2022) Sustainable urban systems: from landscape to ecological processes. Ecol Process 11(1):26

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1:3–14