Bird population changes in urban green spaces explained by regional population trends

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Abstract

Urban bird species represent a subset of the regional species pool, consisting of species that have been able to survive in, or colonise, urban areas. Urban birds are typically resident non-forest species with a broad diet and nesting high in trees or in cavities, and some studies have also claimed that they are large-brained. However, little is known about how urban bird communities change over time. Does the urban environment impose specific selective pressures favouring particular species or ecological groups, or do birds in urban areas simply have population changes reflecting population trends at larger scales? We assessed population changes of 45 breeding land bird species in Oslo, the capital of Norway, based on surveys conducted ca. 15 years apart. Population changes within Oslo most closely matched changes occurring at the regional level (national population trends from Norway and Sweden). Thus, species increasing in Oslo were those that also increased at the regional level. We found no evidence that relative brain size, diet or habitat preferences influenced population trends. However, controlling for regional population trends, there were additional residual effects of nest site and migration: species nesting on the ground or low in bushes had more positive changes than species nesting high in trees or in cavities, and resident species did better than long- or short-distance migrants. These results indicate that urban environments are not isolated islands only influenced by own selection pressures, but are connected with regional population dynamics, most likely through immigration.

Introduction

Urban environments differ substantially from natural habitats (Alberti et al. 2017; Johnson and Munshi-South 2017). Urban species are therefore typically a subset of the regional species pool which have been filtered based on their ability to cope with e.g. altered and artificial habitats, novel food sources, biotic homogenization, novel species interactions and human disturbance (Chace and Walsh 2006; McKinney 2006; Shochat et al. 2006; Croci et al. 2008; Møller 2009; Lowry et al. 2013; Sol et al. 2013; Ferenc et al. 2014; Aronson et al. 2016; Martin and Bonier 2018; Fournier et al. 2020). Among birds, species thriving in urban environments are characterised by having e.g. a broad or generalist diet, nesting high in trees, in cavities and other safe places, and

being resident as opposed to migratory (Chace and Walsh 2006; Croci et al. 2008; Evans et al. 2011; Dale et al. 2015). Several studies have also suggested that species with big brains succeed in urban environments (Carrete and Tella 2011; Maklakov et al. 2011; Callaghan et al. 2019; Sayol et al. 2020), whereas other studies have not found support for this idea (Kark et al. 2007; Evans et al. 2011; Sol et al. 2014; Dale et al. 2015).

However, although we have good insight into what makes an urban bird, we have little knowledge about how urban bird communities change over time. A remarkable exception is the study by Fidino et al. (2022) which compared the bird community in Chicago one hundred years ago and today, showing that birds with a broad diet had increased over time, as well as an increase of those species that also increased at the regional level. The science of urban ecology has developed rapidly over the last decades (Magle et al. 2012; Marzluff 2016), but even at this more limited time-scale there are very few studies of how the composition of urban birdlife has changed because most studies of urban birds have been short-term (Marzluff et al. 2001; Fidino and Magle 2017).

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However, Murgui (2014) found that bird population trends over a period of 15 years in urban parks in Valencia, Spain, matched regional trends.

The population changes that may be expected depend on the history of the urban bird species. Urban bird communities may partly consist of species that have been present in the area from the time the cities were established, and have been able to survive in remant patches of natural vegetation, adapt to changes in vegetation as parks and other urban green spaces were developed, or adapt to general urbanization ('urban survivors'). On the other hand, other species may be recent colonisers of urban areas ('urban colonisers', Tomialojc 1976; Rutz 2008; Evans et al. 2009a, 2010). The population trends of urban bird species may depend on their historical background such that if there are still many 'urban survivors' one may expect a further change towards a species pool with traits that are well adapted to urban life. Specifically, one may expect that some of the 'urban survivors' can go extinct over time due to a lower ability to cope with modern selection pressures in the urban environment (extinction debt). However, if the urban bird community is already composed mostly of species that have traits well adapted to urban life (such as 'urban colonisers'), one may expect that the urban bird community is more or less in equilibrium and will not change much over time if the urban areas have a stable habitat composition and configuration.

These predictions for how urban bird communities may change over time should, however, also take into consideration the population trends of the regional pool of species. Conspecific populations of birds in urban and rural areas are likely to be connected by dispersal, although it has been suggested that urban bird communities are mostly influenced by local features (Clergeau et al. 2001; Evans et al. 2009b). Dispersal between urban and rural populations may lead to synchronous population dynamics. Several studies have found that regional commonness of bird species has a large influence on the composition of urban bird communities (Sol et al. 2014; Dale et al. 2015; Ferenc et al. 2018). Correlated population dynamics may perhaps be most common if urban populations are sinks that receive many immigrants from larger rural populations. Correlated population dynamics could potentially also exist if urban populations are sources, at least if cities are large so that emigration may involve large numbers of individuals and thereby affect rural populations. Thus, for our understanding of the long-term dynamics of urban populations one outstanding question is whether urban environments impose specific selective pressures that favour particular species or ecological groups, or do birds in urban areas have population changes reflecting overall population trends at the regional scale?

We tested these ideas by analysing bird population changes over the last 15 years in Oslo, the capital of Norway. The bird community of urban green spaces in Oslo was surveyed in 2004–2007 (Dale et al. 2015; Dale 2018), and again in 2021 (present study). If the urban bird community was already composed mostly of 'urban colonisers' at the beginning of this period, and if regional population dynamics have little influence on urban bird communities, one may expect that there has been little change during the 15-year period. However, if the bird community still had a number of 'urban survivors' 15 years ago, one may expect that there have been further change towards a bird community with species better adapted to urban conditions. Thus, we expected that occupancy and abundance of 'urban colonisers' would increase at the expense of some 'urban survivors' which may decrease or go extinct. Specifically, based on previous studies of which kinds of birds succeed in urban environments, we predicted that species with the following traits should be expanding: 1) broad or generalist diet (Chace and Walsh 2006; Croci et al. 2008; Jokimäki et al. 2016; Callaghan et al. 2019), 2) nesting high in trees, in cavities and other safe places (Chace and Walsh 2006; Croci et al. 2008; Hedblom and Söderström 2010; Dale et al. 2015; Jokimäki et al. 2016), and 3) being resident as opposed to migratory (Croci et al. 2008; Dale et al. 2015; Jokimäki et al. 2016; but see Evans et al. 2011). Furthermore, we predicted that 4) species inhabiting farmland/open habitats were expected to be favoured over time relative to forest species (in particular relative to species in coniferous forest; Hedblom and Söderström 2010; Dale et al. 2015). Next, we investigated 5) whether brain size influenced population changes to shed more light on the debate about the role of brain size for adapting to urban life (see references above). Finally, we investigated the alternative idea that population changes in urban areas simply follow regional population trends because urban and rural populations are connected through dispersal and therefore respond to the same large-scale factors influencing population size (Murgui 2014; Dale et al. 2015; Ferenc et al. 2018; Fidino et al. 2022).

Materials and methods

Study area

Birds were censused in 93 parks, cemeteries and other green spaces in Oslo, Norway (60°N, 11°E; see map in Dale 2018). This represented nearly all green spaces larger than 1 ha in built-up areas of Oslo. The major exceptions were green areas along two long rivers and one eutrophic lake. The urban green spaces have vegetation varying from intensively managed parks with ornamental deciduous trees and lawns, to green spaces with a mix of managed parkland and remant patches of more or less natural, native forest vegetation. Native forest was dominated by deciduous forest and mixed forest. There were no open areas covered with native

vegetation. The periphery of the city was adjacent to continuous forest (mostly boreal forest dominated by conifers) and some farmland. Oslo had a population of ca. 700,000 in 2021, compared to ca 520,000–550,000 around 2004–2007. Despite the increase in population size, no substantial habitat or vegetation changes in the urban green spaces were observed, and their sizes have been unchanged. Similarly, the forest and farmland areas surrounding Oslo ("Marka") have also not changed substantially due to a strict building ban outside the city perimeter. Thus, changes in the urban bird community are not likely to be driven by habitat changes within or outside the city.

Bird surveys

During the breeding seasons (April–June) of 2003–2007, the 93 urban green spaces were surveyed three times each, mostly in two different years, with two surveys in one year and one survey in another year (Dale et al. 2015; Dale 2018). In 2021, we surveyed all 93 sites twice. To make surveys conducted during 2021 comparable to those conducted in 2003–2007, we matched two surveys done in the same year in the first period ($n=84$ sites, all of these were conducted in 2006 or in 2007) with two surveys in 2021 conducted at the same time of the year (either early, middle or late part of the study period). For the remaining nine sites, surveys in 2021 were matched with surveys done during two different years during 2004–2007. Thus, although the original data collection was conducted during 2003–2007, here we use data originating from 2004 (0.5%), 2005 (1.6%), 2006 (46.2%) and 2007 (51.6%). The average time between the two surveys was 14.51 years. In both 2004–2007 and 2021, 51 surveys were done early (late April – mid-May), 67 during the middle period (mid-May – end of May), and 68 late (June).

Surveys consisted of walking slowly through each site, and paths were chosen to cover each site equally well and such that no part of the site was more than 100 m away from the path used, and were done similarly in both time periods. Surveys were conducted between sunrise and midday. Time spent surveying in each site was approximately the same in 2004–2007 (median 25 min) and 2021 (median 27 min). Surveys were also matched regarding time of day, so that sites in the city centre were visited earlier in the morning than other sites both during 2004–2007 and 2021 in order to avoid traffic noise and human disturbance. Surveys were aimed at detecting potential breeding land bird species. Wetland species and passage migrant species (i.e. those migrating through and not breeding in the city) were excluded. Total number of individuals of each species was recorded, and analyses were based on the highest number recorded of the two surveys for each site. Analyses were also based

on occupancy (presence/absence) in each site, following the main focus of Dale et al. (2015) and Dale (2018).

Species traits

Species were classified according to five variables (habitat preference, nest site selection, migratory behaviour, diet and relative brain size (brain size relative to body mass), see Online Resource 1, Table S1 for details of classification) that we hypothesised could affect their population trend in urban areas. Species were classified into four habitat preferences: (1) breeding predominantly in coniferous forest, (2) breeding predominantly in mixed and deciduous forest, (3) breeding predominantly in farmland habitat, and (4) breeding predominantly in urban areas. Classification was based on Dale et al. (2001) which is the major reference work on the status and distribution of birds in Oslo and Akershus counties. Categories 1–3 were according to species' preferred habitat when breeding outside the city. Thus, analyses referring to e.g. farmland species deal with occurrence in urban green spaces of species that otherwise breed predominantly in farmland areas. The farmland habitat category comprised many species closely associated with humans or human buildings (*Apus apus*, *Pica pica*, *Corvus monedula*, *C. corone*, *Delichon urbica*, *Hirundo rustica*, *Sturnus vulgaris*, *Passer montanus*, *Motacilla alba*). The urban habitat category was used because some species (including *Columba livia*, *Streptopelia decaocto* and *Passer domesticus*) had a predominantly urban distribution, and therefore were not classified as either forest or farmland breeders.

Species were classified in three groups according to nest site: (1) ground or low in bushes (<2 m above ground), (2) high in trees (>2 m above ground) or (3) in cavities or other concealed sites. Information on nest sites relevant for Norwegian conditions were taken from the standard reference work on Norwegian birds (Haftorn 1971).

Migratory status was classified as resident or migratory based on Dale et al. (2001) to take into account local conditions. Species in which a minor part of the population is resident were coded as migratory. Migratory species were further classified as short-distance migrants (wintering in Europe) or long-distance migrants (wintering in Africa; Haftorn 1971; Bakken et al. 2006). Diet was classified as specialist or generalist. Feeding specialists were insectivorous and predatory species. Feeding generalists were omnivorous and granivorous species (many of which also supplement the diet with insects during summer). Classification followed Haftorn (1971), Donald et al. (2006), and Gregory et al. (2007). Classification was also adapted to the present study by focusing on diet during the breeding season. Relative brain size was investigated by including both body mass and brain mass in analyses. Data on body mass and brain mass followed Dale et al. (2015).

Regional species trends

To compare population changes that had occurred within Oslo with regional population trends, we used national data sets for both Norway and Sweden. This was done because there are no local surveys providing data specifically for the surroundings of Oslo. However, we are not aware that any of the species included had population trends in the areas surrounding Oslo that differed from larger-scale trends such as those from the national data sets. Note also that the species trends in the two national data sets were strongly correlated (see below), making it likely that trends in the wider Oslo area followed national trends.

Yearly breeding population indices for both Norway and Sweden were extracted from the Pan-European Common Bird Monitoring Scheme (PECBMS; www.pecbms.info; Brlík et al. 2021) for the period 2007–2017. The starting year of 2007 was chosen because data from Norway are more limited for earlier years (Kålås et al. 2019). The Norwegian data set lacked data for some of the species recorded in Oslo ($n = 35$ of the 45 relevant species were covered; missing species were *Streptopelia decaocto*, *Columba livia*, *Corvus monedula*, *Phylloscopus sibilatrix*, *Sitta europaea*, *Certhia familiaris*, *Passer montanus*, *Coccothraustes coccothraustes*, *Carduelis cannabina* and *C. carduelis*, in general due to small sample sizes). However, the Swedish data set was more useful because more species were included ($n = 44$; *Columba livia* was missing). Population trend for 2007–2017 was calculated as the slope of the regression of the yearly PECBMS index on year where the index was standardised to 1 for 2007 for all species. The Norwegian and Swedish population trends were strongly correlated ($r = 0.54$, $n = 35$, $P = 0.001$). Trends from both data sets were also strongly correlated with a longer-term (1996–2020) Swedish breeding bird index (Green et al. 2021; Norway: $r = 0.41$, $n = 35$, $P = 0.015$; Sweden: $r = 0.77$, $n = 44$, $P < 0.001$).

Statistical analyses

Analyses were based on 45 species that were recorded in at least four sites in 2004–2007 or in 2021. Changes in occupancy (number of sites with presence) and abundance (total number of individuals) were expressed as the ratio between values for the two periods (occupancy or abundance in 2021 divided by 2004–2007). The ratios were log-transformed to reduce skewness and to make data suitable for linear analyses. Log-transformed ratios have positive values if there were population increases and negative values when there were decreases.

Initially, the relationships between the explanatory variables (habitat preference, nest site selection, migratory behaviour, diet, relative brain size and regional population trends) and the population changes recorded in Oslo (occupancy and abundance) were explored with ANOVA-analyses, *t*-tests and Pearson correlation analyses. Relative brain size was assessed by including both brain mass and body mass in analyses (see Dale et al. 2015), and both brain mass and body mass were log-transformed.

Next, GLM analyses were used to assess the main factors influencing population changes in Oslo. Models with different combinations of explanatory variables (habitat preference, nest site selection, migratory behaviour, diet, relative brain size and regional population trends) were compared with AIC_c-values. Model comparisons are presented in Online Resource 1, Tables S2 and S4. Statistical analyses were conducted in JMP Pro Version 16 (SAS 2021).

Results

Overall changes

A total of 8,741 individuals of the 45 focal species were observed in 2021 compared to 8,463 in 2004–2007 (a non-significant increase of 3.3%; average of 194.2 versus 188.1 individuals/species: paired *t*-test: $t = 0.56$, $df = 44$, $P = 0.58$). The mean occupancy of the 45 species was 40.62 sites in 2004–2007 and 40.11 sites in 2021 (a non-significant decrease of 1.3%; paired *t*-test: $t = -0.38$, $df = 44$, $P = 0.71$). The largest increases were shown by *Phylloscopus collybita* (increased from 8 to 110 individuals, and from 7 to 37 sites) and *Turdus philomelos* (increased from 1 to 10 individuals, and from 1 to 7 sites), and the largest decrease by *Carduelis spinus* (decreased from 57 to 4 individuals, and from 21 to 4 sites; Fig. 1). Log-transformed changes in occupancy and abundance were significantly correlated ($r = 0.94$, $n = 45$, $P < 0.001$).

Species traits and regional population trends

Single factor analyses revealed that the 15-year population changes in Oslo were significantly related only to the regional population trend based on Swedish data (Table 1). Species that increased in Oslo were in general those that also increased at the regional level (Fig. 2).

Multivariate analyses indicated that the best models for explaining population changes in Oslo included the regional population trend based on Swedish data (Table 2; Online Resource 1, Table S2). Species increasing in Oslo were in general those that also increased at the regional level. Of the nine species that increased during 2007–2017 according to Swedish breeding bird surveys, their occupancy in Oslo increased from on average 20.1 sites to 26.3 sites (increase of 31%), whereas their abundance increased from on average 41.0 individuals to 67.1 individuals (increase of 63.7%). Of the 35 species that declined, their occupancy in Oslo
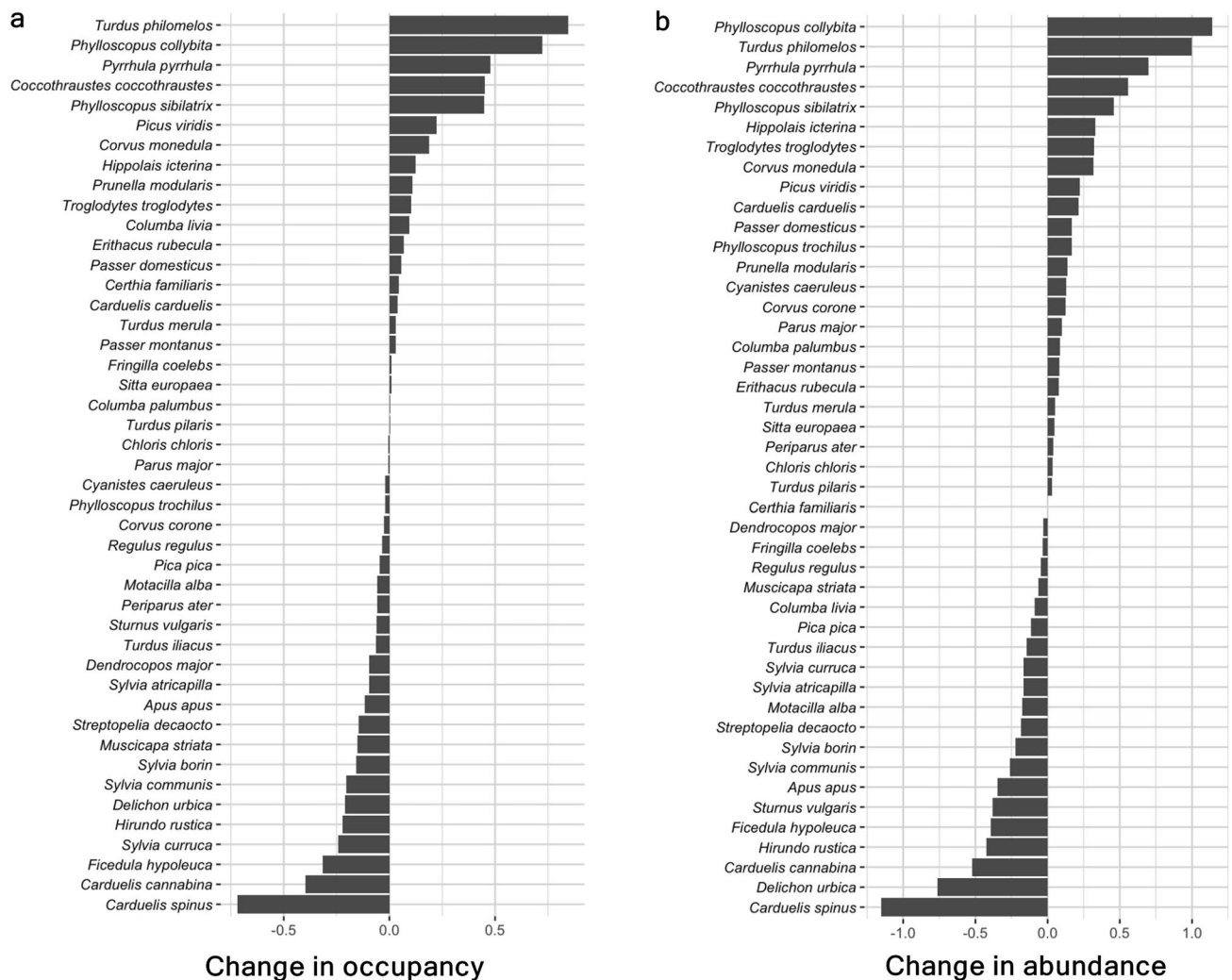
Fig. 1 Changes in **a** occupancy (number of sites with presence) and **b** abundance (total number of individuals) for 45 bird species in Oslo in 2021 compared to during 2004–2007. Species included were those that were recorded in at least four sites in 2004–2007 or in 2021. Changes were measured as the log-transformed ratios of occupancy or abundance in 2021 relative to 2004–2007

declined from on average 46.0 sites to 43.5 sites (decline of 5.4%), whereas their abundance increased from on average 223.1 individuals to 225.8 individuals (increase of 1.2%).

The analysis using changes in abundance in Oslo indicated that there were additional effects of nest site and migration (Table 2). Thus, species nesting on the ground or low in bushes had more positive population changes than species nesting high in trees or in cavities (Table 2). Furthermore, resident species had more positive population changes than long- and short-distance migrants (Table 2). Species nesting on the ground or low in bushes had an average increase in abundance of 80.8% (based on least squares means estimates from a model including nest site, migration and regional trend), whereas species nesting high in trees decreased on average by 33.2% and species nesting in cavities decreased on average by 28.8%.

Resident species increased on average by 70.7%, whereas short-distance migrants decreased by 27.0% and long-distance migrants by 31.0%.

The analyses using regional population trend based on Norwegian breeding bird surveys (only 35 species compared to 44 species for the Swedish data set) showed similar results, although there were more competing models. For occupancy, competing best models included intercept only and diet, whereas for abundance competing best models included regional trend, intercept only, nest site, diet + regional trend, and nest site + migration + diet + regional trend (in decreasing order of model fit; Online Resource 1, Tables S3 and S4). Finally, results were similar to those presented in Table 2 when a longer-term Swedish breeding bird index (1996–2020) was used (Online Resource 1, Table S5).

Table 1 Single factor analyses of the relationships between species traits and regional population trends, and changes in occupancy (number of sites with presence) and abundance (total number of individuals) of 45 bird species in Oslo from 2004–2007 to 2021. Changes were measured as the log-transformed ratios of occupancy or abundance in 2021 relative to 2004–2007. Habitat, nest site and migration were analysed with ANOVA, diet with *t*-test, and relative brain size and regional trends with correlation analyses. Sample size is lower than 45 for analyses of regional trends due to lack of trend data for some species. Significant values are shown in bold

Variable	n	Occupancy		Abundance	
ANOVA/t-test		*F/t*	*P*	*F/t*	*P*
Habitat	45	0.83	0.49	1.40	0.26
Nest site	45	0.59	0.56	1.30	0.28
Migration	45	0.55	0.58	1.06	0.35
Diet	45	-0.54	0.59	-0.60	0.55
Correlation analyses		*r*	*P*	*r*	*P*
Relative brain size[a]	45	0.12	0.44	0.18	0.24
Regional population trends					
Norway	35	0.21	0.25	0.28	0.12
Sweden	**44**	**0.47**	**0.001**	**0.51**	**<0.001**

[a]Partial *r* of brain mass in model also including body mass (both log-transformed)

Table 2 GLMs of the relationships between species traits and regional population trends, and changes in occupancy (number of sites with presence) and abundance (total number of individuals) of 44 bird species in Oslo from 2004–2007 to 2021. Changes were measured as the log-transformed ratios of occupancy or abundance in 2021 relative to 2004–2007. The best models based on AIC_c-comparisons are shown (see Online Resource 1, Table S2 for model comparisons). Regional population trend was based on Swedish breeding bird surveys

Model	Estimate	SE	P
Occupancy			
Regional population trend	3.22	0.91	<0.001
Abundance[a]			
Nest site			
Cavity versus ground/low	-0.40	0.14	0.005
High versus ground/low	-0.43	0.15	0.004
Migration			
Long versus short	-0.02	0.13	0.85
Resident versus short	0.37	0.15	0.012
Regional population trend	4.33	1.31	0.001

[a]A model with only regional population trend had similar AIC_c-value (36.52) as the model shown ($AIC_c = 35.34$)

Discussion

Regional population trends and urban bird community changes

The few previous studies of long-term urban bird population changes have found that regional population trends explain
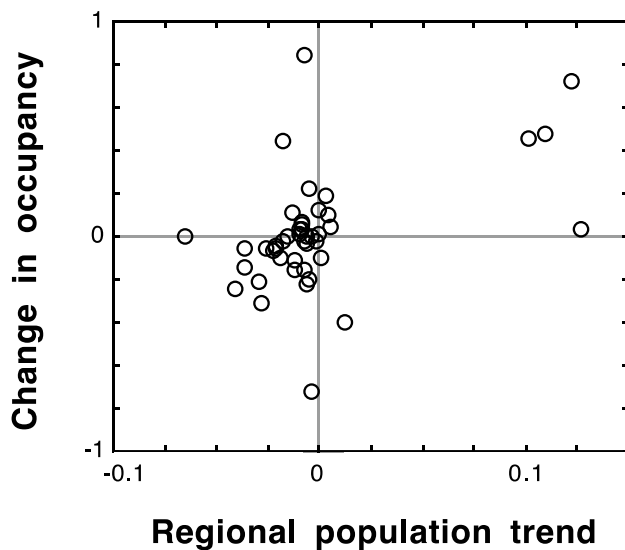

Fig. 2 Population changes of 44 bird species in Oslo between 2004–2007 and 2021 in relation to an index of their regional population trends. Changes in Oslo are based on occupancy (number of sites with presence), and values indicate the log-transformed ratio of occupancy in 2021 relative to 2004–2007. Regional trends are based on changes in Sweden during 2007–2017

much of the changes occurring in urban areas (Murgui 2014; Fidino et al. 2022). The present study confirmed these findings. The analyses of both occupancy and abundance showed that the population changes occurring in Oslo were similar to those occurring at larger scales. Thus, species increasing within Oslo were generally also those that increased at the regional level. The relationships were stronger when using breeding population indices from Sweden than from Norway. The main reason for this was that the Swedish data set had sufficient material to calculate indices for 44 of the 45 species analysed in the present study, whereas the Norwegian data set had enough material for only 35 species. This is due to a much larger field effort in the Swedish breeding bird survey, and the Swedish data are therefore likely also more reliable for the 35 species covered by both national surveys. In addition, the Norwegian data set covers more diverse ecoregions (including maritime and arctic areas) than the Swedish data set, and the more temperate continental conditions in eastern Norway where Oslo is located is covered well by the Swedish data set. Thus, the Swedish population trends may be most useful when analysing changes occurring in Oslo.

The present study compared two time periods where the data for the first time period mostly covered two years, and the last time period covered only one year. Compared to studies assessing changes by yearly surveys, this could make our data set susceptible to annual variation in population size. Among species occurring in Oslo, in particular *Carduelis spinus* may have yearly fluctuations due to variation in food availability. *Carduelis spinus* showed the largest

decrease in occupancy and abundance so that numbers in 2021 were very low. This corresponded to the lowest annual index in the Norwegian bird survey for this species (https://hekkefuglovervakingen.nina.no/hekkefugl/Grønnsisik). However, the effect of regional population trend remained a strong predictor of population changes even if this species was removed from analyses (data not shown).

Species traits

We found no evidence that population changes occurring in Oslo were related to habitat preferences, diet or relative brain size. We observed substantial changes in the bird community in Oslo, with some species increasing strongly whereas others decreased quite a lot. However, large-scale European trends that farmland birds do worse than forest birds (Donald et al. 2006; Kamp et al. 2021) were not mirrored in the trends of urban birds in Oslo. Furthermore, considering that several studies have found that relative brain size has a large impact on adapting to urban conditions and other novel environments (Sol et al. 2005; Maklakov et al. 2011; Sayol et al. 2020), one would have expected that some of the population changes recorded in Oslo were related to brain size. It is remarkable that there was no evidence for this in the present data set. Relative brain size was far from having significant effects in any of the analyses conducted.

On the other hand, there was some evidence that nest site and migration influenced population changes. In analyses of changes in abundance, these traits had significant effects when the effect of the regional population trend was also accounted for. Thus, species nesting on the ground or low in bushes did better than species nesting high in trees or in cavities, and resident species did better than both short- and long-distance migrants. Many other studies have indicated that resident species have been doing well recently, especially compared to long-distance migrants (Sanderson et al. 2006; Vickery et al. 2014; Kamp et al. 2021). In our study, some residents species doing well were *Picus viridis*, *Corvus monedula*, *Coccothraustes coccothraustes* and *Carduelis carduelis*. However, that species nesting on the ground or low should do well was not expected on a general basis because in urban areas such species may in particular be vulnerable to disturbance and predation from in particular people, dogs, cats and rats. In our data set, species nesting on the ground or low which had positive population change were in particular *Phylloscopus collybita*, *Turdus philomelos*, *Phylloscopus sibilatrix*, *Hippolais icterina* and *Troglodytes troglodytes* (all more than doubled in abundance). We can only speculate that some of the negative factors that could impact these species have been relieved recently in Oslo, but because there have been no substantial vegetation changes in the green spaces in Oslo, we believe it cannot be related to changes in availability or quality of nesting habitat. However, a simple explanation may be that some of these species (at least *Phylloscopus collybita*, *Hippolais icterina, Troglodytes troglodytes*) have had a general population increase over large areas, perhaps due to climate change, so that they have also become more common in urban areas. Note, however, that the data represent presence in urban areas without evidence of breeding. Thus, although there was an increase of birds with nest sites on the ground or low, we do not know if they actually breed regularly.

Urban bird community dynamics

The present study indicated that the population dynamics of the bird community in Oslo were correlated to regional bird population trends. This indicates that there must be substantial intraspecific interactions between rural and urban bird populations. Because rural bird populations are much larger than urban populations, at least in Norway and the Oslo region, it appears most likely that the correlated population dynamics are due to dispersal from rural areas into the urban areas. Dispersal among birds occurs most frequently among young individuals and natal dispersal distances are also longest (Paradis et al. 1998). Thus, urban areas are likely to receive young immigrants from rural areas which attempt to establish their first territories, and thereby populate urban green spaces irrespective of whether such sites can have self-sustaining populations or not. Thus, the idea that urban environments are isolated islands where birds are influenced only by idiosyncratic selection pressures is not supported. Rather, urban bird communities are widely connected with rural populations, most likely through immigration from rural areas. The bird community of Oslo therefore appeared to respond to large-scale factors affecting bird populations in northern Europe. This would also include factors operating further south in Europe or in Africa for the migratory species.

However, we also found that some species (those nesting on the ground or low, and resident species) had population changes that differed from what was expected from the regional population trends. This suggests that some selective pressures in urban areas differ from those affecting populations at regional scales. In conclusion, long-term changes in the urban community in Oslo was in particular related to regional population dynamics, but was also influenced by local factors to some degree. We suggest that a pattern where rural populations affect population trends of urban birds is most likely when rural populations are large compared to the urban population, and that the urban areas are of moderate size. For megacities surrounded by highly human-modified landscapes bird populations in areas surrounding cities may have a smaller influence on the dynamics of urban bird communities. The link between urban populations and rural population dynamics should be considered by studies

of evolution in urban environments (Donihue and Lambert 2015; McDonnell and Hahs 2015; Johnson and Munshi-South 2017), because gene flow through dispersal may prevent or slow adaptation to urban conditions.

Declarations

Ethics approval Not applicable.

Competing interests The authors declare that they have no competing interests.

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