RESEARCH ARTICLE



Responses of avian assemblages to spatiotemporal landscape dynamics in urban ecosystems

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Abstract

Context Urbanization and its associated impacts on biodiversity are increasing globally. There is a need to enhance our understanding of species responses to inform strategies for sustainable urbanization.

Objectives Three extensive bird monitoring campaigns took place over the last three decades in the city of Naples, Italy, providing a comprehensive longitudinal dataset to analyse occurrence trends of urban birds. We aimed to assess both species-specific and assemblage-level changes in urban birds according to land cover dynamics.

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variation.

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Methods We extracted bird data for the periods

1990-95, 2000-05, and 2014-18, and explored the

spatial and temporal relationships between bird pres-

ence/avian assemblage composition, and land cover

Results The species richness of breeding birds

remained stable over time, despite a notable species

turnover, influenced by changes in the species' key land cover classes. Species associated with forest and

urban land cover tended to colonise the area, while

those dependent on abandoned and cultivated areas

decreased or went locally extinct. Birds changed their degree of dependence upon their key habitat type over time, as species from marginal and open habitat types

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D. E. Chamberlain Department of Life Sciences and Systems Biology, University of Turin, Via Accademia Albertina 13, 10123 Turin, Italy needed larger amounts of habitat to persist within the area, while forest species showed an opposite trend. *Conclusions* Habitat-driven changes in avian assemblages within the urban landscape led to an increase in forest-associated species, and a decrease in birds associated with declining habitat types. Our findings may inform urban planning to promote more wildlife-friendly cities, which for our study area should prioritise open and marginal habitats.

Keywords Birds · Landscape ecology · Management · Marginal habitat · Species richness · Urbanization

Introduction

The rate of urbanization in terms of expansion of the built environment has many negative impacts, including changes in land cover, pollution levels, hydrological cycles, biogeochemical cycles, local climate, and biodiversity (Grimm et al. 2008; Aronson et al. 2014). The increasing human population, and the proportion of that population that lives in urban areas, are driving increases in the rate of urbanization in many parts of the world (United Nations 2015). There is thus a need to develop urban areas in a more sustainable way to minimise impacts on the environment and improve the living conditions of urban dwellers. Indeed, the development of sustainable cities is one of the United Nations' Sustainable Development Goals to be achieved by 2030 (United Nations 2018). To achieve this, there needs to be a sound knowledge base to inform the development of strategies to address these goals.

One of the most evident impacts of urbanization is on biodiversity, which is typically lower in urban areas compared to other habitats. Urbanization is a threat to habitats adjacent to urban areas as well, as new development expands. A further consequence of urbanization can also be the 'infilling' of undeveloped habitat fragments within cities, which may be parks and other amenity areas, including unmanaged and informal semi-natural habitat, but also marginal lands such as brownfield sites (i.e., abandoned, formerly developed land, often industrial) and scrubby areas (Anderson and Minor 2017) which may be important reservoirs of urban biodiversity (Zuñiga-Palacios et al. 2020). Thus relatively biodiverse habitats may become increasingly fragmented within the urban landscape. Despite the generally negative impact of urbanization, the impoverished biodiversity in urban areas may still have value. For those species that can persist, urban environments may hold important populations compared to more natural habitats (e.g., Mason 2000; Pomeroy and Kibuule 2017). Furthermore, urban biodiversity is associated with a range of ecosystem services (Dearborn and Kark 2009; Belaire et al. 2015), and there is increasing evidence that urban habitats which are relatively rich in biodiversity have health benefits for humans (Marselle et al. 2021).

Birds are probably the most studied group of organisms in an urban context. Urbanization tends to favour certain biological traits (Santini et al. 2019), whilst others are filtered out, thus urban bird communities generally show characteristic features, especially in terms of diet and nesting strategy (e.g., Patankar et al. 2021; Lakatos et al. 2022). Whilst there is an increasing evidence base for urban exploiters and their key habitats in urban areas, much of this is based on the gradient approach, whereby bird communities and habitats are sampled along urbanization gradients of decreasing cover of artificial surfaces, typically from city centres to peri-urban, rural or even natural areas outside the city (McKinney 2000, Bàtary et al. 2018). The temporal effects of urbanization are then inferred based on a space-fortime substitution approach (Blois et al. 2013) i.e., the spatial variations from non-urbanized to urbanized bird communities along the gradient are assumed to be analogous to the development of non-urban to urban habitat over time. However, urban areas are usually highly dynamic in terms of land cover, being characterized by renovations, expansions, variable management of green and blue spaces, and urban agriculture, resulting in a rich mosaic of different habitat types that may show high temporal and spatial variation (Barot et al., 2019; Knapp et al., 2021; McKinney 2008). The assumptions underlying the space-for-time substitution approach may therefore be overly simplistic.

Detecting how animals respond to such dynamic environments is paramount to managing urban wildlife and the ecosystem services it provides (e.g. Ancillotto et al., 2019), yet data from long time series are needed to detect such responses, and results may vary significantly depending on the duration of the time frame selected (Weiserbs and Jacob 2007; Fidino and Magle 2017). Studies that analyse changes in urban bird populations and their key habitats over time are scarce. This is largely due to a lack of historical data - urban bird research was not widespread before the 21st Century (Marzluff 2017), and urban areas have often not been included in monitoring studies, at least until relatively recently. Those longer-term studies that exist tend to be focused on specific urban habitats (in particular private gardens, e.g., Cannon et al. 2005; Plummer et al. 2019), and are geographically biased (Marzluff 2017), with relatively few studies having been carried out in southern Europe (Tzortzakaki et al. 2018). Existing examples of studies on Mediterranean urban bird communities have included gradient approaches to assess biotic homogenization (Sorace and Gustin 2008) and analyse seasonal dynamics (Caula et al. 2008) and identification of habitat features associated with species richness (Tzortzakaki et al. 2018) and nest sites (Marlès Magre et al. 2019). Most studies in this region have not, however, considered long-term trends in urban bird populations. Exceptions include a 23-year study on the impacts of surrounding urbanization on wetland birds (Ferrarini et al. 2021), a 26-year study on changes in species composition in a single park (Battisti and Dodaro 2016), and an 8-year study on population changes of alien parrot species (Hernández-Brito et al. 2022).

In this study, we analyse trends in the occurrence of birds and land cover changes in a large Mediterranean city over three decades in a period of urban expansion. We analysed overall changes in the bird community, and changes in the occurrence of individual species, to assess the potential impacts of urbanization on key bird habitats within the urban environment, and crucially how dependence on these habitats varies over time. Whilst there have been several studies that have considered habitat associations in urban areas, we are unaware of studies that have considered how dependency on key habitats changes over time within urban areas. Based on existing evidence, we hypothesise that city-scale changes in land cover that have occurred over the last decades in our study area will have driven consequent changes in the bird assemblage. We predict that expanding urbanization will have led to a reduction in open-space species, and an increase in species that dwell in rocky areas or

forests, i.e., those species characterised by traits that may be expected to exploit urban environments, as seen in other contexts (Clergeau et al. 2006; Møller 2009; Murgui, 2014; Litteral and Shochat 2017; Lakatos et al. 2022). Furthermore, we predict that dependency on species' key habitats will increase as the area of those habitats is reduced and fragmented due to urbanization.

Materials and methods

Study area

We chose the city of Naples (Southern Italy, 40°50' N, 14°10'E) as a model to test the effects of land cover modifications on urban bird assemblages and species' relationships with the land cover over 28 years, using standardized data from bird atlases. Naples provides a good example of long-term bird monitoring, since bird presence data have been collected for the preparation of three bird atlases in the last three decades, respectively in 1990-95 (Fraissinet 1995), 2000-2005 (Fraissinet 2006), and 2014–2018 (Fraissinet and Capasso 2020). Naples is one of the largest urban areas in Europe and is the third-ranked Italian city according to the number of inhabitants. The city covers an area of ca. 117 km² and has a human population size of 959,188 inhabitants (as of December 2019; www.dati.istat.it) and a population density of 8,179 inhabitants/km². It lies along the Tyrrhenian Sea coast and comprises 8 km of coastline. Elevation ranges from 0 to 457 m a.s.l., and the climate is typically Mediterranean, with hot and dry summers and precipitation concentrated in autumn. Naples has also undergone significant land-use changes over the last three decades, with an evident expansion of built-up areas to the detriment of (semi-)natural ones (Mazzoleni et al. 2001; di Gennaro et al. 2019), so its territory provides an important opportunity to test hypotheses on the temporal and spatial effects of urbanization on bird communities. The city's geographic scale is large enough to represent an effective model for many other European urban areas.

Land cover mapping

The land cover classes represented within the metropolitan area of Naples are mainly humanmodified, with built-up areas strongly dominating the landscape, which is characterised by a mosaic of vegetation assemblages, including both natural patches and recreational green spaces, and small agricultural areas. Three land cover maps were created at different times (2018, 2006, 1995) through photointerpretation of digital orthophotos and aerial photogrammetric stereo pairs (AGEA 2014: https:// www.agea.gov.it; 40 cm spatial resolution) and cartographic restitution with a polygon vector data model, classified according to the CORINE legend (European Environment Agency – EEA: https://www. eea.europa.eu/data-and-maps/data/corine-biotopes) into 24 classes. Once the topology of the polygons had been verified, before the definitive drafting of the map, field checks were carried out. The work was done in ArcGIS 10.3 and Arcview 3.2 (Esri Inc.), keeping a 1:1500 scale. The 3 maps were then produced in the same geographical reference system (UTM WGS 84, zone 33, EPSG Authority), to the same legend (CORINE Land Cover/Biotopes, Online Resource 1), and the same scale ratio (1: 4000). For spatial and overlay analyses, all the vector maps were rasterized at 1 m grid cell size and the land cover classes were amalgamated into the following 5 classes which were felt to better represent the key landscape types for birds:

- 1. Urban areas (Urb): residential areas including infrastructures and paved roads, characterized by impervious surfaces, with small green patches (<0.3 ha) e.g., private gardens
- 2. Non-intensive farmland (Nif): traditionallymanaged crops including orchards, vineyards, and vegetable gardens, usually separated by hedgerows and small patches of woodland and grassland
- 3. Wooded areas (War): areas with extensive tree cover, natural or managed, i.e., recreational areas such as public parkland, historic villas, and botanical gardens. Such areas comprised native broadleaved tree species (*Quercus* spp., *Castanea sativa*), conifers (*Pinus pinea, P. halepensis* and *P. pinaster*), and non-native tree species (e.g.,

Robinia pseudoacacia, Ailanthus altissima, Eucalyptus spp.)

- 4. Cropland (Cro): intensively managed agricultural areas, featuring herbaceous cultivations, also comprising greenhouses
- 5. Abandoned fields (Afi): pioneer vegetation colonizing recently abandoned areas such as former agricultural areas, fallows, and wastelands, characterized by herbaceous species and low shrubs (e.g., *Rubus ulmifolius*).

We excluded poorly represented land-use types such as mining sites, landfills, and water bodies, each accounting for <5% of the entire urban territory.

We overlaid land cover maps on the bird sampling grid, and land cover composition within each grid square was quantified as the per cent of each of the five land-use classes, separately for each sampling session. All procedures were implemented in ArcGis 10.3.1.

We ran a series of repeated measures ANOVAs to assess whether the amounts of different land cover classes within each sampled square varied among the three periods, considering all results with p < 0.05 as significant, and applying a Tukey's post hoc test with Bonferroni correction to compare individual periods (expressed as per cent amount of land cover per grid square).

Bird surveys and description of bird assemblages

Surveys of breeding birds were conducted following protocols of the European Birds Census Council for ornithological atlases, each campaign lasting for 4 full reproductive seasons (February to May). Data on bird presence were collected adopting the same protocol for all the three atlases, covering the whole study area evenly by overlaying a 142 square grid (each covering 1 km²) on the city's geographic map (Fraissinet 1995, 2006) (Fig. 1). Surveyors visited each grid square 8.5 times on average within the same campaign, totalling 1,217 visits and 359 survey days across the entire study. Within each grid square, surveyors adopted an array of different techniques, such as mobile visual and acoustic transects, visits at dusk, and stationary hearing points, to maximise the chances of detecting all species. Bird detectability may vary greatly among species within an assemblage (Johnston et al. 2014), yet the multiple-visit-multiple-technique protocol we



Fig. 1 Map of the urban area of Naples, with the 1 km UTM square grid overlaid. A: land cover in 1995; B: land cover in 2018

adopted should confer sufficient confidence that single-square species inventories (i.e., presence/absence records in our sample) are reliable (Fraissinet 2006).

We quantified assemblage diversity across the three sampling sessions (1990-95, 2000-05, and 2014-18) by calculating species richness (S) and the Index of Ornithological Value (IOV), which assesses an avian assemblage's conservation value by evaluating its composition weighted for species' conservation status at global and/or local scales (Massa et al. 2004). The index is a useful tool to facilitate the identification of areas of higher conservation value for birds, regardless of species composition, and thus those in need of more urgent protection. This index is calculated as follows: $IOV = Stot [(SSpec1 \times 1) + ($ $SSpec2 \times 0.75$ + ($SSpec3 \times 0.50$) + ($SNonSpec^{E} \times 0$. 25) + (SCR × 1) + (SEN × 0.75) + (SVU × 0.50) + (SN $T \times 0.25$ + S147 × 100–1, where Stot is the number of breeding bird species, SSpec1, SSpec2, SSpec3 e SNonSpec^E are the numbers of bird species falling respectively in the SPEC1, SPEC2, SPEC3 and NonSPEC^E categories as defined by BirdLife (2017). Such categories indicate the prioritization degree of bird species according to their conservation status at the EU level, ranging from SPEC1, indicating higher priority (unfavourable conservation status and populations concentrated in Europe) to NonSPEC^E, indicating species whose conservation status is favourable and does not raise any concern. SCR, SEN, SVU, and SNT are the numbers of bird species assigned to different risk classes (CR, EN, VU, NT respectively) by the Italian IUCN red list (Gustin et al. 2019); and S147 is the number of bird species included in Annex I of the EU 2009/147/EC Birds Directive. The value of the index is relative to the study area and depends on the number of species per area, potentially including negative values, with higher values indicating greater conservation value.

Bird assemblage variation in time

We examined whether the bird assemblage changed throughout the study period and whether different ecological groups of species contributed to such changes. For visualizing the differences in assemblage composition among the three-time intervals, we used non-metric multidimensional scaling (NMDS), which is an ordination technique that locates samples in a multidimensional space based on a dissimilarity matrix derived from the Bray-Curtis index values. Such a matrix was obtained by comparing species composition at the grid square scale across all three samples. We then performed an Analysis of Similarity (ANOSIM), a randomization technique that calculates the probability that a sampling unit (i.e., a grid square) belongs to a given group of samples (in our case, sampling campaigns) based on intra- and inter-group variances. Significant test results (p < 0.05) indicate that groups differ significantly in composition. As the last step, we ran Similarity Percentage analyses (SIMPER) to calculate the relative importance of each bird category to the detected changes, following the classification obtained by the species-specific relationship between birds and land cover classes (see below). Similarly, we also tested whether species associated with different land-use classes showed a disproportionate tendency to go extinct or to colonise the study area. We did so by running a chi-squared test on a contingency table on the numbers of species associated with each land class category that respectively went extinct or colonised the area in at least one interval between sampling campaigns. Any species that went extinct in the first interval and that recolonized the area during the second was counted as belonging to both categories.

Species' relationships with land cover and time

We built single species Generalized Linear Mixed Models (GLMM) to evaluate the effect of land cover composition on species' probability of presence in each square. We did not partition the probability of detection and that of presence, thus we assume that detectability was constant across the study area and over time and that probabilities derived from the models can be used as relative probabilities of occurrence, although we use the term 'probability of occurrence' for convenience. For each species separately, we first modelled the probability of occurrence as a function of land cover composition inside each grid square, following a backwards stepwise procedure until a Minimum Adequate Model (MAM) was obtained (i.e., a model featuring only significant terms) to identify the land cover class with which a given species was most associated. Models were built with a zero-inflated binomial error distribution and a logit link function (Yau et al. 2003), using presence/absence data as the response variable, the amount of each of the five land-use classes in each square as the explanatory variables, and square identity as a random effect. Each species was then assigned to a specific land cover class, i.e., the class featured in the MAM which explained most of the variance in presence probability among those with significant effects, which was termed the 'key land cover class'. When more than one significant landuse class contributed equally (i.e., showing Δ residual deviance < 10%), we assigned the species to the land cover class with the highest effect size. As a second step, we reran a model for each species by including, as explanatory variables, the amount of key land cover class, the sampling year and their interaction term; we considered the latter as an indicator of potential changes in the species' dependency upon their key land cover class. We excluded from these analyses the species known to be dependent on scarcely represented (< 2%) land cover classes, poorly mapped habitats (e.g., water sites), or only recorded occasionally. Species for which no land class had any significant effect on their probability of presence were also excluded from further analyses. The same procedure was applied to species richness and IOV values, in such cases building models with Poisson and Gaussian error distributions, respectively. We did not consider any measure of spatial autocorrelation since the study area was relatively restricted, so we assumed that individual birds may potentially reach any square grid cell comprising suitable habitat. We then ran a chi-square test on a contingency table to assess differences in the proportion of species showing negative, positive, or no changes in their affinity to land-use classes (i.e., a 3×5 table); a significant chi-squared test was then followed by an analysis of residuals to determine the contribution of each category to the test's significance.

GLMs and GLMMs were run in R 3.2.2 using the package *nlme* (Pinheiro et al. 2011), while all other tests were run in Past 3.0 (Hammer et al. 2001).

Results

Land cover mapping

Across the entire study area, land cover changed over the 28 years considered: urban areas increased (+7.8%), and so did cropland (+26.4%) and wooded areas (+17.4%), while non-intensive farmland and abandoned fields decreased by 41.6 and 28.8%, respectively. Significant changes occurred at the grid square scale for all the considered land-use classes (Urban areas: $F_{2,141} = 21.45$, p < 0.001; Wooded areas: $F_{2.141} = 17.21$, p<0.01; Non-intensive farmland: $F_{2.141} = 11.43$, p<0.01; Afi: $F_{2.141} = 10.99$, p<0.05), except Cropland ($F_{2,141} = 6.54$, p = n.s.). In all significant cases, differences were only evident when comparing data from 1995 to 2018 (all Tukey's p < 0.01). Namely, the mean urban land cover per square increased from 53.4 ± 30.7 to 57.6 ± 32.3 ha, and the mean wooded surface cover increased from 7.4 ± 13.0 to 8.7 ± 14.9 ha. Non-intensive farmland decreased from 13.2 ± 14.2 to 7.7 ± 13.1 ha and mean abandoned field cover decreased from 5.4 ± 9.3 to 1.4 ± 3.9 ha per square.

Bird assemblage variation in time

Species richness and IOV at the grid square scale showed no significant variation in time (p>0.05), yet for species richness, we found a positive effect of increasing amounts of both wooded areas (Estimate: 0.21 ± 0.05 , p<0.05) and non-intensive farmland (Estimate: 0.09 ± 0.02 , p<0.05). The six most common species did not change in any of the three sampling sessions and are all well-known urban adapters or exploiters, i.e., the endemic Italian sparrow Passer italiae (91.5-99.2% of occupancy), the rock pigeon Columbia livia var. domestica (79.8–94.3%), the European blackbird Turdus merula (86.8–93.6%), the European serin Serinus serinus (85.4-94.3%), the blackcap Sylvia atricapilla (72.2-88.0%), and the greenfinch Chloris chloris (65.2-80.9%). However, the bird assemblage in the urban area of Naples did not remain stable over time, with 10 and 12 species respectively becoming extinct and colonizing the area between the first and

Fig. 2 Non-metric multidimensional scaling of the bird assemblage within 1 km square grid (n = 142) in the urban area of Naples at three times intervals; filled circles: 1990–1995; empty diamonds: 2000– 2005; empty squares: 2014–2018. Ellipses represent 95% confidence intervals around each group's centroid second sampling campaigns, while 6 extinctions and 6 colonisations (including 3 re-colonisation events) occurred in the second interval.

Bird assemblages differed significantly among the three samples (ANOSIM: r=0.30, p<0.001, based on 9999 permutations; Fig. 2). Specifically, significance was mainly driven by the differences between the first (1990–1995) and the third (2013–2018) bird atlases (p < 0.001), while all other comparisons were not significant. The ecological groups that contributed the most to differences were birds associated with wooded areas $(39.9 \pm 8.2\%)$, cropland $(25.4 \pm 4.2\%)$ and abandoned fields $(17.7 \pm 4.9\%)$, with smaller differences due to species using non-intensive farmland $(8.9 \pm 2.3\%)$ and urban areas $(7.1 \pm 4.0\%)$. This differential increase in forest species' contribution to the bird assemblage mostly involved increases in numbers of grid squares or novel colonisations of the study area, while the changes in species occurrence associated with cropland and abandoned fields mostly consisted of a decrease in occupancy or extinctions at a grid square scale. Namely, changes in assemblage composition were only clear when comparing the first atlas with the third one, with negligible differences



between the first and the second. The proportion of species going extinct in at least one interval was significantly biased towards species associated with cropland (9 extinction versus 3 colonisation events), species associated with wooded areas showing higher proportions of colonisation events (3 extinction versus 9 colonisation events: $X^2 = 6.25$, p < 0.05).

Species' relationships with land cover and time

Forty-nine bird species were recorded in the study area (i.e., in > 5% of grid cells; see Online Resource 2) and were thus considered for quantitative modelling; additional species were excluded because they were dependent on water sites (n=9), were introduced (n=1), or only recorded occasionally (n=17); see Online Resource 3). Species were grouped into five categories corresponding to the key land cover classes that most influenced the probability of occurrence (Fig. 3; see Online Resource 4 for models' details). At the grid square scale, most species were closely dependent on the amount of wooded surface occurring in each square (n=20), followed by species associated with cropland (n=3), non-intensive farmland (n=9), abandoned fields (n=7), and urban areas (n=3). Seven species were not associated with any land-use class. For all these species, we only detected positive relationships between the probability of occurrence and the amount of a given landuse class. Models for 24 species featured more than one land-use class that significantly affected species occupancy, yet the effect size of additional land cover classes was negligible (Δ residual deviance < 10% in all cases), hence it was possible to assign a single key land cover class for these species.

Time had significant effects on species' dependency upon their key land cover class in 40.0% of the species analysed. Of these, 33.3% (n=6) increased their probability of occurrence in a grid square for a given amount of favoured landuse class over time, while the remaining 66.7% (n = 12) showed a decrease in the same value. For example, the occurrence of the Blue tit Cyanistes caeruleus in a grid square with 25.0% of wooded areas increased from $42.0 \pm 12.5\%$ in 1995 to $70.8 \pm 15.2\%$ in 2005 and up to $88.2 \pm 7.8\%$ in 2018. In other words, a lower amount of the key land cover class was required to achieve the same probability of occurrence in the later period. Conversely, the probability of occurrence of the Fan-tailed warbler Cisticola juncidis in a grid square with 25.0% of cropland dropped from $95.0 \pm 2.2\%$ in 1995 to $88.5 \pm 5.9\%$ in 2005 and $71.5 \pm 18.7\%$



Fig. 3 Estimated probability of occurrence of five bird species in the urban area of Naples (upper row) as a function of the amount of different key land-use classes (lower row) within a 1×1 km square, grid at three-time intervals (years 1995, 2005, 2018), calculated using binomial generalized linear mixed models (shaded areas indicate 95% confidence intervals). From left to right: Eurasian jay (*Garrulus glandarius*), response to wooded areas; Fan Tailed warbler (*Cisticola juncidis*) response to cropland; Common Swift (*Apus apus*), response to urban land cover; Goldfinch (*Carduelis carduelis*), response to nonintensive farmland; Nightingale (*Luscinia megarhyncos*), response to abandoned fields. Silhouettes were taken from phylopic.org under a public domain license. Photos of land cover classes by Maurizio Fraissinet in 2018, i.e., a higher cover of the key land cover class was required to achieve the same probability of occurrence in the later period, thus dependency on cropland increased over time. On average, birds associated with abandoned fields, cropland, and non-intensive farmland needed greater amounts of their key land cover class per square km to reach a given value of occurrence probability, in contrast to species associated with forest and urban areas, which needed lower amounts of their key land cover class. Species showed disproportionate changes in dependency on their key land cover class ($X^2 = 10.89$, p < 0.05), with birds depending upon abandoned fields and non-intensive farmland showing an increase in dependency more often than expected in comparison to species favouring other land cover classes.

Discussion

By assessing bird species distribution and land cover composition with consistent methods across 28 years, we provide strong evidence that urban bird assemblages are influenced by fine-scale changes in land cover, at least in highly dynamic and modified landscapes such as cities, and that changes in avian assemblages are strongly biased towards specific changes in land cover classes and their associated species. The comparison of bird assemblages at different time intervals allowed us to highlight the importance of long-term studies to detect such changes in biological communities, as evidenced by the lack of significant differences between the year 1990-95 and the years 2000-05, i.e., after 10-15 years. This is particularly true if such studies aim to assess trends in extinction and colonization rates within a given area (Fidino and Magle 2017; Hedblom and Murgui 2017; Ferenc et al. 2018). The bird assemblage in Naples was relatively stable over time only in terms of species richness and overall conservation value, whereas species composition significantly changed temporally, as also observed in other studies set in urban regions (Travis 2003; Fidino and Magle 2017). While most species occurring in Naples were associated with wooded habitat, it is worth noticing that non-intensive farmland (a land cover class representing < 10% of each grid square, on average) also significantly contributed to overall species richness, highlighting the importance of such marginal habitat types to urban wildlife (e.g., Turo et al. 2021).

The most common bird species in Naples remained stable in our study system across 28 years and comprised taxa associated with specific land-use classes that are widespread across the urban landscape we investigated, such as wooded and built-up areas. Conversely, birds more closely associated with open and semi-open land-use types such as agricultural land and abandoned fields, despite significantly contributing to fine-scale species richness, were those experiencing the most evident declines, and consequently were more likely to go locally extinct. Such negative trends are probably linked to the fast replacement of these land-use types with urban areas due to human demographic expansion (i.e., infilling), as well as to the development of wooded areas that follow land abandonment, as also evident at broader scales (Suárez-Seoane et al. 2002; Dyulgerova et al. 2015). Similarly, the range expansion of forest birds seems to be a widespread phenomenon in urban areas (Malher and Lesaffre 2007; Evans et al. 2009; Murgui 2014). Forest species were more likely to colonize the urban area of Naples throughout the study period and less likely to go locally extinct. Specifically, two of the only three forest species that disappeared from the study area over 28 years, i.e., the European cuckoo (Cuculus canorus) and the coal tit (Periparus ater), naturally occurred in the area with very low numbers. The local extinction of the common nuthatch (Sitta europaea) is possibly due to indirect competition for nesting sites by the introduced rose-ringed parakeet Psittacula krameri (Strubbe and Matthysen 2009; Mori et al. 2017; Ancillotto et al. 2018), also present in Naples since the 1990s (Fraissinet et al. 2000; Pârâu et al. 2016). Conversely, cropland colonisers (n=3) were only very adaptable species such as the common starling (Sturnus vulgaris), or species with very large and relatively stable populations across their European range (i.e., the common hoopoe Upupa epops, and the European bee-eater Merops apiaster; Ieronymidou et al. 2015).

Our analyses highlight that species may change their dependency upon their key land cover classes at high landscape resolution within the urban landscape. Decreases in dependency on habitats have been previously interpreted as a plastic response by highly adaptable bird species at large scales (e.g., national:

Ward et al. 2018) i.e., a species may rely less upon a favoured land-use class by getting used to or invading new ones (e.g., by synurbization). Conversely, increasing dependency should indicate a species demographically retreating, and being increasingly restricted to optimal areas featuring favourable conditions or larger amounts of habitat. Such changes in dependency in our case are likely to reflect those in population size or time since synurbization (Møller et al. 2012), possibly leading to land-use class saturation by demographically expanding species (decreasing dependency), or decreased occupancy even in optimal areas by demographically crashing species (increasing dependency) or due to sensitivity to habitat fragmentation, even though such hypotheses are still to be confirmed (Batáry et al. 2018).

Our analyses relied on the assumption of constant detectability and did not consider the occupancy of species in the study area before the first data collection campaign, both aspects that may influence subsequent occupancy estimations and actual dynamics. Whilst we have no reason to suppose that detectability may have changed over time, we nevertheless advise caution in the interpretation of our results since other factors besides association to specific land cover classes may affect a species' likelihood to go extinct in urban areas. Moreover, assessing dependency upon specific land cover classes as we did does not take into account habitat quality e.g., in terms of resource availability, which may also have huge effects on bird occupancy and is particularly likely to change in agricultural and developing urban areas (e.g., use of pesticides, agricultural intensification, etc.; Assandri et al. 2019). Other factors that may also play a role in shaping the urban bird assemblage, and that we did not consider, are the pool of available species in the neighbouring natural areas, their general conservation status and population size, as well as landscape configuration within and around the city itself such as habitat-specific connectivity, although understanding the contributions of these potential drivers would require highly intensive ecological research. All these factors highlight that a deeper understanding of bird assemblages and their spatiotemporal dynamics needs to rely on a holistic approach, possibly paired with long-term monitoring campaigns, thus paving further research avenues for the study of urban wildlife.

Management and conservation implications

Our analysis highlights biased changes in avian assemblages within the urban landscape, with a progressive switch to increasing proportions of forestassociated species (e.g., great, and blue tits, greatspotted woodpecker), corresponding to a decrease in birds associated with land cover classes more prone to be replaced, such as fallows and agricultural areas (e.g., warblers and nightingale). Such species-specific relationships and land cover dynamics at a fine scale within an urban landscape also provide a methodological exercise that may inform land-use managers and urban planners. From our analysis of almost three decades of bird monitoring, a biased effect of landuse changes was evident, with a decrease in birds from open habitat types such as overgrown abandoned fields and non-intensive farming. Such marginal land-use classes host a high diversity of plant and animal species even in urban areas (Anderson and Minor 2017; Zuñiga-Palaciosa et al. 2020), particularly invertebrates and their associated predators (Bodsworth et al. 2005), thus providing important refuge areas for wildlife living in cities. Besides, urban landscape managers often regard fallows and overgrown vegetation patches as wasteland, thus available for other uses such as urban development. Consequently, abandoned fields and overgrown areas are generally replaced at faster rates than are other land cover classes within cities, e.g., by recreational green spaces and wooded or built-up areas, as also evident in our case study. We highlight that the marginal habitats are those most jeopardized in urban areas, which is especially concerning since they provide fundamental ecosystem services within cities worldwide e.g., by sustaining populations of pollinators important for agriculture (Bennet and Lovell 2019), and insectivorous taxa (including birds; Villaseñor et al. 2020) that may suppress crop pests and other insects potentially affecting human health (Heyman et al. 2017; Philpott and Bichier 2017; Ancillotto et al. 2019). Thus, assessing the relationship between land cover classes and wildlife is an important management asset for landscape management in wildlifefriendly cities (Villaseñor et al. 2021). We suggest that the protection and enhancement of marginal habitats within urban areas should thus form part of a strategy for the sustainable development of cities in the face of a growing urban population.

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Data availability The datasets generated during and/ or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

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

Ethical approval Not applicable.

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