www.nature.com/scientificreports

scientific reports

Check for updates

OPEN

Different traits shape winners and losers in urban bird assemblages across seasons

Riccardo Alba[1,2,8]✉, Fabio Marcolin[1,3,4,5,8], Giacomo Assandri[6], Luca Ilahiane[7], Francesca Cochis[1,2], Mattia Brambilla[7], Diego Rubolini[7] & Dan Chamberlain[1,2]

Urbanisation is a major driver of global biodiversity decline, profoundly affecting animal communities. While most studies on bird communities have primarily focused on the breeding season, we aimed to identify species responses and their associated traits by adopting a stratified design and using a multi-season approach considering a gradient from highly urbanised city centres to the urban–rural fringe across six Italian cities. We found that bird assemblages exhibited different responses to urbanisation according to season. Winners (i.e. species positively affected by urbanisation) were characterised by traits such as colonial nesting, high productivity and longevity. In winter, these species displayed generalist foraging strategies and solitary behaviour. Losers (i.e. species negatively affected by urbanisation) tended to be insectivorous, ground-nesting and short-distance migratory species. Interestingly, intra-specific variations emerged, with wintering populations of some species exploiting highly urbanised areas despite not breeding there. Urban adapters, although not strictly winners, displayed resilience by navigating a range of urban conditions, effectively exploiting intermediate levels of urbanisation. This study provides novel insights into the complex ecological dynamics occurring within the urban matrix in different seasons. Our findings emphasise the importance of adopting a multi-season approach in research and urban planning to better understand species responses and develop more effective, sustainable strategies for biodiversity conservation in urban environments.

Keywords Community ecology, Green spaces, Green cities, Imperviousness, Urban biodiversity, Urban gradient

Urbanisation is one of the main worldwide threats to biodiversity, which is increasing at a disproportionate rate compared to other land use changes globally[1,2]. Future projections suggest that by 2050, 68% of the world's population will be living in urban areas[3]. Significant land use changes are thus expected to accommodate the expanding urban population, with substantial pressures on Earth's ecosystems[4,5] and alterations of ecosystem characteristics and functions[6,7]. Overall negative effects on biodiversity are predicted[8–11], thus adequate urban planning strategies are needed to accommodate both biodiversity requirements and growing human populations across the globe without increasing environmental injustice[2]. Even though the urban environment generally shows a reduced taxonomic diversity of animal communities in comparison to more natural habitats[12], different levels of biodiversity can be found within the heterogeneous urban matrix. Whilst areas with a high cover of impervious surface (e.g. city centre or highly urbanised areas) generally host fewer species, green spaces of cities are characterised by a higher biodiversity[13–15], with different degrees of species richness mainly dictated by vegetation composition and habitat management[16]. Green spaces such as urban parks can also act as refugia for rare and threatened species[17,18].

Birds show high levels of environmental adaptability[19] and behavioural flexibility[20], thus making them one of the most successful taxonomic groups in urban environments[21–23]. Bird populations in highly urbanised areas

[1]Department of Life Sciences and System Biology, University of Turin, Via Accademia Albertina 13, 10123 Turin, Italy. [2]NBFC, National Biodiversity Future Center, 90133 Palermo, Italy. [3]Forest Research Centre and Associated Laboratory TERRA, School of Agriculture, University of Lisbon, Lisbon, Portugal. [4]CIBIO/InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, School of Agriculture, University of Lisbon, Lisbon, Portugal. [5]CIBIO/InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, University of Porto, Vairão, Portugal. [6]University of Eastern Piedmont, Alessandria, Italy. [7]Department of Environmental Sciences and Policy, University of Milan, Milan, Italy. [8]Riccardo Alba and Fabio Marcolin contributed equally to this work. ✉email: riccardo.alba@unito.it

typically consist of few common species (i.e. urban exploiters, hereafter winners), whilst specialised species (i.e. urban avoiders, hereafter losers) are generally filtered out by urbanisation, remaining only in green spaces or rural habitats outside the city[12,24–26]. These dynamics might lead to biotic homogenisation in highly urbanised areas whereby more widespread generalist species become dominant[27,28]. This process is mainly driven by filtering of species traits[29] so that winners possess the necessary traits to exploit resources and ecological conditions that losers cannot[30]. Winners tend to exhibit generalist habitat selection and foraging behaviour[31,32], usually being characterised by larger size, omnivorous diet, longer life-span and non-migratory behaviour, as well as other ecological and life-history traits that allow them to thrive in the urban environment[29,33–35]. On the contrary, losers possess traits of specialist species such as a narrow foraging niche, and they tend to be long-distance migrants or ground nesters[31,32], traits that are negatively affected by urban landscape development (especially vegetation characteristics and lack of extensive untouched natural areas), and which ultimately influence species responses to urbanisation[36–38]. Thus, urban landscape features and the expansion of cities play critical roles in shaping urban bird communities.

While urban bird ecology has been widely studied, there are still key gaps in our understanding of how seasonal changes influence species responses to urbanisation. Most urban ornithological studies have focused on the impact of urbanisation during the breeding period[37,39–41], with few taking into account bird communities year-round with consideration of seasonal effects, although there has been a slight increase in the number of studies in recent years[31,35,42]. Research on dynamics involving urban bird communities in other periods of the year is uncommon[43,44], even though in temperate climates, winter is likely to be a critical period since trophic resources typically diminish. Moreover, the role of species traits in mediating these seasonal responses has been under-investigated, particularly in relation to both breeding and non-breeding dynamics. Addressing these gaps is crucial for a more comprehensive understanding of urban biodiversity and its conservation implications. Nonetheless, the provision of supplementary food is common in some urban areas, whether deliberate (such as through bird feeders, in particular areas of the world) or unintentional (e.g. garbage or areas where discarded food accumulates), which might reduce the risk of starvation and enhance the survival chances of birds[45,46]. Another benefit of urban living in winter is the urban heat island effect, where urban areas experience higher air temperatures compared to their surrounding areas, which might help birds reduce thermoregulatory costs[47] and lower the propensity of urban bird species to migrate[48].

We aimed to explore the seasonal dynamics of urban bird assemblages and species traits in different urban habitats by comparing species responses to urbanisation across seasons using a set of six Italian cities distributed along a wide latitudinal range as a model system. Furthermore, we subsequently focused on species-specific responses to identify urban-tolerance plasticity of winners and losers. Our study, by adopting a stratified sampling design based on land use and land cover, provides new insights into the intra-specific variation in response to urbanisation based on the season, and contributes to the few studies that adopted a multi-season approach, considering non-breeding season responses. Species traits, in interaction with time since urban colonisation, are known to affect population trajectories of urban breeding birds[49]. Similarly, they could affect the species' ability to dwell in the cities in relation to the different phases of their life cycle, leading to seasonal patterns. Many studies investigating these dynamics have successfully utilised citizen science data[43] or have used multiple observers across different cities[50,51]. Our study uses the same professional surveyors across all cities, thus ensuring consistent data quality, i.e. avoiding temporal biases, variability in detection rates and lack of training[52–54], providing a complementary perspective to previous studies. No extensive survey on urban bird communities across cities and across seasons has ever been carried out in Italy. Furthermore, deliberate provision of bird food is rare in Italy and more in general in Southern Europe[55,56], a factor that can have significant effects on bird responses to urbanisation in the non-breeding season[50], thus adding relevance to our study.

We hypothesised that species composition would change between the two seasons along an urbanisation gradient, these changes being mainly dictated by species traits characterising ecological niche (i.e. ecological and life-history traits). In particular, we wanted to identify the traits of winners and losers in the urban environment and whether they changed according to season. We also wanted to test if responses to urbanisation are consistent across seasons in the same species or whether different intra-specific patterns can be observed. Given the predicted increase in urbanisation at the global scale, shedding light on these dynamics throughout the full annual cycle will help to improve our understanding of how the urban landscape shapes the dynamics of bird communities in different seasons. This will be critical for the sustainable management of urban environments and for the development of biodiversity-friendly strategies that take into account urban biodiversity.

Materials and methods

Study area and stratified study design

We sampled bird assemblages in six Italian cities covering a latitudinal gradient of approximately 550 km along the Italian peninsula (Fig. 1). A standardised sampling design was adopted to select sites along a green area size-fragmentation gradient by imposing a 1×1 km^2 grid on each city[57]. A gradient of green space area and a gradient of fragmentation degree of individual green spaces, each divided into four strata, were merged to create a 4×4 design[58]. We subsequently selected 1-km squares for each of the 16 combinations of green space area and fragmentation randomly. In each 1-km square, we selected three points, ideally one in green spaces, one in highly impervious-covered areas (i.e. roads and residential or industrial buildings) and one on the border between the two habitats. The number of cells and the numbers of points varied from city to city as not every combination of the stratified design was always available, and there were sometimes access difficulties. Furthermore, points were not located in highly touristic locations where large numbers of pigeons and their potential deliberate feeding could have biased the sampling. We surveyed a total of 72 cells with 47 points in Turin (45°04′ N, 7°40′ E), 45 in Milan (45°27′ N, 9°11′ E), 34 in Florence (43°46′ N, 11°15′ E), 35 in Rome (41°53′ N, 12°28′ E), 32 in Naples (40°50′ N, 14°14′ E) and 27 in Campobasso (41°43′ N, 14°49′ E) for a total of 220 points. We extracted

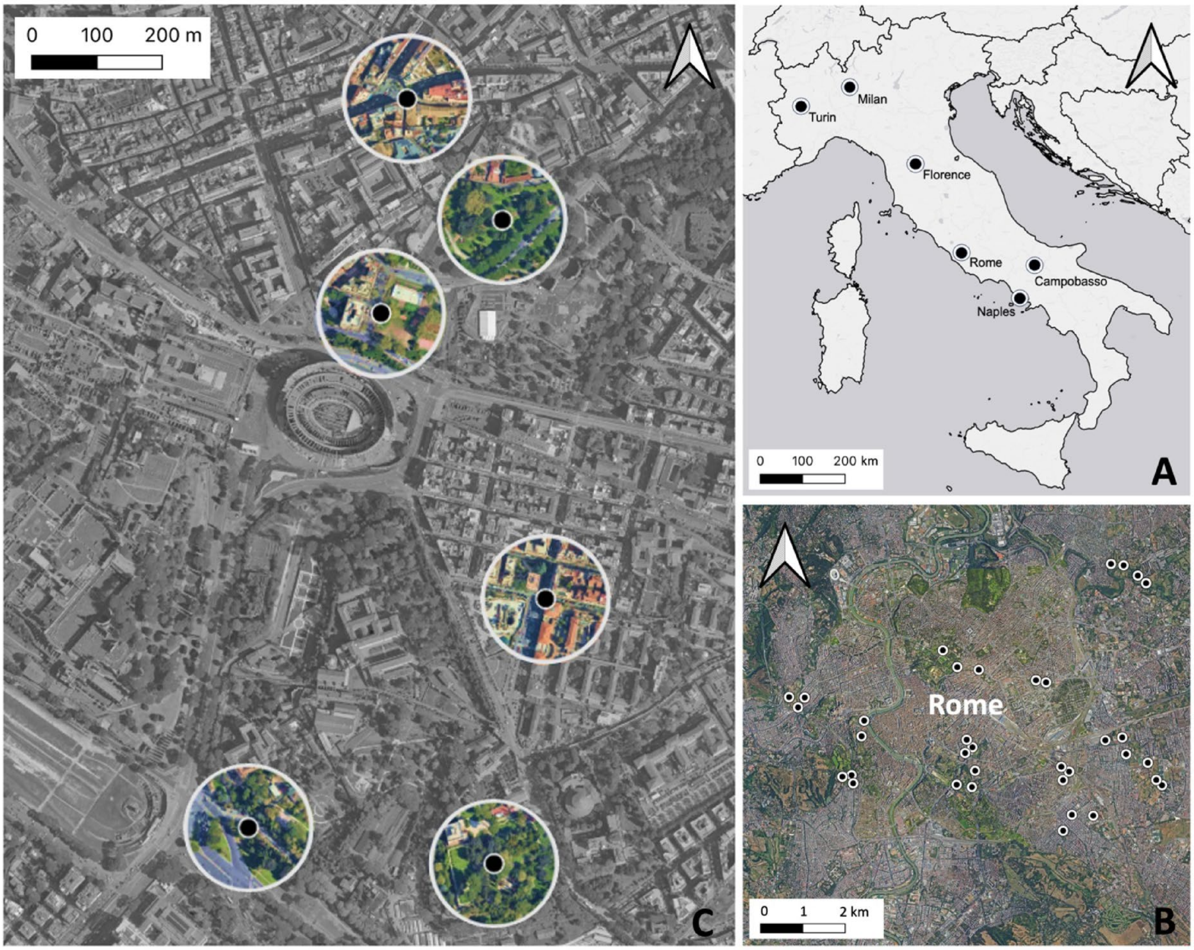

Fig. 1. Study design and details on sampling methodology. Location of the six cities surveyed in the Italian peninsula (**A**), details of the study design within the city of Rome, as an example (**B**) and point counts (black dots) and the 100 m buffer (white circle) with land use (**C**). Map designed in QGIS Software (datum and projection: EPSG:3003—Monte Mario/Italy zone 1).

land-use data for each point within a 100-m radius buffer (see Bird surveys) and calculated the % cover of impervious surface areas (imperviousness) by aggregating urban area categories (e.g. residential areas, roads, industrial areas). We used the most recent land cover data available for each region, prioritising datasets with the highest level of detail and accuracy. Where possible, we relied on regional land use maps (e.g., Piemonte 2021 for Turin https://www.geoportale.piemonte.it, Lombardia 2018 for Milan https://www.dati.lombardia.it) and the Copernicus Urban Atlas (2018) https://land.copernicus.eu/local/urban-atlas for the other 4 cities. Additionally, we validated the land cover classifications by cross-referencing them with high-resolution satellite orthoimagery and subsequent field validation to ensure correspondence with actual conditions during the study period. In this way, we created an imperviousness (i.e. urbanisation) gradient that ranged from less impervious areas with high green space cover (e.g. urban parks, natural areas such as woodland/shrubland remnants in the suburbs) to highly impervious areas (e.g. historical city centres, densely populated areas, industrial areas). To assess if low impervious areas were also more likely to be green spaces, we conducted a correlation test between imperviousness % and green spaces % which resulted in a high correlation (Pearson's $r = -0.999$, p-value < 0.001). See Table S1 for details on the land use categories and their aggregation for the imperviousness gradient.

Bird surveys

For each point, we used standardised 10-min point counts with a 100 m fixed-radius[59] which were carried out within the first five hours of the day twice during the breeding season in April–June 2023, and once during the following winter in December 2023–January 2024, for a total of 660-point visits. During the wintering season, we also carried out an extra 5-minute survey immediately after the standard point count period where the observer walked around within the fixed radius and noted any additional species located to increase species detection due to lower singing activity outside the breeding season. We carried out two surveys in the breeding period to account for seasonal variations in the bird community (i.e. some resident species breed in early spring, while others, especially migrant species, breed later). We removed species that were exclusively migratory and not breeding in the area based on the Italian checklist of breeding birds[60] and expert opinion. For both seasons, we removed individuals flying over that were not explicitly using the surveyed habitat and non-terrestrial species (e.g. waterfowl, rallids, herons[61]) from the dataset.

Traits

We extracted data on 11 species-specific traits for the breeding and wintering seasons from the literature[62–65]. We only retrieved traits related to species ecology, resource use and life-history that could have a biologically meaningful effect on the adaptation to the urban environment. These were: foraging strata generalism, diet, migratory strategy, body mass, life span, fledgling period, nest type, degree of sociality during and outside the breeding period, number of broods per year and mean clutch size (see Table 1 for details). Prior to analyses, all numerical trait variables were scaled and tested for possible multicollinearity by applying a Spearman correlation test. All traits showed low correlation coefficients ($r_s < 0.6$) and were thus retained in the analyses (see Fig. S1 and S2 for correlation plots and matrixes).

Statistical analyses

We first tested whether bird species occurrence probability changed along the urbanisation gradient and whether these patterns varied according to season by fitting Generalized Linear Mixed Models (GLMMs) using the *lme4* R package[66] specifying a binomial distribution, using presence/absence data for each species as the response variable and imperviousness, season and their interaction as explanatory variables. We tested for non-linearities in responses to imperviousness by incorporating the quadratic term and its interaction with season when visual inspection of scatterplots suggested the possible existence of non-linear associations. We then selected the best model between a model with and without the quadratic term, based on the lowest AIC. Point identity and city were included in each model as nested random factors. We classified winners based on significantly positive linear responses to urbanisation and losers based on significantly negative responses ($p < 0.05$). When species showed a non-significant response to urbanisation, or when a non-linear response was significant, we classified them as urban adapters. If the species was absent from a given city due to biogeographical reasons, we carried out the analyses on a subset of cities to avoid zero redundancy in data and model fit problems. GLMMs were carried out on 32 species which had a reasonable sample size and showed no problems of convergence (≥ 10% of the total sample size i.e. ≥ 22 occurrences in the 220 points).

We subsequently assessed whether bird species composition varied along the urban gradient in breeding and wintering periods, and how bird traits were related to urbanisation using the *mvabund* R package[67]. For the first analysis, for each season separately we carried out a multivariate Generalized Linear Model (MGLM) by specifying a negative binomial distribution with the *manyglm* function using the bird species abundance matrix as the response and the imperviousness gradient (as singular-column matrix) as the predictor. For the bird traits, we carried out a fourth-corner analysis using the *traitglm* function for each season, by adding a third matrix (i.e. trait data) to the previous analysis. In this way, it was possible to identify specific traits associated

Trait	Explanation	Season	Justification	Source
Foraging strata generalism	Discrete (1 to 7: sum of the number of strata used by a given species. Categories: water below surface, water around surface, ground, understory, mid-high, canopy, aerial)—scaled	B, W	Three-dimensional use of the urban environment gives insights about the ability of a given species to use resources and exploit habitat structures	Wilman et al.[62]
Diet	Categorical (6 classes: granivore, herbivore aquatic, invertivore, vertivore, aquatic predator, omnivore)	B, W	Diet affects competition dynamics within an urban bird assemblage and is related to the habitat	Tobias et al.[65]
Migratory strategy	Categorical (3 classes: resident, short-distance migrant, long-distance migrant)	B, W	Migrants are associated with seasonal use of resources and higher specialisation which might be detrimental in an urban context	Tobias et al.[65]
Body mass	Continuous (grams)—scaled	B, W	Proxy of ecophysiological conditions, resource exploitation, life history and tolerance to disturbance and dispersal ability	Tobias et al.[65]
Life span	Continuous (years)—scaled	B, W	Longevity in birds is correlated with brain size, so it indirectly affects life-history and resource use	Storchová and Hořák[63] and Bird et al.[64]
Fledgling period	Continuous (days)—scaled	B, W	Age at fledgeling reflects resource stability and colonisation ability in a urban context	Storchová and Hořák[63]
Nest type	Categorical (5 classes: ground, cavity, open, close to ground, closed-arboreal)	B, W	Nest site availability differs among urban habitats and affects predation exposure and inter-specific competition	Storchová and Hořák[63]
Association degree during nesting (ADN)	Categorical (3 classes: solitary, semi-colonial, colonial)	B	ADN has effects on predation exposure, interspecific competition, reproductive outcome and resource use during the breeding period	Storchová and Hořák[63]
Association degree outside the breeding nesting (AOBS)	Categorical (3 classes: gregarious, in pairs, solitary)	W	AOBS has effects on predation exposure, interspecific competition and resource use during winter	Storchová and Hořák[63]
Broods per year	Continuous (number of broods)—scaled	B, W	Number of broods per year is affected by phenology and resource seasonality and can be associated with urbanisation tolerance	Storchová and Hořák[63]
Clutch size	Continuous (number of eggs)—scaled	B, W	Clutch size evolved in response to environment and resource constraints and stability	Storchová and Hořák[63]

Table 1. Summary of bird traits with explanation of the variable, season for which the trait was used (B = breeding, W = wintering), justification for its inclusion and source.

with winners and losers, based on the association degree of each trait to the urbanisation gradient[67]. For both analyses, we carried out chi-squared tests by bootstrapping with 999 repetitions and tested the significance of the imperviousness gradient on bird traits by adding a LASSO (Least Absolute Shrinkage and Selection Operator) penalty to improve model fit. LASSO is an optimisation algorithm that performs both variable selection and regularisation in order to enhance the prediction accuracy and interpretability of the statistical model and removes non-significant interactions[67]. We then created a heatmap for bird traits for each season to visually represent the results. Goodness-of-fit was assessed in the analyses by checking for patterns in model residuals by means of a variogram[68]. All analyses were performed using R software 4.3.1[69].

Results

In our surveys, we recorded a total of 18,594 individual birds and a total of 119 species, 93 during the breeding surveys and 79 during the winter period. The 5 most abundant species during the breeding season were feral pigeon *Columba livia* (1225 individuals), Italian sparrow *Passer italiae* (946 individuals), European starling *Sturnus vulgaris* (512 individuals) and Eurasian blackbird *Turdus merula* (456 individuals). In winter, the most abundant were pigeon (1327 individuals), European starling (464 individuals), Italian sparrow (400 individuals), hooded crow *Corvus cornix* (336 individuals) and European robin *Erithacus rubecula* (312 individuals).

Species-specific responses

Species-specific responses to the urbanisation gradient were generally stronger in the breeding season than in the winter (Figs. 2 and 3). Significant effects of imperviousness, both linear and non-linear, were reported for most species (n = 26, 81%), whilst fewer showed a significant seasonal change in occurrence (n = 17, 53%). Winners (Fig. 2A) were represented by species that are closely associated with human settlements and highly impervious areas such as pigeon, yellow-legged gull *Larus michahellis* and black redstart *Phoenicurus ochruros* (only in the breeding season). A higher number of species was categorised as losers (Fig. 2B) which were negatively affected by urbanisation; these were species mainly tied to forested and green spaces (e.g. short-toed treecreeper *Certhia brachydactyla*, Eurasian nuthatch *Sitta europea*, Eurasian green woodpecker *Picus viridis*). A large number of species emerged as urban adapters (Fig. 3), most of them showing non-linear responses,

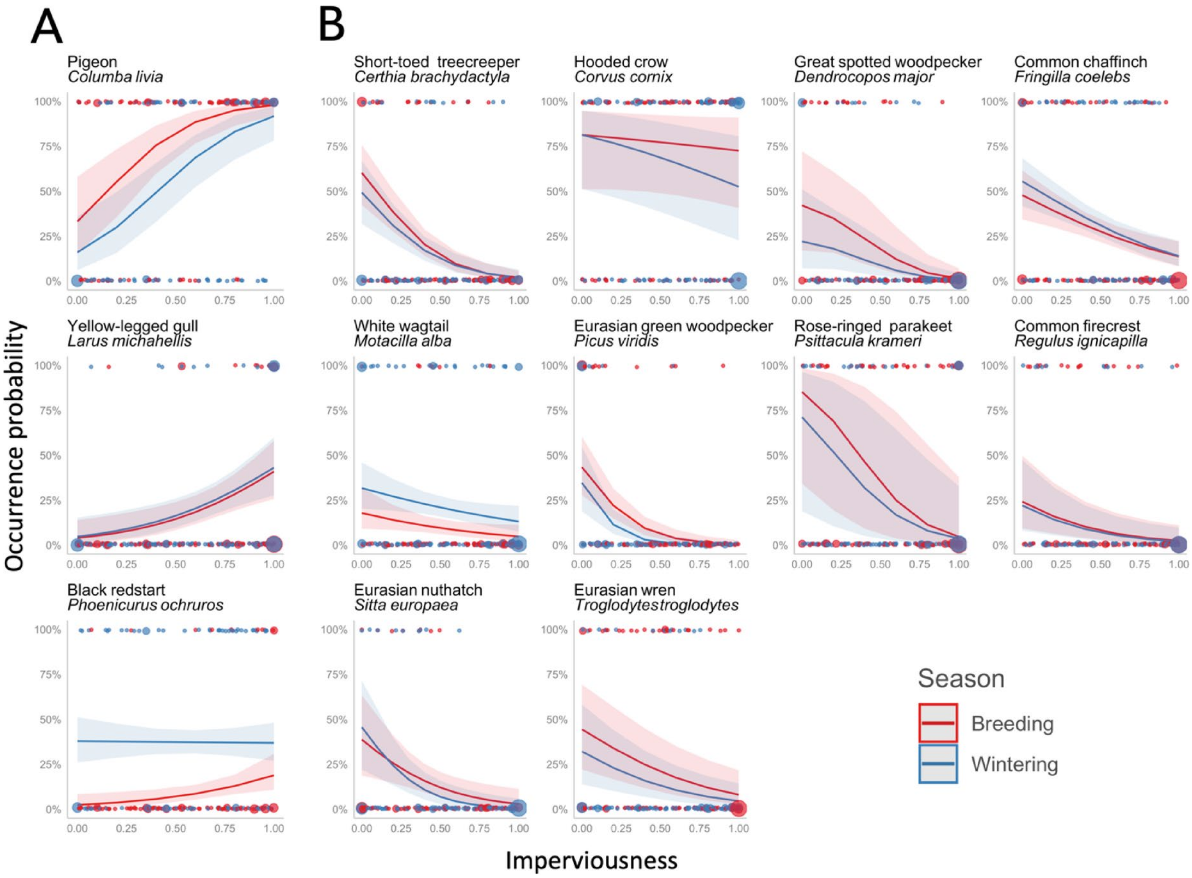

Fig. 2. Regression plots from the species-specific GLMMs with occurrence probability in relation to the imperviousness gradient across seasons for winners (**A**) and losers (**B**). Point identity and city were added as nested random factors in the models. Winners were classified based on significantly positive linear responses to urbanisation and losers based on significantly negative responses. For black redstart (*Phoenicurus ochruros*) a significant ($p < 0.05$) interaction between imperviousness and season was highlighted. See Table S2 for results.

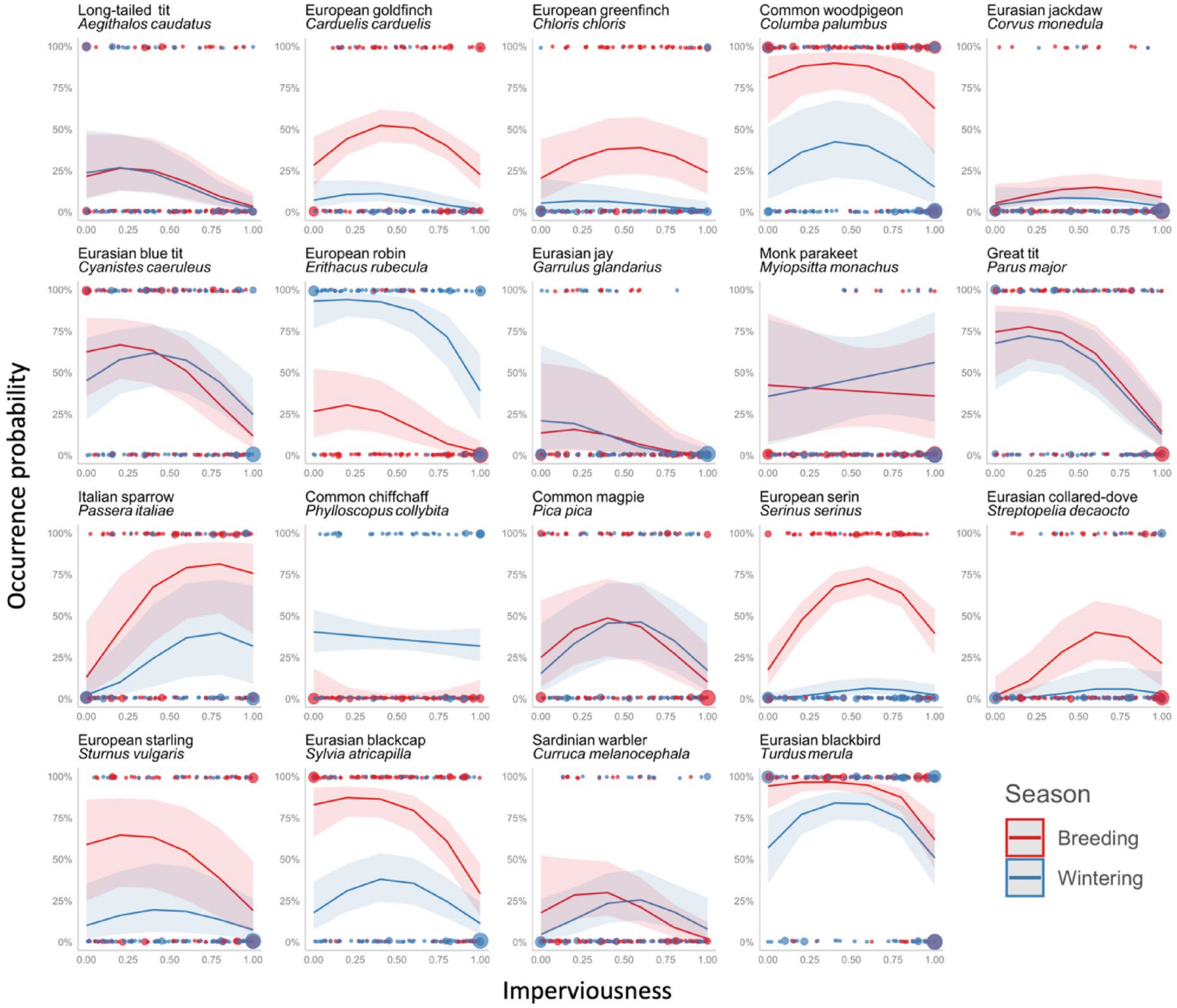

Fig. 3. Regression plots from the species-specific GLMMs with occurrence probability in relation to the imperviousness gradient across seasons for urban adapters. Point identity and city were added as nested random factors in the models. Urban adapters were classified based on non-significant or significantly non-linear responses to urbanisation. For blue tit (*Cyanistes caeruleus*), blackcap (*Sylvia atricapilla*), Sardinian warbler (*Curruca melanocephala*) and blackbird (*Turdus merula*) a significant ($p < 0.05$) interaction between imperviousness and season was highlighted. See Table S2 for results.

but there were a few with non-significant responses (i.e. European greenfinch *Chloris chloris*, Eurasian jackdaw *Corvus monedula*, Eurasian jay *Garrulus glandarius*, monk parakeet *Myiopsitta monachus*, common chiffchaff *Phylloscopus collybita*). See Table S2 for species-specific model outputs.

Bird species composition and traits

There was significant variation in bird species composition and bird traits across the urban gradient, both during the breeding (composition: $\chi^2 = 8.95$, p-value = 0.003; traits: $\chi^2 = 7.00$, p-value = 0.027) and winter (composition: $\chi^2 = 7.71$, p-value = 0.035; traits: $\chi^2 = 5.78$, p-value = 0.030) seasons. Abundance increased with increasing urbanisation during the breeding season in species which breed colonially, have a greater number of broods per year, a longer life span and, to a lesser extent, closed arboreal nesting and a granivorous diet. Invertivores, ground- and close to ground-nesting species, short-distance migrants and non-colonial species were more abundant in areas of low impervious cover (i.e. higher cover of green spaces). During winter, species with a greater number of broods per year, solitary behaviour and the ability to use multiple foraging strata had higher abundances with increasing urbanisation. On the contrary, species with larger clutch sizes and short-distance migrant species were more abundant in green spaces (Fig. 4).

Discussion

Our hypotheses were largely supported by our results. We predicted that bird species composition would change along an urbanisation gradient across seasons and that these changes would be modulated by ecological and life-history traits, with winners and losers distinguishable in the urban environment. Our study confirmed that

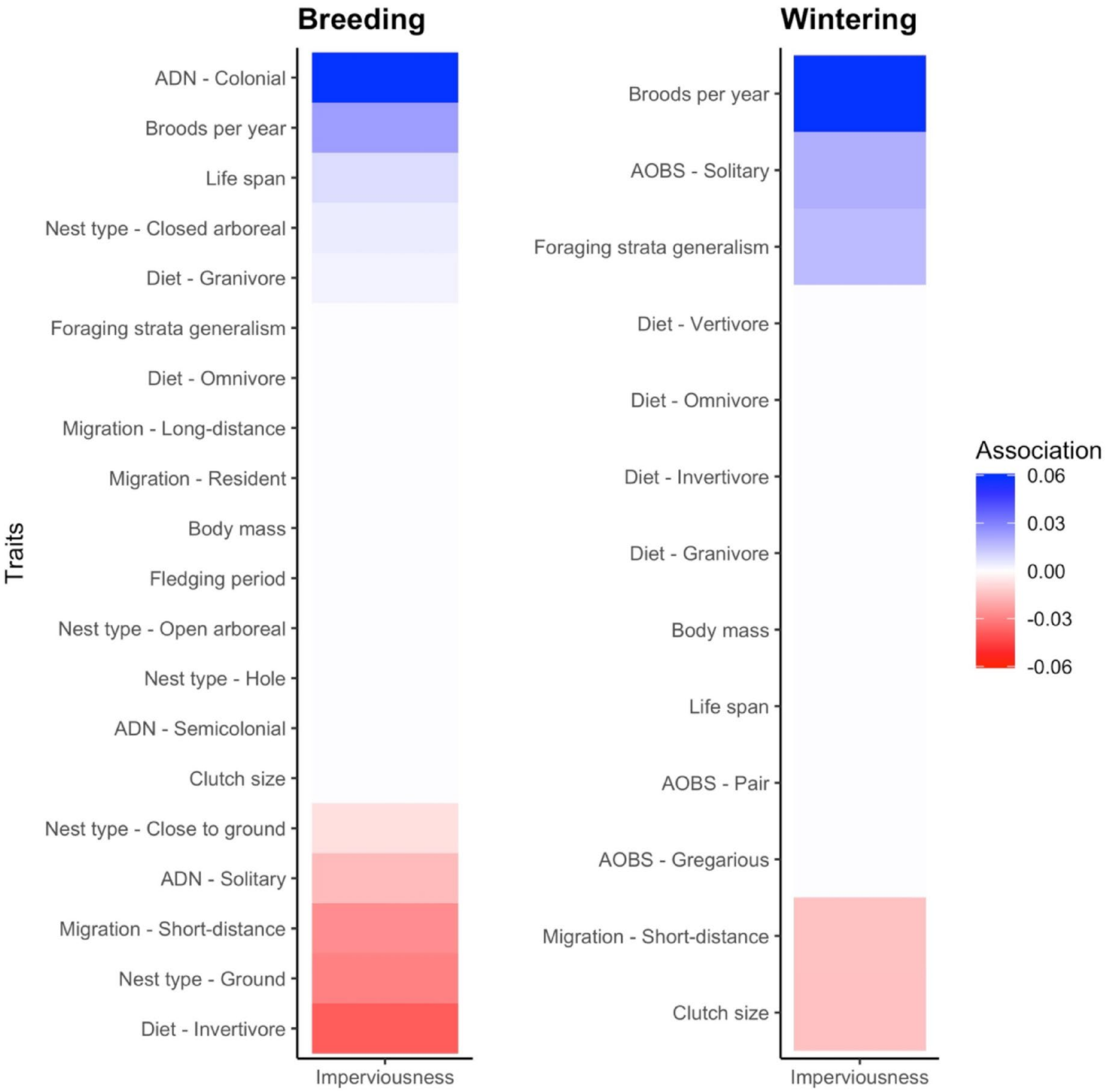

Fig. 4. Heatmaps of the relationships between bird traits and the imperviousness gradient for the breeding and wintering seasons derived from the fourth-corner analysis with a LASSO penalty. White cells represent non-significant associations whereas darker colours represent stronger associations, with blue representing positive correlations (i.e. traits associated with highly impervious areas) and red negative ones (i.e. traits associated with green spaces). ADN is the association degree during nesting whilst AOBS is the association degree outside the breeding season. See Table 1 for further details on traits.

bird communities vary along the urban gradient in both the breeding and wintering seasons, and that species traits significantly influence these responses. However, rather than a clear-cut division into winners and losers, most species appeared to be urban adapters, typically occurring at intermediate levels of urbanisation. Moreover, we observed notable intra-specific differences between the breeding and wintering seasons, suggesting that individual species may shift their responses to urbanisation throughout the annual cycle. Together, these findings underscore the complexity of urban bird community dynamics and highlight the importance of accounting for seasonal variations..

We found that being a colonial species and having a higher number of broods per year were the traits most closely associated with winners[31,70], whilst solitary breeders tended to be filtered out from highly urbanised areas. Colonialism and sociality may facilitate the exploitation of urban areas through improved detection of food sources and avoidance of predators[34,71]. Furthermore, a higher number of broods during an extended breeding season was a winning trait. Species that are able to exploit the trophic resources in urban areas and are favoured by higher temperatures are more likely to show extended breeding seasons (e.g. 3 broods for the Italian sparrow and up to 5 for the feral pigeon). This in turn is associated with an advancement in reproductive phenology of urban in comparison to rural birds[72,73]. Somewhat anomalously, in winter, species with large clutch sizes were less associated with urban areas. This result likely arose because many small passerines (with relatively large clutch sizes) are migrant species that leave the city in winter (see below), whereas species with small clutches (in particular pigeons) remain.

Species nesting close to or on the ground were negatively affected by urbanisation. The loss of large open habitats within cities, together with higher nest predation pressure caused by corvids, cats and dogs and disturbance by human activities, is the main cause of the poor survival of urban ground nesting species[74,75]. Nesting in vegetation above the ground (either in open or enclosed nests) is beneficial for urban-tolerant species[47,74], with documented switches in nest sites in some species in newly colonised urban habitats[76]. We found a positive effect of closed arboreal nests (e.g. magpie, monk parakeet), which is possibly a preferred strategy in comparison to cavity nesting due to the lower availability of natural cavities (i.e. mostly in trees) in highly impervious areas[77], although some species can adapt to nest in non-natural cavities in buildings (e.g. jackdaw, Italian sparrow, pigeon).

Food availability can change drastically along the urbanisation gradient and especially in different seasons. Insectivorous birds were generally classed as losers because they were associated with areas with a great cover of green spaces, likely due to the difficulties in finding adequate food resources where impervious cover is high. However, some species manage to adapt to these conditions and to exploit new food sources provided by human activities, e.g. garbage, bird feeders[46]. Flexibility in diet, and the ability to learn and adapt, which can be correlated with a bigger brain size and a longer lifespan in some bird species, are successful features in an urban context[35,78,79] because individuals might respond promptly to new ecological challenges[80]. Indeed, species that were more generalist in their foraging strata (i.e. exploiting all available strata in the urban environment) were more abundant in urbanised areas in winter, suggesting greater flexibility in foraging habitat selection when trophic resources become scarcer. We also found that a granivorous diet was associated with more urbanised areas[34,47,81] during the breeding season. Some studies argue that this might be due to benefits from supplementary feeding[82,83]. However, it would seem more likely that such effects might be more evident in winter[50] when natural food resources are scarcer and when supplementary feeding is more widespread[84] yet there was no effect of granivorous diet in the winter in our study. Furthermore, supplementary feeding in Italy (and southern Europe in general) is not as popular as in northern European countries or the USA[55,56]. The positive effect of granivorous diet in the breeding season may instead have been influenced by the abundance of seed-producing ornamental plants[85,86] which are widespread in the city. It is still possible to find intact native herbaceous patches in Italian cities, widely used by granivorous species breeding in highly urbanised areas such as the European serin *Serinus serinus*. Also, many granivorous species, such as the Italian sparrow and the feral pigeon, have developed a broad trophic niche to exploit a wide range of artificial food, which is abundant in cities.

Negative effects of non-native bird species on native urban bird communities are still not fully supported[87], yet studies have shown potential competition for nest sites[88,89] and effects on foraging behaviour of native avifauna[90]. There is also evidence that native bird communities are more affected by habitat loss and disturbance in human-modified environments than by competition with non-native species such as parakeets, which may have limited negative effects on native avifauna[86]. The two non-native species of parakeets we found in our study area showed different traits which resulted in different responses to urbanisation. The monk parakeet is a colonial breeder that nests in the canopy of highly urbanised areas and has a higher number of broods per year, and can thus be considered a winner. The rose-ringed parakeet on the other hand can be considered a loser as it is more tied to green spaces of cities, in particular large parks, and is a solitary breeder, nesting in cavities. This species does, however, show a strong link to human-modified habitats in its non-native range[86], and it is probably less likely to occur in natural or near-natural habitats which were not considered in our study.

Interesting patterns emerged from species-specific models in relation to urbanisation, showing that species were more generalist in the non-breeding season. Regarding migratory status and phenology, some short-distance migrant species that used highly urbanised areas during the breeding period were no longer present during the winter, moving from highly urbanised areas where they nest to winter in areas where trophic resources are likely less limiting (e.g. finches like European goldfinch *Carudelis carduelis*, European greenfinch and European serin, common woodpigeon *Columba palumbus* and European starling). Some species did not breed in the most impervious areas of the city or were scarce breeders in at least some of our cities, but were present in winter (e.g. European robin, black redstart, common chiffchaff). Callaghan et al.[43] and Sorte et al.[91] highlighted a greater use of urban areas during the non-breeding season by migrants in cities (i.e. urban tolerance increases during the winter). Indeed, many bird species associated with green spaces (e.g. common firecrest *Regulus ignicapilla*, common chaffinch *Fringilla coelebs*, European robin, Eurasian blackbird) were classified as short-distance migrants and were negatively affected by urbanisation in our study.

This study has identified winners, losers and urban adapters in the context of an urbanisation gradient across six southern European cities during the breeding and non-breeding seasons, thus addressing the bias towards northern European cities, evident from the literature[44] and by considering seasonal effects, which are rarely considered in urban gradient studies that are usually undertaken in the breeding season[40,41]. Many of the traits that we identified as being associated with either winners or losers were consistent with findings of other studies from different geographical locations (e.g. generalists[33] and more social species[43] were winners, while short-distance migrants[75] and ground-nesters[33,75] were losers). However, there were also some notable differences (e.g. no advantage for granivores in the winter[33] or for species with a large clutch size[31,35]). Interestingly, urban adapters, while not classified strictly as winners, showed the ability to exploit urban environments. Their intermediate level of tolerance to urbanisation might allow them to utilise resources across a variety of urban gradients, adapting behaviours and foraging strategies that allow them to persist in cities. In this sense, urban adapters could be considered secondary winners as their flexible strategies provide them with resilience in increasingly human-dominated landscapes.

Species classified in our sample of cities may not be considered winners, losers or urban adapters in other regions. This could be due to methodological differences, although it is very likely that region-specific factors have an important influence. A particular aspect that is likely to be important is the relative scarcity of supplementary feeding in Italy compared to the majority of similar studies that show a marked bias towards northern Europe and North America where this practice is more widespread[55,56]. Studies in countries such as Italy therefore offer the opportunity to assess impacts of urbanisation without the likely profound influence of supplementary feeding which can extend to non-urban areas[92]. Broadening the seasonal and geographic scope of urbanisation impact research, ideally using standardised methods, would increase our understanding of the traits that promote winners and losers in different contexts. This could inform urban planning and management strategies to maintain high-levels of avian diversity in urban environments[33] and urban biodiversity more generally.

Data availability

The datasets generated during and/or analysed during the current study are available in the Zenodo repository, DOI https://doi.org/10.5281/zenodo.15343590.

Received: 28 November 2024; Accepted: 28 April 2025

References

1. Simkin, R. D. et al. Biodiversity impacts and conservation implications of urban land expansion projected to 2050. *Proc. Natl Acad. Sci. USA* 119, e2117297119 (2022).
2. United Nations. World Cities Report 2022. (2022). https://unhabitat.org/sites/default/files/2022/06/wcr_2022.pdf
3. United Nations. World Urbanisation Prospects: The 2018 Revision (2018). https://population.un.org/wup/Publications/Files/WUP2018-Report.pdf
4. Foley, J. A. et al. Global consequences of land use. *Science* **309**, 570–574 (2005).
5. Grimm, N. B. et al. Global change and the ecology of cities. *Science* **319**, 756–760 (2008).
6. Gaston, K. J., Davies, Z. G. & Edmondson, J. L. Urban environments and ecosystem functions. In *Urban Ecology* (ed. Gaston, K. J.) 35–52 (Cambridge University Press, 2010).
7. van Vliet, J. Direct and indirect loss of natural area from urban expansion. *Nat. Sustain.* **2**, 755–763 (2019).
8. McDonald, R. I., Kareiva, P. & Forman, R. T. The implications of current and future urbanisation for global protected areas and biodiversity conservation. *Biol. Conserv.* **141**, 1695–1703 (2008).
9. Shochat, E. et al. Invasion, competition, and biodiversity loss in urban ecosystems. *BioScience* **60**, 199–208 (2010).
10. Seto, K. C., Güneralp, B. & Hutyra, L. R. Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proc. Natl. Acad. Sci. USA* **109**, 16083–16088 (2012).
11. Li, G. et al. Global impacts of future urban expansion on terrestrial vertebrate diversity. *Nat. Commun.* **13**, 1628 (2022).
12. Ibáñez-Álamo, J. D. et al. Global loss of avian evolutionary uniqueness in urban areas. *Glob. Change Biol.* **23**, 2990–2998 (2017).
13. Chamberlain, D. E. et al. Determinants of bird species richness in public green spaces. *Bird. Study* **54**, 87–97 (2007).
14. F Aronson, M. et al. A global analysis of the impacts of urbanisation on bird and plant diversity reveals key anthropogenic drivers. *Proc. R. Soc. B.* **281**, 20133330 (2014).
15. Beninde, J., Veith, M. & Hochkirch, A. Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. *Ecol. Lett.* **18**, 581–592 (2015).
16. Aronson, M. F. et al. Biodiversity in the city: key challenges for urban green space management. *Front. Ecol. Environ.* **15**, 189–196 (2017).
17. Ives, C. D. et al. Cities are hotspots for threatened species. *Glob. Ecol. Biogeogr.* **25**, 117–126 (2016).
18. Lepczyk, C. A. & Aronson, M. F. & La sorte, F. A. Cities as sanctuaries. *Front. Ecol. Environ.* **21**, 251–259 (2023).
19. Møller, A. P. Successful city dwellers: a comparative study of the ecological characteristics of urban birds in the Western Palearctic. *Oecologia* **159**, 849–858 (2009).
20. Slabbekoorn, H. & Peet, M. Birds sing at a higher pitch in urban noise. *Nature* **424**, 267 (2003).
21. Lepczyk, C. A. & Warren, P. S. (eds) *Urban Bird Ecology and Conservation* (Univ. of California Press, 2012).
22. Magle, S. B. et al. Urban wildlife research: past, present, and future. *Biol. Conserv.* **155**, 23–32 (2012).
23. Fischer, J. D., Schneider, S. C., Ahlers, A. A. & Miller, J. R. Categorizing wildlife responses to urbanization and conservation implications of terminology. *Conserv. Biol.* **29**, 1246–1248 (2015).
24. Devictor, V. et al. Functional biotic homogenization of bird communities in disturbed landscapes. *Glob. Ecol. Biogeogr.* **17**, 252–261 (2008).
25. McKinney, M. L. Effects of urbanisation on species richness: a review of plants and animals. *Urban Ecosyst.* **11**, 161–176 (2008).
26. Sol, D. et al. The worldwide impact of urbanisation on avian functional diversity. *Ecol. Lett.* **23**, 962–972 (2020).
27. McKinney, M. L. Urbanisation as a major cause of biotic homogenization. *Biol. Conserv.* **127**, 247–260 (2006).
28. Hahs, A. K. et al. Urbanisation generates multiple trait syndromes for terrestrial animal taxa worldwide. *Nat. Commun.* **14**, 4751 (2023).
29. Croci, S., Butet, A. & Clergeau, P. Does urbanisation filter birds on the basis of their biological traits? *Condor* **110**, 223–240 (2008).
30. Blair, R. B. Land use and avian species diversity along an urban gradient. *Ecol. Appl.* **6**, 506–519 (1996).
31. Callaghan, C. T. et al. 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 urbanisation. *Oikos* **128**, 845–858 (2019).
32. Callaghan, C. T. et al. Avian trait specialization is negatively associated with urban tolerance. *Oikos* **129**, 1541–1551 (2020).
33. Evans, K. L. et al. What makes an urban bird? *Glob. Change Biol.* **17**, 32–44 (2011).
34. Kark, S., Iwaniuk, A., Schalimtzek, A. & Banker, E. Living in the city: can anyone become an 'urban exploiter'? *J. Biogeogr.* **34**, 638–651 (2007).
35. Neate-Clegg, M. H. et al. Traits shaping urban tolerance in birds differ around the world. *Curr. Biol.* **33**, 1677–1688 (2023).
36. Ikin, K., Knight, E., Lindenmayer, D. B., Fischer, J. & Manning, A. D. Linking bird species traits to vegetation characteristics in a future urban development zone: implications for urban planning. *Urban Ecosyst.* **15**, 961–977 (2012).
37. Jokimäki, J., Suhonen, J., Jokimäki-Kaisanlahti, M. L. & Carbó-Ramírez, P. Effects of urbanisation on breeding birds in European towns: impacts of species traits. *Urban Ecosyst.* **19**, 1565–1577 (2016).
38. Dale, S. Urban bird community composition influenced by size of urban green spaces, presence of native forest, and urbanisation. *Urban Ecosyst.* **21**, 1–14 (2018).
39. Cavalli, M., Isacch, J. P., Baladrón, A. V., Biondi, L. M. & Bó, M. S. Differing nest-defence behaviour in urban and rural populations of breeding burrowing owls. *Emu* **116**, 428–434 (2016).
40. Gryz, J. & Krauze-Gryz, D. Influence of habitat urbanisation on time of breeding and productivity of Tawny Owl (*Strix aluco*). *Pol. J. Ecol.* **66**, 153–161 (2018).

41. de Satgé, J. et al. Urbanisation lowers great tit (*Parus major*) breeding success at multiple spatial scales. *J. Avian Biol.* **50**, e02248 (2019).
42. La Sorte, F. A., Clark, J. A., Lepczyk, C. A. & Aronson, M. F. Collections of small urban parks consistently support higher species richness but not higher phylogenetic or functional diversity. *Proc. R. Soc. B* **290**, 20231424 (2023).
43. Callaghan, C. T., Cornwell, W. K., Poore, A. G., Benedetti, Y. & Morelli, F. Urban tolerance of birds changes throughout the full annual cycle. *J. Biogeogr.* **48**, 1503–1517 (2021).
44. Moreno-Contreras, I. et al. Disentangling the drivers of urban bird diversity in the non-breeding season: A general synthesis. *Glob. Change Biol.* **30**, e17421 (2024).
45. Brittingham, M. C. & Temple, S. A. Use of winter bird feeders by black-capped chickadees. *J. Wildl. Manag.* **56**, 103–110 (1992).
46. Robb, G. N. et al. Winter feeding of birds increases productivity in the subsequent breeding season. *Biol. Lett.* **4**, 220–223 (2008).
47. Chace, J. F. & Walsh, J. J. Urban effects on native avifauna: a review. *Landsc. Urban Plan.* **74**, 46–69 (2006).
48. Partecke, J. & Gwinner, E. Increased sedentariness in European blackbirds following urbanisation: a consequence of local adaptation? *Ecology* **88**, 882–890 (2007).
49. Grünwald, J. et al. Ecological traits predict population trends of urban birds in Europe. *Ecol. Indic.* **160**, 111926 (2024).
50. Ibáñez-Álamo, J. D. et al. Biodiversity within the city: effects of land sharing and land sparing urban development on avian diversity. *Sci. Total Environ.* **707**, 135477 (2020).
51. Ibáñez-Álamo, J. D. et al. Urban landscape organization is associated with species-specific traits in European birds. *Sci. Total Environ.* **908**, 167937 (2024).
52. Courter, J. R. et al. Weekend bias in citizen science data reporting: implications for phenology studies. *Int. J. Biometeorol.* **57**, 715–720 (2013).
53. Kelling, S. et al. Taking a 'big data' approach to data quality in a citizen science project. *Ambio* **44**, 601–611 (2015).
54. Lewandowski, E. & Specht, H. Influence of volunteer and project characteristics on data quality of biological surveys. *Conserv. Biol.* **29**, 713–723 (2015).
55. Jones, D. N. *The Birds at my Table* (Cornell University Press, 2017).
56. Reynolds, S. J. et al. Garden bird feeding: insights and prospects from a north-south comparison of this global urban phenomenon. *Front. Ecol. Evol.* **5**, 24 (2017).
57. ISPRA. Carta Copertura del Suolo ISPRA 2021. https://www.isprambiente.gov.it/it/attivita/suolo-e-territorio/suolo/copertura-del-suolo/carta-nazionale-di-copertura-del-suolo (2021).
58. Dondina, O. et al. Spatial and habitat determinants of small-mammal biodiversity in urban green areas: lessons for nature-based solutions. *Urban Urban Green.* **104**, 128641 (2025).
59. Bibby, C. J. *Bird Census Techniques* (Elsevier, 2000).
60. Baccetti, N. & Fracasso, G. CISO-COI check-list of Italian birds-2020. *Avocetta* **45**, 1–12 (2021).
61. Marcolin, F., Lakatos, T., Gallé, R. & Batáry, P. Fragment connectivity shapes bird communities through functional trait filtering in two types of grasslands. *Glob Ecol. Conserv.* **28**, e01687 (2021).
62. Wilman, H. et al. EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecol. Arch. E095–178 Ecol.* **95**, 2027–2027 (2014).
63. Storchová, L. & Hořák, D. Life-history characteristics of European birds. *Glob. Ecol. Biogeogr.* **27**, 400–406 (2018).
64. Bird, J. P. et al. Generation lengths of the world's birds and their implications for extinction risk. *Conserv. Biol.* **34**, 1252–1261 (2020).
65. Tobias, J. A. et al. AVONET: morphological, ecological and geographical data for all birds. *Ecol. Lett.* **25**, 581–597 (2022).
66. Bates, D. et al. Package 'lme4'. *Convergence* **12**, 1–2 (2015).
67. Wang, Y. I., Naumann, U., Wright, S. T. & Warton, D. I. mvabund–an R package for model-based analysis of multivariate abundance data. *Methods Ecol. Evol.* **3**, 471–474 (2012).
68. Dormann, C. F. et al. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* **30**, 609–628 (2007).
69. R Core Team. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria (2023). https://www.R-project.org/
70. Coleman, S. L. & Mellgren, R. L. Neophobia when feeding alone or in flocks in zebra finches, *Taeniopygia guttata*. *Anim. Behav.* **48**, 903–907 (1994).
71. Sol, D. Do successful invaders exist? Pre-adaptations to novel environments in terrestrial vertebrates. *Biol. Invasions* **193**, 127–141 (2007).
72. Partecke, J., Van't Hof, T. & Gwinner, E. Differences in the timing of reproduction between urban and forest European Blackbirds (*Turdus merula*): result of phenotypic flexibility or genetic differences? *Proc. R Soc. Lond. B Biol. Sci.* **271**, 1995–2001 (2004).
73. Chamberlain, D. E. et al. Avian productivity in urban landscapes: a review and meta-analysis. *Ibis* **151**, 1–18 (2009).
74. Jokimäki, J. & Huhta, E. Artificial nest predation and abundance of birds along an urban gradient. *Condor* **102**, 838–847 (2000).
75. Lakatos, T., Chamberlain, D. E., Garamszegi, L. Z. & Batary, P. No place for ground-dwellers in cities: A meta-analysis on bird functional traits. *Glob. Ecol. Conserv.* **38**, e02217 (2022).
76. Yeh, P. J., Hauber, M. E. & Price, T. D. Alternative nesting behaviours following colonisation of a novel environment by a passerine bird. *Oikos* **116**, 1473–1480 (2007).
77. Blewett, C. M. & Marzluff, J. M. Effects of urban sprawl on Snags and the abundance and productivity of cavity-nesting birds. *Condor* **107**, 678–693 (2005).
78. Maklakov, A. A., Immler, S., Gonzalez-Voyer, A., Rönn, J. & Kolm, N. Brains and the city: big-brained passerine birds succeed in urban environments. *Biol. Lett.* **7**, 730–732 (2011).
79. Sol, D., Bartomeus, I. & Griffin, A. S. The paradox of invasion in birds: competitive superiority or ecological opportunism? *Oecologia* **169**, 553–564 (2012).
80. Sol, D., González-Lagos, C., Moreira, D., Maspons, J. & Lapiedra, O. Urbanisation tolerance and the loss of avian diversity. *Ecol. Lett.* **17**, 942–950 (2014).
81. Paton, G. D., Shoffner, A. V., Wilson, A. M. & Gagné, S. A. The traits that predict the magnitude and spatial scale of forest bird responses to urbanisation intensity. *PLoS One* **14**, e0220120 (2019).
82. Jokimäki, J., Clergeau, P. & Kaisanlahti-Jokimäki, M. L. Winter bird communities in urban habitats: a comparative study between central and Northern Europe. *J. Biogeogr.* **29**, 69–79 (2002).
83. Fuller, R. A., Warren, P. H., Armsworth, P. R., Barbosa, O. & Gaston, K. J. Garden bird feeding predicts the structure of urban avian assemblages. *Divers. Distrib.* **14**, 131–137 (2008).
84. Jones, D. N. & Reynolds, S. J. Feeding birds in our towns and cities: a global research opportunity. *J. Avian Biol.* **39**, 265–271 (2008).
85. McKinney, M. L. Urbanisation, biodiversity, and conservation: the impacts of urbanisation on native species are poorly studied, but educating a highly urbanised human population about these impacts can greatly improve species conservation in all ecosystems. *Bioscience* **52**, 883–890 (2002).
86. Marcolin, F., Segurado, P., Chamberlain, D. & Reino, L. Testing the links between bird diversity, alien species and disturbance within a human-modified landscape. *Ecography* e06886 (2023).
87. Menchetti, M. & Mori, E. Worldwide impact of alien parrots (Aves Psittaciformes) on native biodiversity and environment: a review. *Ethol. Ecol. Evol.* **26**, 172–194 (2014).

88. Strubbe, D. & Matthysen, E. Invasive ring-necked parakeets (*Psittacula krameri*) in Belgium: habitat selection and impact on native birds. *Ecography* **30**, 578–585 (2007).
89. Hernández-Brito, D., Carrete, M., Popa-Lisseanu, A. G., Ibáñez, C. & Tella, J. L. Crowding in the city: losing and winning competitors of an invasive bird. *PLoS One* **9**, e100593 (2014).
90. Peck, H. L., Pringle, H. E., Marshall, H. H., Owens, I. P. & Lord, A. M. Experimental evidence of impacts of an invasive parakeet on foraging behavior of native birds. *Behav. Ecol.* **25**, 582–590 (2014).
91. La Sorte, F. A., Tingley, M. W. & Hurlbert, A. H. The role of urban and agricultural areas during avian migration: an assessment of within-year temporal turnover. *Glob. Ecol. Biogeogr.* **23**, 1225–1234 (2014).
92. Shutt, J. D., Trivedi, U. H. & Nicholls, J. A. Faecal metabarcoding reveals pervasive long-distance impacts of garden bird feeding. *Proc. R. Soc. B* **288**, 20210480 (2021).

Acknowledgements

We thank Luca Bajno for help during fieldwork and land use analysis. R.A., F.C. and D.C. were supported by the National Biodiversity Future Centre - NBFC [funded by the European Union - NextGenerationEU under the National Recovery and Resilience Plan (NRRP) M4C2 Investment Line 1.4: "Strengthening of research facilities and creation of "national R&D champions" on some Key Enabling Technologies", project CN_00000033]. L.I., M.B. 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: Strenghtening of research structures and creation of R&D "innovation ecosystems", set up of "territorial leaders in R&D", project ECS_00000037).

Author contributions

R.A., F.M., G.A., D.C. conceived the study; R.A., F.M., G.A., L.I. conducted the fieldwork; R.A. analysed data with inputs from F.M. and D.C. All authors contributed to the drafts and gave final approval for publication. R.A. and F.M. share first authorship.

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/s41598-025-00350-6.

Correspondence and requests for materials should be addressed to R.A.

Reprints and permissions information is available at www.nature.com/reprints.