

The effect of urbanization on the functional and scale-sensitive diversity of bird assemblages in Central India

Manoj Kale¹, Nandkishor Dudhe², Marco Ferrante³, Tatiana Ivanova⁴, Raju Kasambe², Irina S. Trukhanova⁵, Prosun Bhattacharya¹ and Gabor L. Lövei^{3,*}

¹ Department of Sustainable Development and Environmental Science and Engineering, KTH Royal Institute of Technology, Teknikringen, 76, SE-100 44, Stockholm, Sweden

² Bombay Natural History Society, Hornbill House, Shaheed Bhagat Singh Road, Mumbai, 400001, Maharashtra, India

³ Department of Agroecology, Aarhus University, Flakkebjerg Research Centre, Forsøgsvej 1, DK-4200 Slagelse, Denmark

⁴ ICPO 'Biologists for Nature Conservation', 24 line V. O. 3–7, 199106 St Petersburg, Russia

⁵ Applied Physics Laboratory, Polar Science Center, University of Washington, 1013 NE 40th St., Seattle, WA 98105, USA

(Received 5 April 2018; revised 28 August 2018; accepted 28 August 2018; first published online 26 September 2018)

Abstract: Diversity changes can be evaluated at various spatial scales, and the relationship between changes in diversity at the local, landscape and regional scales is not evident. The overall patterns of functional and beta diversity of bird assemblages were evaluated along a five-stage urbanization gradient, censused over the months of January to April in the years 2010–2013, in and around Amravati city, Deccan Plateau, Central India. We expected the abundance of large and predatory species to decline along the gradient, and urbanization to homogenize species richness at the landscape level. Overall, 112,829 birds belonging to 89 species were identified in the region, and species richness decreased from the rural forest (73 species) to more urbanized areas (lowest at the centre of Amravati city with 29 species). Along the urbanization gradient, bird assemblages contained more small species, and the share of frugivorous and omnivorous species also increased, while that of insectivorous species decreased. Diversity partitioning indicated that of the overall pattern, local (alpha) diversity accounted for 50.1% of the total (gamma) diversity, and urbanization stages another 36.2%; the contribution of within-stage, local diversity was rather small (2.7%), indicating fairly homogeneous assemblages.

Key Words: anthropogenic activities, Aves, biotic homogenization, disturbance, forest-urban gradient, frugivory, Indian Peninsula, omnivory, scale-sensitive diversity, size effects

INTRODUCTION

Urbanization dramatically transforms natural environments, perpetuating habitat loss and fragmentation worldwide and changing the original flora and fauna, but also concentrating resources and energy (Wagner 2008). Together with increased density of humans, urbanized areas have higher temperatures, modified precipitation regimes, altered nutrient cycling and increased concentration of various xenobiotics (McKinney 2006). Urbanization also promotes biotic homogenization, as only a few, usually non-native, species can tolerate the urban conditions (McKinney 2006). As more than half of the world's population lives in cities (United Nations 2014), urban biodiversity is particularly valuable, both

as a link between humans and nature and for providing ecosystem services (Millennium Ecosystem Assessment 2005).

In general, higher levels of urbanization cause a decline in ecosystem services (Eigenbrod *et al.* 2011, Ferrante *et al.* 2014) and in biodiversity (see Ahrné *et al.* 2009 for bumble bees; McKinney 2008 for plants; Marzluff 2001 for invertebrates and vertebrates excluding birds; Sol *et al.* 2014 for birds), although negative effects are not universal (Magura *et al.* 2010, Marzluff 2005, McKinney 2008).

Birds are a flagship group in studies of urbanization on biodiversity, being a favoured group by many people, taxonomically well-known, and quick to react to environmental changes in easily detectable ways (Chazdon *et al.* 2009, Gibson *et al.* 2011). Bird densities show both negative (Aronson *et al.* 2014) and positive (Galushin 1971, Marzluff 2001, Sengupta *et al.* 2014) responses

* Corresponding author. Email: gabor.lovei@agro.au.dk

to urbanization, and avian species richness can decrease with increasing urbanization (Chace & Walsh 2006), or peak at intermediate levels of urbanization (Jokimäki & Suhonen 1993, Marzluff 2005).

Our knowledge on the effects of urbanization on birds originates mostly from studies in the northern hemisphere (Aronson *et al.* 2014), while most biodiversity resides at lower latitudes (Huston 1994), where the fastest growth in urbanization also occurs (United Nations 2014). Decreasing bird diversity was detected also in Central America (MacGregor-Fors 2008) and Asia (Lin *et al.* 2011).

To analyse effects of urbanization on bird assemblages in Central India, we used an urbanization gradient approach (Clergeau *et al.* 1998, Jokimäki & Suhonen 1993, Liker *et al.* 2008) to examine the factors influencing bird assemblages.

We tested the following hypotheses: increasing omnivory and herbivory hypothesis (H1): as urbanization advances, much of the original diversity, including plants and their associated arthropods is destroyed (Wagner 2008), so we expected that raptors and insectivores will decline, and omnivores and plant/seed eaters will increase as urbanization advances. Support for this hypothesis was found when examining the effects of urbanization on ground beetles in Denmark (Elek & Lövei 2007). We also expected that the average body size of birds will gradually decrease with advancing urbanization (the decreasing body size hypothesis, H2). Urban habitats are characterized by larger and more frequent environmental fluctuations, and higher degrees of disturbance (McKinney 2006), causing smaller windows of opportunity, which can be better exploited by smaller species, and their relative abundance will increase as urbanization advances. Large species are expected to diminish or disappear altogether (Cardillo *et al.* 2005). Finally, we expected that as urbanization progresses, beta diversity will decrease (H3) – the assemblages will be more similar to each other with fewer local differences. This can be interpreted as a version of the homogenization hypothesis (McKinney 2006): bird assemblages in more urbanized habitats will be less different from each other than in the original, rural, forest-associated habitats.

METHODS

Study area

The study was conducted in the area of Amravati city (Figure 1), in the state of Maharashtra, on the Deccan Plateau in Central India (20°56'–20°93'N, 77°45'–77°75'E, 343 m asl). This area is characterized by a tropical wet and dry climate with a mean annual

temperature of 27°C, and a mean annual precipitation of 874 mm. The summer lasts from March to June, the monsoon season from July to October, and the winter from November to March. An urbanization gradient of five stages was selected on the basis of built-up surface and vegetation composition, as these two parameters are usually considered reliable indicators of human disturbance level (Pickett *et al.* 2011). The five-stage gradient included (1) rural forest, (2) industrial, (3) peri-urban, (4) suburban and (5) urban area (0%, 0–20%, <35%, 35–50%, >50% of built-up area, respectively, identified from Google Earth). Our selected stages were characterized by similar plant communities, although the dominant species were different. The rural forest was a forest reserve (20°53'N, 77°47'E) classified as Southern Tropical Dry Deciduous Forest by Champion & Seth (1968), and dominated by *Aegle marmelos* Correa, *Azadirachta indica* A.Juss., *Butea monosperma* Taub., *Calotropis procera* Aiton, *Cassia fistula* L. and *Gliricidia sepium* Kunth. The land between the studied forest reserve and the urbanized area was occupied by rain-fed croplands of mixed cropping. The industrial stage (20°53'N, 77°45'E) was located at the south-eastern part of Amravati city, comprising an area of 200 ha, which was allocated by the government for industrial development. This area was under construction, and changed considerably for the duration of the study. The roads were tarmac, the average size of individual land parcels much bigger than in other areas. Nevertheless, the plant community was represented by the same dominant tree species during our study: *Ailanthus excelsa* Roxb., *Eucalyptus obliqua* L'Herit., *Leucaena leucocephala* de Wit, *Psidium guajava* L. and *Ziziphus mauritiana* Lam. The periurban stage (20°53'N, 77°45'E) was located at the periphery of Amravati city, with separate houses, plots of land and streets with little or no asphalt; and less than 35% of the surface was occupied by buildings. Virtually all individual households had gardens and kept domestic animals. The most common plant species were *Ficus benghalensis* L., *Ficus racemosa* L., *Ficus religiosa* L., *Lantana camara* L., *Millettia pinnata* Panigrahi and *Tamarindus indica* L. The suburban stage (20°56'N, 77°46'E) was a residential area dominated by the tree species *Delonix regia* Raf. and *Michelia champaca* L. and by the fruit trees *Annona squamosa* L., and *Mangifera indica* L. In this area, 35–50% of the total surface was covered with tarmac or occupied by buildings. Several individual households kept domestic animals and cultivated vegetable gardens. The urban stage (20°55'N, 77°45'E) was densely populated, including also the historical centre of the city, and more than 50% of the surface was covered with buildings. It was characterized by tree species of *A. indica*, *Cocos nucifera* L., *F. religiosa*, *Polyalthia longifolia* Sonn. and *Terminalia catappa* L. The centre of Amravati was ~6–7 km from the forest area, 4–5 km from the

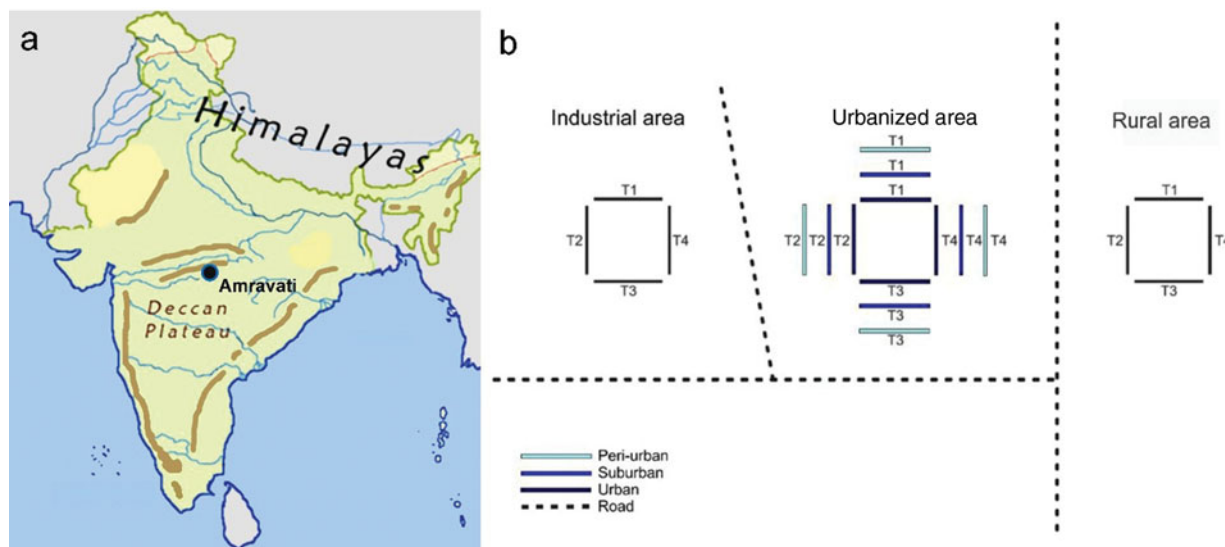


Figure 1. Location of Amravati city, Maharashtra State, on the Deccan Plateau, India (left panel), and the arrangement of census paths (right panel). Transects were indicated by “T”.

suburban stage, 2–3 km from the peri-urban stage and 4–8 km from the industrial area.

Bird survey methods

Bird presence and abundance were recorded during the breeding season (January–April), between 2010–2013, along four transects at each of the five urbanization stages (Verner 1985). Each transect was 3 km long and 50 m wide, and was walked at the same speed on sunny days from 06h00 to 09h00 on three days of each of the four months in each of the four years. Identification of birds was done using field guides (Ali 2002, Grimmett *et al.* 2001). Some species belonging to raptor, quail and warbler families (5–10% of the total number of observations) were excluded from the analysis as their species identification was uncertain. Additionally, data on several waterbirds (*Actitis hypoleucos* L., *Amaurornis phoenicurus* Pennant, *Ardeola grayii* (Sykes), *Bubulcus ibis* L., *Egretta garzetta* L. and *Pseudibis papillosa* (Temminck)) were excluded (2.6% of the total number of observations) as not all urbanization stages provided suitable habitat for them.

Statistical analysis

We selected the maximum numbers counted of each species over the three days of surveys in each month as representative of the bird abundance at that urbanization stage in that month. We tested for significant differences between the four months per year using Wilcoxon paired

t-tests. As none of the comparisons showed significant differences, we kept the maximum value for each species. Diversity within transect and between urbanization stage was examined using an additive partitioning method (Lande 1996). This method considers α - (i.e. diversity at transect/year level) and β -diversity as additive components of the γ - (i.e. regional) diversity, and express them in the same units of species richness. This allows direct comparisons between α - and β -diversity within the same study (Crist & Veech 2006) as well as between studies, when diversity is expressed as proportions (Anderson *et al.* 2011). As very little (2.7%) of the diversity was explained by differences among transects within an urbanization stage, we considered only year and urbanization stage as a factor in further analyses. We compared bird species richness for each urbanization stage/year using the Jaccard dissimilarity index (Magurran 2003: Eq. 1).

$$C_j = a / (a + b + c) \quad (\text{Eq. 1})$$

Where *a* is the number of species shared between two urbanization stages, and *b* and *c* the number of species found at only one of the stages (Henderson & Southwood 2016). In order to construct the dendrogram, we used ‘average linkage’ clustering method (Izenman 2008).

Although N-mixture models are technically appropriate to estimate absolute abundance by incorporating probability of detection (Barker *et al.* 2017), estimating the actual population size in each stage of the urbanization gradient was not the aim of this study. Moreover, N-mixture models do not perform well under low probabilities of detection (Duarte *et al.* 2018). Therefore, we tested for differences in species richness and abundance using generalized linear mixed models, with bird size class

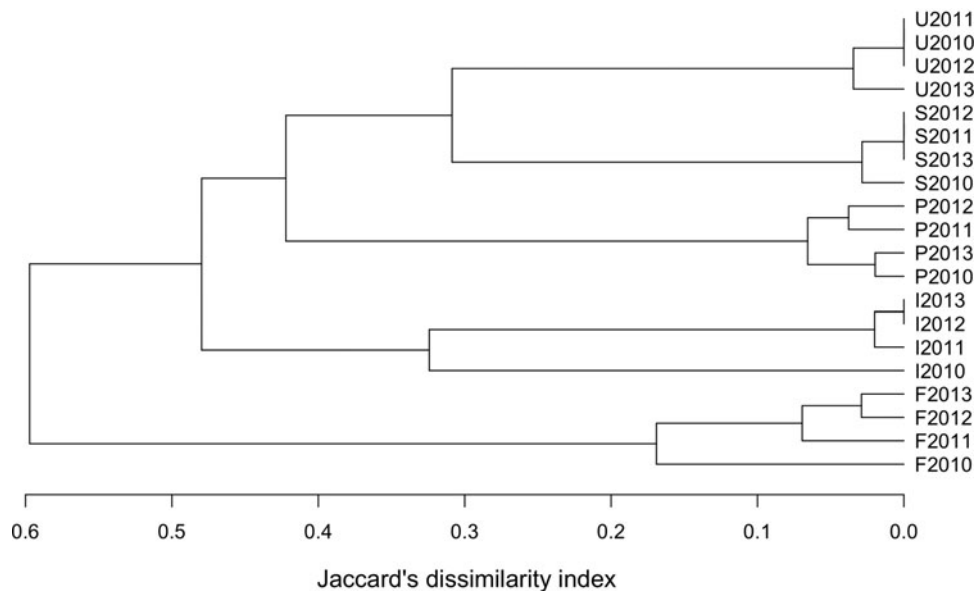


Figure 2. Jaccard's dissimilarity indices for the bird species richness along the five-stage urbanization gradient, observed during censuses in 2010–2013, in and around Amravati city, Maharashtra State, India.

and foraging preference as random factors. Foraging preferences were categorized as: insectivorous, omnivorous, predatory (when feeding on other vertebrates such as fish or mammals), herbivorous and frugivorous. Bird body size classes (a proxy for several categories of resource use, Peters 1986) were categorized as: small (6–45 g), medium (45–120 g), large (120–300 g) and very large (> 300 g). Both categorizations were based on guilds and categories in Wilman *et al.* (2014). We tested if species presence/absence and total bird abundance varied along the five-stage gradient between years using binomial and Poisson distributions, respectively. To account for overdispersion, the Poisson GLM standard errors were corrected using a quasi-GLM model where the variance was given by $\phi \times \mu$, where μ is the mean and ϕ the dispersion parameter (Zuur *et al.* 2009). Model selection was done through backward selection, by comparing AICs. All calculations were made using the R program version 3.0.2, and the package *vegan*.

RESULTS

During four years, our study assemblage included 89 bird species along the urbanization gradient, the majority of them were year-round residents (Appendix 1). The total species richness was higher in the rural (forest) and industrial zone stages, followed by the peri-urban, suburban and urban ones (73, 73, 54, 35 and 29 species, respectively). However, the number of species in the industrial zone decreased considerably after the first year of census, while the other stages did not show such

striking between-year differences (Figure 2). The overall assemblage was composed of insectivorous species (44%), omnivores (31%), predators (10%), herbivores (9%) and frugivores (6%). Considering size distribution, nearly half of the species (48%) were small, while 24% were of medium size, 17% large and 11% very large.

If abundance of individuals was considered, we observed almost the opposite of the trend observed for species richness: the urban stage had the highest number (41 670 individuals), followed by the suburban (24 409 ind.), peri-urban (17 749 ind.), forest (15 562 ind.) and industrial (13 439 ind.) habitats. These values were directly comparable, because of the identical sampling effort at the various urbanization stages. Variation in abundance per year showed idiosyncratic patterns for each of the urbanization stages (Table 1). In the forest area in 2010 we observed fewer individuals than in the subsequent years; while in the industrial zone, the assemblage in 2010 showed a much higher number than later. In 2010, the record of bird individuals in the suburban area was more similar to 2013, due to the presence of large flocks of *Hirundo concolor* observed in those years. In the peri-urban area, the trend was the same as in the suburban one, but the dominant species was *Columba livia* throughout the study period. Finally, bird abundance in the urban area in 2010 was closer to 2011 than to the remaining years.

The mean species richness per year of each of the foraging categories was always higher in the rural forest, with the exception of frugivorous species; the same was not found for bird count (Table 1). Along all the stages of the gradient there were more small species than big ones

Table 1. Species richness and numbers of individuals by foraging category along the urbanization gradient near Amravati city, Maharashtra State, India, censused between 2010 and 2013. Values are yearly means \pm SD.

Parameter and urbanization stage	Frugivores	Herbivores	Insectivores	Omnivores	Predators
Species richness					
Rural	2.8 \pm 0.5	7.5 \pm 0.6	28.8 \pm 1.7	19.8 \pm 1.0	8.3 \pm 1.5
Industrial	5.0 \pm 0.0	5.3 \pm 0.5	21.3 \pm 7.9	18.3 \pm 2.5	5.5 \pm 1.0
Peri-urban	2.0 \pm 0.0	4.0 \pm 0.0	23.3 \pm 0.5	17.3 \pm 0.5	4.8 \pm 0.5
Suburban	2.0 \pm 0.0	3.0 \pm 0.0	12.0 \pm 0.0	13.3 \pm 0.5	4.0 \pm 0.0
Urban	1.0 \pm 0.0	3.0 \pm 0.0	8.8 \pm 0.5	12.0 \pm 0.0	4.0 \pm 0.0
Numbers of individuals					
Rural	22.0 \pm 24.1	60.0 \pm 64.1	14.7 \pm 30.5	39.8 \pm 70.5	4.9 \pm 2.2
Industrial	14.5 \pm 8.2	20.6 \pm 39.8	11.9 \pm 45.0	43.6 \pm 117	10.7 \pm 27.6
Peri-urban	11.2 \pm 22.0	24.2 \pm 25.8	18.4 \pm 40.7	47.8 \pm 86.4	9.7 \pm 17.0
Suburban	9.8 \pm 17.2	61.5 \pm 113	29.3 \pm 23.0	69.6 \pm 127	11.6 \pm 27.0
Urban	24.2 \pm 50.5	331 \pm 891	7.8 \pm 22.8	73.0 \pm 204	5.6 \pm 9.0

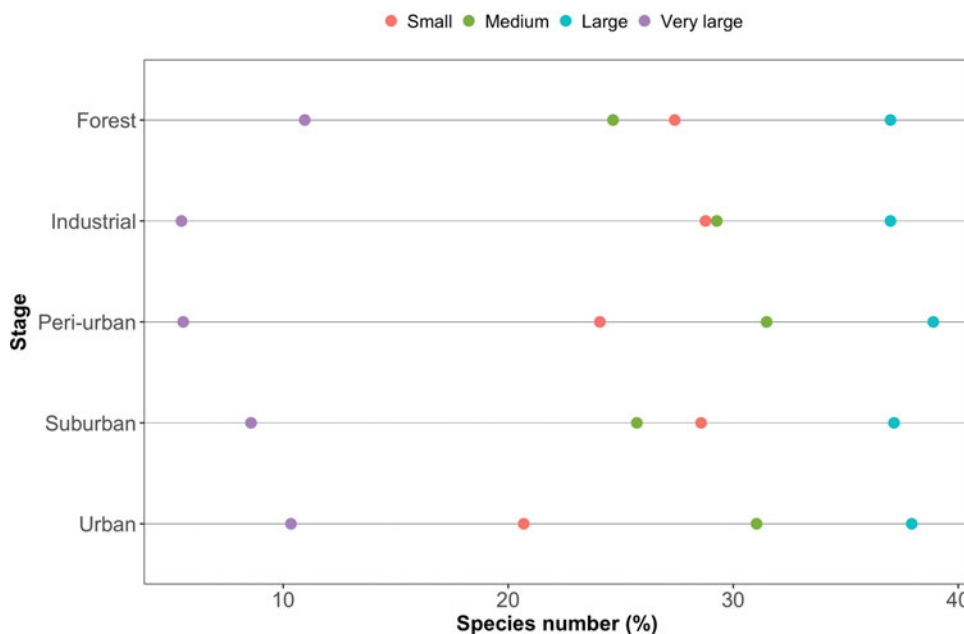


Figure 3. The composition by size classes of the bird assemblages along the five-stage urbanization gradient, observed during censuses in 2010–2013, in and around Amravati city, Maharashtra State, India.

(small > medium > large > very large, Figure 3). The foraging preference pattern was common to the gradient too (insectivores > omnivores > predators > herbivores > frugivores), with the only exception being the suburban stage (omnivores > insectivores > predators > herbivores > frugivores, Figure 4). Although forest and industrial areas had the same species richness, the proportion of foraging categories was different. We found more predatory and herbivorous species in the forest than in the industrial area (9 and 8 vs. 7 and 6 species, respectively), and more insectivorous and frugivorous ones in the industrial than forest area (33 and 5 vs. 31 and 3 species, respectively). Very large species were found mostly in the forest area, whereas in the industrial stage they were replaced by medium-sized species. The results of the

logistic regression showed that species presence/absence was significantly affected by urbanization stage (Table 2). Species number in the rural forest area was significantly higher than in all the other stages (with the exception of the industrial area in 2010). Moreover, temporal effect in year 2011 and 2012 was observed independently of the urbanization stage. Bird abundance was significantly higher in the urban and suburban stages compared with all the others (Table 3).

The additive diversity partitioning indicated that of the overall diversity (gamma-diversity), alpha diversity (local diversity, i.e. at transect level) contributed 50.1% to the total diversity. Only 2.7% was explained by between-transect differences, and the remaining 36.2% by differences between urbanization stages.

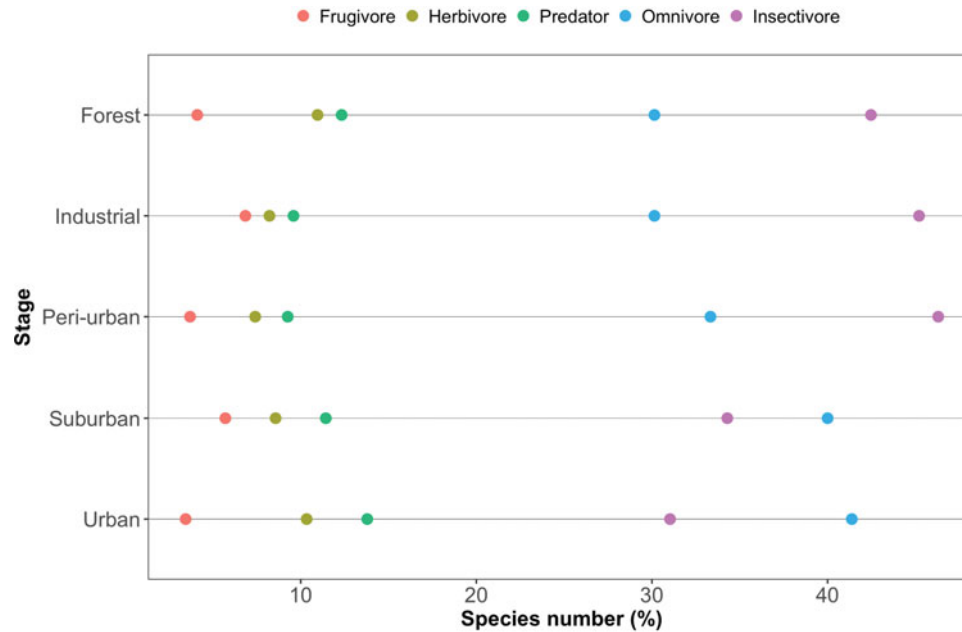


Figure 4. The composition by feeding categories of the bird assemblages along the five-stage urbanization gradient, observed during censuses in 2010–2013, in and around Amravati city, Maharashtra State, India.

Table 2. Summary results of the logistic regression for bird assemblages at Amravati city and surroundings, Maharashtra State, central India. The response variable of the model was presence/absence of species, and urbanization stage and year were fixed factors. Only significant values are shown.

	Estimate	Pr(> z)
(Intercept)	0.65	<0.001
Peri-urban	− 0.62	<0.001
Suburban	− 1.24	<0.001
Urban	− 1.43	<0.001
2011	0.35	0.035
2012	0.35	0.035
Industrial:2011	− 1.06	<0.001
Industrial:2012	− 1.12	<0.001
Industrial:2013	− 0.98	<0.001

Table 3. Summary result of the generalized linear model (Poisson family), with bird abundance as response variable, and urbanization stage as the fixed factor for the bird assemblages at Amravati city and surroundings, Maharashtra State, central India. Only significant values are shown.

	Estimate	Pr(> z)
(Intercept)	1.36	<0.001
Suburban	0.48	0.008
Urban	0.80	<0.001

DISCUSSION

By using an urbanization gradient, we found that bird species richness was negatively affected by urbanization, while the opposite was true for bird abundance, which is

in accordance with previous results (reviewed in Marzluff 2001). In this study, we provided evidence that this pattern is true also for tropical regions. We registered a higher species richness in general than found in similar studies in the temperate zone, which is not surprising, as India's avian biodiversity contains 13% of the world species richness, ~1300 species (Grimmett *et al.* 2001). The bird fauna of the various urbanization stages in this region originates from the rural bird fauna. Here we detected the effects of filtering mechanisms (Clergeau *et al.* 2006) that influenced the composition of bird assemblages in various urbanization stages.

We found support for H1, as the share of omnivorous and herbivorous species increased, both in terms of number of species and of individuals as urbanization progressed. The few species that are adapted to the overabundance of certain resources in urban centres will have a higher success than insectivores or predators as hypothesized. Although Galushin (1971) was impressed by the high number of predatory birds in New Delhi, he also commented on the very high numbers of the black kite (*Milvus migrans*), which are linked to carrion and rubbish, and that hunting birds are much more rare.

Consistently with our H2, large species were mostly restricted to the rural forest and in some cases, the industrial zones, and these hardly ever occurred in the more urbanized areas. This generated assemblages composed of smaller sized species – but still, the small insectivores (of which there are many in India, see Ali 2002) were lacking. One reason could be that the insect food supply could be smaller in urban settings. An indirect

indication of this is the loss of large carabid beetle species, and the generally decreasing trend of species sizes along, for example, temperate forest urbanization gradients (Magura *et al.* 2010). Carabids form an important food resource for birds (Lövei & Sunderland 1996), and trends found in this family could reflect the overall trends of arthropod sizes with increasing levels of urbanization.

Diversity partitioning indicated that local (α) diversity contributed 50.1% to the overall (γ) diversity of 89 species identified in the region of study. Another 36.2% was found at urbanization stage level and only 2.7% of the diversity was found at within-stage level (β diversity), indicating fairly homogeneous assemblages. By partitioning β diversity into components, we found species richness (species loss) was more important than species replacement for the pattern of β diversity along the urban gradient. The urbanization in this region may create very similar conditions for birds, because the within-zone spatial variability contributed little to the overall pattern of diversity. Bird assemblages are strongly affected by habitat structure and availability of food. The supply of anthropogenic food in an urban centre and water in the gardens of residential suburban and peri-urban areas may contribute to bird richness (Blair 1996, McKinney 2002). Furthermore, structural biodiversity across urban parks and rural forest could also be important determinants (Diaz *et al.* 2005, Newton 1994).

The basis of such changes can be behavioural. The reactions of the Acadian flycatcher (*Empidonax vireescens*) to urbanization in Ohio, USA, include higher levels of turnover in site occupancy, smaller-sized birds settling in urban areas, that show lower site fidelity and higher nest predation (Rodewald *et al.* 2013). This is probably true for between-species situations as well, but this hypothesis needs testing.

Our results could be extended by a systematic analysis of bird functional diversity in tropical areas, to test whether biotic homogenization also occurs under tropical conditions, and whether the reduced bird diversity would profoundly influence the functioning of urban ecosystems. With the continuing decline of biodiversity worldwide (Butchart *et al.* 2010), and the increasing urbanization, especially in the megadiverse regions of the world (Puppim de Oliveira *et al.* 2010), biodiversity-friendly management of urban areas could bring substantial global benefits.

ACKNOWLEDGEMENTS

We thank K. Morey, M. Nawarkhele and C. Shrivastav for help during fieldwork, C. H. Knudsen for preparing the map, and the anonymous reviewers for comments. Author contributions: MK, ND, RK and PB designed

the study, fieldwork was performed by MK, ND and RK, data analysis by MF, IT, TI and GL and writing by MK, MF, IT and GL, with comments from the other authors. Authorship is by the first-and-last principle.

LITERATURE CITED

- ALI, S. 2002. *The book of Indian birds*. (Thirteenth, revised edition). Bombay Natural History Society, Mumbai. 354 pp.
- AHRNÉ, K., BENGTTSSON, J. & ELMQVIST, T. 2009. Bumble bees (*Bombus* spp.) along a gradient of increasing urbanization. *PLoS ONE* 4:e5574.
- ANDERSON, M. J., CRIST, T. O., CHASE, J. M., VELLEND, M., INOUE, B. D., FREESTONE, A. L., SANDERS, N. J., CORNELL, H. V., COMITA, L. S., DAVIES, K. E., HARRISON, S. P., KRAFT, N. J. B., STEGEN, J. & SWENSON, N. G. 2011. Navigating the multiple meaning of β diversity: a roadmap for the practicing ecologist. *Ecology Letters* 14:19–28.
- ARONSON, M. E. J., LA SORTE, F. A., NILON, C. H., KATTI, M., GODDARD, M. A., LEPCZYK, C. A., WARREN, P. S., WILLIAMS, N. S. G., CILLIERS, S., CLARKSON, B., DOBBS, C., DOLAN, R., HEDBLUM, M., KLOTZ, S., KOOIJMANS, J. L., KÜHN, I., MACGREGOR-FORS, I., MCDONNELL, M., MÖRTBERG, U., PYŠEK, P., SIEBERT, S., SUSHINSKY, J., WERNER, P. & WINTER, M. 2014. A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B* 281:20133330.
- BARKER, R. J., SCHOFIELD, M. R., LINK, W. A. & SAUER, J. R. 2017. On the reliability of N-mixture models for count data. *Biometrics* 74:369–377.
- BLAIR, R. B. 1996. Land use and avian species diversity along an urban gradient. *Ecological Applications* 6:506–519.
- BUTCHART, S. H. M., WALPOLE, M., COLLEN, B., VAN STRIEN, A., SCHARLEMANN, J. P. W., ALMOND, R. E. A., BAILLIE, J. E. M., BOMHARD, B., BROWN, C., BRUNO, J., CARPENTER, K. E., CARR, G. M., CHANSON, J., CHENERY, A. M., CSIRKE, J., DAVIDSON, N. C., DENTENER, F., FOSTER, M., GALLI, A., GALLOWAY, J. N., GENOVESI, P., GREGORY, R. D., HOCKINGS, M., KAPOS, V., LAMARQUE, J. F. ET AL. 2010. Global biodiversity: indicators of recent declines. *Science* 328:1164–1168.
- CARDILLO, M., MACE, G. M., JONES, K. E., BIELBY, J., BININDA-EMONDS, O. R. P., SECHREST, W. & ORME, D. L. 2005. Multiple causes of high extinction rate in large mammal species. *Science* 309:1239–1241.
- CHACE, J. F. & WALSH, J. J. 2006. Urban effects on native avifauna: a review. *Landscape Urban Planning* 74:46–69.
- CHAMPION, H. G. & SETH, K. S. 1968. *A revised survey of the forest types of India*. Government of India Press, New Delhi. 404 pp.
- CHAZDON, R. L., PERES, C. A., DENT, D., SHEIL, D., LUGO, A. E., LAMB, D., STORK, N. E. & MILLER, S. 2009. The potential for species conservation in tropical secondary forests. *Conservation Biology* 23:1406–1417.
- CLERGEAU, P., SAVARD, J.-P. L., MENNECHEZ, G. & FALARDEAU, G. 1998. Bird abundance and diversity along an urban-rural gradient:

- a comparative study between two cities on different continents. *The Condor* 100:413–425.
- CLERGEAU, P., CROCI, S., JOKIMÄKI, J., KAISANLAHTI-JOKIMÄKI, M-L & DINETTI, M. 2006. Avifauna homogenisation by urbanisation: analysis at different European latitudes. *Biological Conservation* 127:336–344.
- CRIST, T. O. & VEECH, J. A. 2006. Additive partitioning of rarefaction curves and species-areas relationships: unifying α -, β - and γ -diversity with sample size and habitat area. *Ecology Letters* 9:923–932.
- DIAZ, I. V., ARMESTO, J. J., REID, S., SIEVING, K. E. & WILLSON, M. F. 2005. Linking forest structure and composition: avian diversity in successional forests of Chiloé Island, Chile. *Biological Conservation* 123:91–101.
- DUARTE, A., ADAMS, M. J., PETERSON, J. T. 2018. Fitting N-mixture models to count data with unmodeled heterogeneity bias, diagnostics, and alternative approaches. *Ecological Modelling* 374:51–59.
- EIGENBROD, E., BELL, V. A., DAVIES, H. N., HEINEMYER, A., ARMSWORTH, P. R. & GASTON, K. J. 2011. The impact of projected increases in urbanization on ecosystem services. *Proceedings of the Royal Society B* 278: 2301–2308.
- ELEK, Z. & LÖVEI, G. L. 2007. Patterns in ground beetle (Coleoptera: Carabidae) assemblages along an urbanisation gradient in Denmark. *Acta Oecologica* 32:104–111.
- FERRANTE, M., LO CACCIATO, A. & LÖVEI, G. L. 2014. Quantifying predation pressure along an urbanisation gradient in Denmark using artificial caterpillars. *European Journal of Entomology* 111:649–654.
- GALUSHIN, W. M. 1971. A huge urban population of birds of prey in Delhi, India. *Ibis* 113:522.
- GIBSON, L., LEE, T. M., KOH, L. P., BROOK, B. W., GARDNER, T. A., BARLOW, J., PERES, C. A., BRADSHAW, C. J. A., LAURANCE, W. F., LOVEJOY, T. E. & SODHI, N. S. 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478:378–383.
- GRIMMETT, R., INSKIPP, C. & INSKIPP, T. 2001. *Pocket guide to the birds of the Indian Subcontinent*. Oxford University Press, New Delhi. 384 pp.
- HENDERSON, P. A. & SOUTHWOOD, T. R. E. 2016. *Ecological methods*. (Fourth edition). John Wiley & Son, Chichester. 632 pp.
- HUSTON, M. A. 1994. *Biological diversity*. Cambridge University Press, Cambridge. 682 pp.
- IZENMAN, A. J. 2008. *Modern multivariate statistical techniques. Regression, classification and manifold learning*. Springer, Berlin. 740 pp.
- JOKIMÄKI, J. & SUHONEN, J. 1993. Effects of urbanization on the breeding bird species richness in Finland: a biogeographical comparison. *Ornis Fennica* 70:71–77.
- LANDE, R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76:5–13.
- LIKER, A., PAPP, Z., BÓKONY, V. & LENDVAI, Á. Z. 2008. Lean birds in the city: body size and condition of house sparrows along the urbanization gradient. *Journal of Animal Ecology* 77:789–795.
- LIN, Y.-P., CHANG, C.-R., CHU, H.-J. & CHENG, B.-Y. 2011. Identifying the spatial mixture distribution of bird diversity across urban and suburban areas in the metropolis: a case study in Taipei Basin of Taiwan. *Landscape and Urban Planning* 102:156–163.
- LÖVEI, G. L. & SUNDERLAND, K. D. 1996. The ecology and behaviour of ground beetles. *Annual Review of Entomology* 41:231–256.
- MACGREGOR-FORS, I. 2008. Relation between habitat attributes and bird richness in a western Mexico suburb. *Landscape and Urban Planning* 84:92–98.
- MAGURA, T., LÖVEI, G. L. & TÓTHMÉRÉSZ, B. 2010. Does urbanisation decrease diversity in ground beetle (Carabidae) assemblages? *Global Ecology and Biogeography* 19:16–26.
- MAGURRAN, A. E. 2003. *Measuring biological diversity*. Blackwell Publishing, Oxford. 264 pp.
- MARZLUFF, J. M. 2001. Worldwide urbanization and its effects on birds. Pp. 19–47 in Marzluff, J. M., Bowman, R. & Donnelly, R. (eds). *Avian ecology in an urbanizing world*. Kluwer Academic Publishers, Norwell.
- MARZLUFF, J. M. 2005. Island biogeography for an urbanizing world: how extinction and colonization may determine biological diversity in human-dominated landscapes. *Urban Ecosystems* 8:157–177.
- MCKINNEY, M. L. 2002. Urbanization, biodiversity and conservation. *Bioscience* 52:883–890.
- MCKINNEY, M. L. 2006. Urbanization as a major cause of biotic homogenization. *Biological Conservation* 127:247–260.
- MCKINNEY, M. L. 2008. Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosystems* 11:161–176.
- MILLENNIUM ECOSYSTEM ASSESSMENT 2005. *Ecosystem and human well-being: synthesis*. Island Press, Washington, DC. 155 pp.
- NEWTON, I. 1994. The role of nest sites in limiting the numbers of hole nesting birds: a review. *Biological Conservation* 70:265–276.
- PETERS, R. H. 1986. *The ecological implications of body size*. Cambridge University Press, Cambridge. 329 pp.
- PICKETT, S. T., CADENASSO, M., GROVE, J., NILON, C., POUYAT, R., ZIPPERER, W. & COSTANZA, R. 2001. Urban ecological systems: linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. *Annual Review of Ecology and Systematics* 32:127–157.
- PUPPIM DE OLIVEIRA, J. A., BALABAN, O., DOLL, C. N. H., MORENO-PEÑARANDA, R., GASPARATOS, A., IOSSIFOVA, D. & SUWA, A. 2010. Cities and biodiversity: perspectives and governance challenges for implementing the Convention on Biological Diversity (CBD) at the city level. *Biological Conservation* 144:1302–1313.
- RODEWALD, A. D., KEARNS, L. J. & SHUSTACK, D. P. 2013. Consequences of urbanizing landscapes to reproductive performance of birds in remnant forests. *Biological Conservation* 160:32–39.
- SENGUPTA, S., MONDAL, M. & BASU, P. 2014. Bird species assemblages across a rural urban gradient around Kolkata, India. *Urban Ecosystems* 17:585–596.
- SOL, D., GONZÁLEZ-LAGOS, C., MOREIRA, D., MASPONS, J. & LAPIEDRA, O. 2014. Urbanisation tolerance and the loss of avian diversity. *Ecology Letters* 17:942–950.
- UNITED NATIONS. 2014. *World urbanization prospects: the 2014 revision. Highlights*. (ST/ESA/SER.A/352). United Nations, New York. 32 pp.
- VERNER, J. 1985. Assessment of counting techniques. *Current Ornithology* 2:247–302.
- WAGNER, L. N. (ed.) 2008. *Urbanization: 21st century issues and challenges*. Nova Science Publishers, New York. 242 pp.

- WILMAN, H., BELMAKER, J., SIMPSON, J., DE LA ROSA, C., ZUUR, A. F., IENO, E. I., WALKER, N. J. & SAVELIEV, A. 2009. GML and RIVADENEIRA, M. M. & JETZ, W. 2014. EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. *Ecology* 95:2027.
- GAM for count data. Pp. 209–243 in Gail, M., Krickeberg, K., Samet, J. M., Tsiatis, A. & Wong, W. (eds). *Mixed effects models and extensions in ecology with R*. Springer Science and Business Media, New York.

Appendix 1. List of the birds observed along the urbanization gradient in Amravati city, Maharashtra State, central India, with their food preferences, and body size class. Species nomenclature follows Ali (2002). Food preference and body size extracted from Wilman *et al.* (2014). Body size classes: small (6–45 g), medium (45–120 g), large (120–300 g) and very large (> 300 g).

Family	Species	Status	Food preference	Body size class
Phasianidae	<i>Francolinus pondicerianus</i>	Resident	Omnivore	Large
Phasianidae	<i>Francolinus pictus</i>	Resident	Omnivore	Large
Phasianidae	<i>Pavo cristatus</i>	Resident	Omnivore	Very large
Picidae	<i>Jynx torquilla</i>	Resident	Insectivore	Small
Picidae	<i>Dinopium benghalense</i>	Resident	Insectivore	Medium
Megalaimidae	<i>Megalaima haemacephala</i>	Resident	Omnivore	Small
Bucerotidae	<i>Ocyrceros birostris</i>	Resident	Omnivore	Very large
Upupidae	<i>Upupa epops</i>	Resident	Insectivore	Medium
Coraciidae	<i>Coracias benghalensis</i>	Resident	Insectivore	Large
Halcyonidae	<i>Halcyon smyrnensis</i>	Resident	Predator	Medium
Meropidae	<i>Merops orientalis</i>	Resident	Insectivore	Small
Cuculidae	<i>Clamator jacobinus</i>	Winter migrant	Omnivore	Medium
Cuculidae	<i>Hierococcyx varius</i>	Resident	Insectivore	Medium
Cuculidae	<i>Cacomantis passerinus</i>	Resident	Insectivore	Small
Cuculidae	<i>Eudynamis scolopacea</i>	Resident	Frugivore	Large
Centropodidae	<i>Centropus sinensis</i>	Resident	Insectivore	Large
Psittacidae	<i>Psittacula eupatria</i>	Resident	Herbivore	Large
Psittacidae	<i>Psittacula krameri</i>	Resident	Herbivore	Medium
Psittacidae	<i>Psittacula cyanocephala</i>	Resident	Herbivore	Medium
Apodidae	<i>Apus affinis</i>	Resident	Insectivore	Small
Strigidae	<i>Athene brama</i>	Resident	Predator	Medium
Caprimulgidae	<i>Caprimulgus asiaticus</i>	Resident	Insectivore	Small
Columbidae	<i>Columba livia</i>	Resident	Omnivore	Very large
Columbidae	<i>Treron phoenicoptera</i>	Resident	Frugivore	Large
Columbidae	<i>Streptopelia decaocto</i>	Resident	Frugivore	Large
Columbidae	<i>Streptopelia tranquebarica</i>	Resident	Frugivore	Medium
Columbidae	<i>Streptopelia chinensis</i>	Resident	Herbivore	Large
Columbidae	<i>Streptopelia senegalensis</i>	Resident	Omnivore	Medium
Pteroclididae	<i>Pterocles indicus</i>	Resident	Herbivore	Large
Burhinidae	<i>Burhinus oedicnemus</i>	Resident	Insectivore	Very large
Charadriidae	<i>Vanellus malabaricus</i>	Resident	Insectivore	Large
Charadriidae	<i>Vanellus indicus</i>	Resident	Insectivore	Large
Accipitridae	<i>Elanus caeruleus</i>	Resident	Predator	Large
Accipitridae	<i>Milvus migrans</i>	Resident	Predator	Very large
Accipitridae	<i>Accipiter badius</i>	Resident	Predator	Large
Accipitridae	<i>Circaetus gallicus</i>	Resident	Predator	Very large
Accipitridae	<i>Pernis ptilorhynchus</i>	Resident	Insectivore	Very large
Accipitridae	<i>Butastur teesa</i>	Resident	Predator	Very large
Falconidae	<i>Falco tinnunculus</i>	Resident	Predator	Large
Laniidae	<i>Lanius excubitor</i>	Resident	Insectivore	Medium
Laniidae	<i>Lanius vittatus</i>	Resident	Insectivore	Small
Laniidae	<i>Lanius schach</i>	Resident	Insectivore	Medium
Corvidae	<i>Corvus splendens</i>	Resident	Omnivore	Very large
Corvidae	<i>Pericrocotus cinnamomeus</i>	Resident	Insectivore	Small
Corvidae	<i>Pericrocotus erythropygus</i>	Resident	Insectivore	Small
Corvidae	<i>Dicrurus macrocercus</i>	Resident	Insectivore	Medium
Corvidae	<i>Rhipidura aureola</i>	Resident	Insectivore	Small
Corvidae	<i>Terpsiphone paradisi</i>	Resident	Insectivore	Small
Corvidae	<i>Aegithina tiphia</i>	Resident	Insectivore	Small
Muscicapidae	<i>Monticola solitarius</i>	Winter Migrant	Insectivore	Medium
Muscicapidae	<i>Ficedula parva</i>	Winter Migrant	Omnivore	Small

Appendix 1. Continued

Family	Species	Status	Food preference	Body size class
Muscicapidae	<i>Copsychus saularis</i>	Resident	Insectivore	Small
Muscicapidae	<i>Saxicoloides fulicata</i>	Resident	Insectivore	Small
Muscicapidae	<i>Phoenicurus ochruros</i>	Winter Migrant	Omnivore	Small
Muscicapidae	<i>Saxicola caprata</i>	Resident	Insectivore	Small
Muscicapidae	<i>Cercomela fusca</i>	Resident	Insectivore	Small
Sturnidae	<i>Sturnus pagodarum</i>	Resident	Omnivore	Medium
Sturnidae	<i>Sturnus roseus</i>	Winter Migrant	Omnivore	Medium
Sturnidae	<i>Sturnus contra</i>	Resident	Omnivore	Medium
Sturnidae	<i>Acridotheres tristis</i>	Resident	Omnivore	Medium
Hirundinidae	<i>Hirundo concolor</i>	Resident	Insectivore	Small
Hirundinidae	<i>Hirundo smithii</i>	Resident	Insectivore	Small
Pycnonotidae	<i>Pycnonotus cafer</i>	Resident	Omnivore	Small
Cisticolidae	<i>Cisticola juncidis</i>	Resident	Insectivore	Small
Cisticolidae	<i>Prinia sylvatica</i>	Resident	Insectivore	Small
Cisticolidae	<i>Prinia socialis</i>	Resident	Insectivore	Small
Cisticolidae	<i>Prinia inornata</i>	Resident	Insectivore	Small
Zosteropidae	<i>Zosterops palpebrosus</i>	Resident	Frugivore	Small
Sylviidae	<i>Orthobomus sutorius</i>	Resident	Omnivore	Small
Sylviidae	<i>Chrysomma sinense</i>	Resident	Omnivore	Small
Sylviidae	<i>Turdoides caudatus</i>	Resident	Omnivore	Small
Sylviidae	<i>Turdoides malcolmi</i>	Resident	Omnivore	Medium
Sylviidae	<i>Turdoides striatus</i>	Resident	Omnivore	Medium
Alaudidae	<i>Eremopterix grisea</i>	Resident	Omnivore	Small
Alaudidae	<i>Ammomanes phoenicurus</i>	Resident	Insectivore	Small
Alaudidae	<i>Mirafra cantillans</i>	Resident	Omnivore	Small
Nectarinidae	<i>Nectarinia zeylonica</i>	Resident	Herbivore	Small
Nectarinidae	<i>Nectarinia asiatica</i>	Resident	Herbivore	Small
Passeridae	<i>Motacilla alba</i>	Winter Migrant	Insectivore	Small
Passeridae	<i>Motacilla cinerea</i>	Winter Migrant	Insectivore	Small
Passeridae	<i>Motacilla madaraspatensis</i>	Resident	Insectivore	Small
Passeridae	<i>Anthus rufulus</i>	Resident	Insectivore	Small
Passeridae	<i>Passer domesticus</i>	Resident	Omnivore	Small
Passeridae	<i>Petronia xanthocollis</i>	Resident	Omnivore	Small
Passeridae	<i>Ploceus philippinus</i>	Resident	Omnivore	Small
Passeridae	<i>Lonchura malabarica</i>	Resident	Herbivore	Small
Fringillidae	<i>Melophus lathami</i>	Resident	Omnivore	Small
Accipitridae	<i>Circus macrourus</i>	Winter Migrant	Predator	Very large
Accipitridae	<i>Dendrocitta vagabunda</i>	Resident	Omnivore	Medium