The interaction of imperviousness and habitat heterogeneity drives bird richness patterns in south Asian cities

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Abstract

Bird species richness has often been used as an indicator of urbanisation effects on biodiversity in North America and Europe, but similar studies are rare in rapidly urbanising regions in the tropics. Here we assess the effect of different urban environmental factors on local resident bird species richness at different spatial extents in South Asian cities. Bird data at 57 urban locations distributed across 11 cities were retrieved from the available literature. Different variables assessing the degree of urbanisation and urban habitat factors were measured, at 1000 m and 5000 m radius scale extent, for each urban location. We investigated how resident bird species richness was affected by urban environmental predictors by fitting linear regression models in a Bayesian framework. Our model suggested strong positive influence of the interaction between habitat Shannon metric (a proxy of habitat heterogeneity) and proportion of impervious surface (a proxy of human built-up and settlement extent) on local resident bird richness at both spatial scales. Increasing values of habitat Shannon metric positively related to increasing bird richness, but only when the proportion of impervious surface was very high. Our results suggest that areas with a high degree of urbanisation necessitate an increase of habitat heterogeneity to maintain high local bird diversity. Increasing the quality and the compositional variability of remaining bird habitat patches in highly built-up areas should be a major conservation concern within cities of South Asia.

Keywords Urbanisation · Urban habitat · Habitat heterogeneity · Tropical region · Indian sub-continent

Introduction

Natural and near-natural ecosystems are globally changing toward man-made urban ecosystems, with increasing interaction between human and natural systems (Kareiva et al. 2007; Strohbach et al. 2014). Urbanisation is a challenge to biodiversity and conservation that has long attracted the attention of ecologists (Blair 1996; McKinney 2002; Chace and Walsh 2006; McKinney 2008; Faeth et al. 2011). Several researchers suggested that urban biodiversity is affected directly by habitat conversion or indirectly through the effects of human population growth at local, regional and global scales (McKinney

2002; Ricketts and Imhoff 2003). These impacts, however, may be different in different taxonomic groups and across distinct geographic and climatic zones (Faeth et al. 2011).

Birds are the most studied taxon in urban ecology (Strohbach et al. 2009) and are commonly used as an indicator to assess the effect of urbanisation on biodiversity and on species community structure (Evans et al. 2009; Garaffa et al. 2009; Ferenc et al. 2014). Bird species richness is affected negatively by urbanisation (Blair 1996; Lepczyk et al. 2008; Garaffa et al. 2009; Silva et al. 2015), and positively by the presence of green areas, such as city parks, gardens, and green alleys (Chace and Walsh 2006; Donnelly and Marzluff 2006; Evans et al. 2009; Silva et al. 2015). In densely urbanised areas, however, green spots are shrinking, and native vegetation within city parks is often replaced with exotic plants (Chace and Walsh 2006; Sjöman et al. 2012). These changes are of conservation concern, as they may cause a decline of native bird species in urban sites (Chace and Walsh 2006). Consequently, urban ecologists have repeatedly stressed the importance of maintaining an intermediate degree of urbanisation for the conservation of birds and overall

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biodiversity (Jokimäki and Suhonen 1993; Blair 1996; Niemelä 1999; Crooks et al. 2004).

Several studies have highlighted that bird species richness and abundance can vary along gradients of urbanisation and peak in intermediate urban or suburban areas, because of different intensity of land use and different availability of resources, such as food, cover, and nesting sites (Blair 1996; Evans et al. 2007; McKinney 2008; Silva et al. 2015). The suburban matrix broadly supports the coexistence of different urban exploiters and the occurrence of complex avian community structure (Blair 2001; Jokimäki and Suhonen 1993; Clergeau et al. 2006; Faeth et al. 2011; Verma and Murmu 2015). Variation in bird diversity, however, is affected by the different adaptability and flexibility of individual bird species to urbanisation, which often results in the gradual replacement of native specialists with common generalist birds as urbanisation levels increase (McKinney 2008; Redowald and Gehrt 2014; Concepción et al. 2016). Birds with narrow ecological niches are sensitive to increasing urbanisation and almost never occur in urban areas unless natural areas occur nearby (Redowald and Gehrt 2014). Conversely, birds with flexible behaviour to increasing urbanisation have broader ecological niches and occur across the urban landscape, since they gain advantages from high habitat heterogeneity and low competition and predation rates (McKinney 2008; Redowald and Gehrt 2014). Consequently, in increasingly urbanised areas, native generalist bird presence is replaced by increasing abundance of common urban dwellers, such as rock dove (*Columba livia* f. *domestica*), house sparrow (*Passer domesticus*), common starling (*Sturnus vulgaris*), which depends on the human resources (Jokimäki and Suhonen 1993; Blair 1996; Evans et al. 2007; Garaffa et al. 2009; Lepczyk et al. 2017). The gradual decline in native bird species richness in highly urban areas is thus largely explained by the loss of natural habitat and by reduction and modification of resource availability (Chace and Walsh 2006; Sandström et al. 2006; Lepczyk et al. 2008; Silva et al. 2015).

Urban-rural gradient studies commonly assess the degree of urbanisation as a simplified measure of complex urban habitat structures (Beninde et al. 2015). This approach has the advantage of generalising varied urban landscapes easily; however, the individual effects of underlying specific habitat features and their heterogeneity remain unnoticed (McDonnell and Hahs 2009; Fuller and Gaston 2009; Beninde et al. 2015). In urban areas, vegetation composition is directly maintained by human intervention at the local scale, and avian diversity is mainly driven by such vegetation structures and green habitat patches at both local and city scales (Chamberlain et al. 2007; Murgui 2007; van Heezik et al. 2013; Ferenc et al. 2014). In highly built-up areas, green habitat patches are spatially fragmented and isolated, and they lack heterogeneity at a broader scale; since high bird diversity requires large geographic ranges and diverse foraging sites (McKinney 2008),

highly built-up areas often lead to a decline of avian richness within cities (Niemelä 1999; Jokimäki 1999). Indeed, bird diversity is associated with local habitat characteristics as well as with the interplay between habitat diversity and degree of urbanisation at multiple spatial scale extents (Jokimäki and Huhta 1996; Fontana et al. 2011; Meffert and Dzioc 2013; Lepczyk et al. 2017). Consequently, the improvement of quality and structural complexity of existing green patches of bird habitat in highly built-up areas is essential to favour the recovery of overall avian diversity within cities.

Our current understandings of patterns and processes of avian diversity in urbanised areas mainly derive from numerous studies conducted in North American and European cities (Grimm et al. 2008; Faeth et al. 2011). In contrast, similar knowledge is scant in cities of tropical areas (Marzluff 2016). This lack of understanding of urban biodiversity drivers outside of temperate regions has been documented in recent reviews (Faeth et al. 2011; Aronson et al. 2014; Beninde et al. 2015; Lepczyk et al. 2017). Because urban development differs according to urban status, geographic condition and land use heterogeneity at different spatial scales, it is unclear whether the results deriving from temperate zones can be extrapolated to other parts of the world (Lepczyk et al. 2017; Leveau et al. 2017; Demographia 2019).

The world's urban human population is projected to reach 66% by 2050, and nearly 90% of this increase is predicted to occur in Asia and Africa (United Nations 2014). Asia already has the highest percentage of urban population and built-up areas of any continent (Demographia 2019). South Asia, in particular, is one of the fastest-growing regions in the world (World Bank 2018), mainly owing to the presence of megacities like Delhi, Dhaka, Kolkata, Karachi and Mumbai. These cities are thus highly vulnerable in terms of sustainable urban management. Although South Asia accounts for about 13% of the world's bird species diversity (Grimmett et al. 2011), the loss of urban biodiversity is commonly considered as a secondary issue, as the foremost priorities are related to social and economic challenges. Hence, studying the drivers of bird diversity in South Asia would greatly contribute to improving the general understanding of the consequences of urbanisation on bird species richness in rapidly urbanising regions.

In this paper, we aimed to investigate the effect of different urban environmental factors on local scale bird species richness within cities of South Asia, using data from published literature. Bird species diversity varies spatially with environmental conditions (Jokimäki and Huhta 1996; Meffert and Dzioc 2013), and avian patterns in urban areas should be considered at multiple spatial scales (Jokimäki 1999). We thus hypothesise that environmental predictors at different scale extents may affect bird species richness differently. Several studies indicated a negative effect of build-up proportions on bird species richness. Conversely, increasing habitat heterogeneity was frequently found to be beneficial for birds within

cities (Rebele 1994; McKinney 2008; Evans et al. 2009; Meffert and Dziok 2013; Beninde et al. 2015; Lepczyk et al. 2017). We therefore predict that the interactions between impervious surface and heterogeneity in habitat patches may positively influence bird species richness at both small and large spatial scale extents. Since birds rely on available suitable habitat, increasing the level of heterogeneity in highly urban areas would benefit bird richness at smaller spatial scale. Birds, however, are highly mobile and depend on a broader area for foraging. Thus, we further predict that habitat heterogeneity at a large spatial scale extent would be also important and would favor bird species richness in urban areas.

Methods

Compilation of bird data

We obtained bird species checklists for multiple urban areas located in South Asian cities from published literature. Using ‘Web of Science’, we searched for urban bird studies by ‘TOPIC: (bird), Refined by TOPIC: (urban) AND TOPIC: (South Asia)’. To improve the number of hits, we searched again with city names – 20 cities, following the ranking of largest built-up urban areas based on population density (Demographia 2019) and 30 cities, considering major and biggest cities by country according to ‘World Atlas of cities’ (www.worldatlas.com/citypops.htm). We further explored studies published in local journals in English which were not covered by Web of Science, using Google Scholar. Overall, we found a total of 54 publications among which we selected 24 references (ESM_Table 1), i.e. those that presented an observation of overall bird species at any urban locality. Only eight studies were directly urban-focused, whereas others were general bird surveys. Few studies reported bird lists for multiple localities, while others reported birds for a single locality (ESM_Table 1,2). We then associated geographic location coordinates (latitude, longitude) to the reported localities. In absence of information from the source, we used the maps and location details provided in the papers to acquire GPS (Geographic Positioning System) coordinates. When multiple studies were found for the same location, we reconciled all bird records to generate one unique checklist for that location. As a result, we obtained 57 urban locations with available bird checklists from the sources, distributed across 11 cities (Fig. 1; ESM_Table 2). All the selected locations fulfilled specific requirements: i) information was available to derive the geographic position; ii) study area size was $\leq 5 \text{ km}^2$; iii) survey was performed over less than 10 years, to minimise variation in the spread of observation duration; iv) survey period includes the year

2000 onwards, to minimise temporal mismatch among study years and environmental variables.

Within a given locality, a potential issue is the occurrence of both migratory birds and resident birds, and the presence of birds of different origin (i.e. native vs. exotic). To avoid bias, our analysis focused on the number of native resident birds only, i.e. non-exotic species which occur at a given locality throughout the year (hereafter “resident birds”). To identify the origin and migration status of birds, we used species fact sheets and range maps available from BirdLife International (BirdLife International 2016, 2019). Preliminary analyses, however, showed that the number of all bird species (defined as all birds observed within a locality, either native or non-native, resident or migratory) strongly and positively correlated (Pearson’s $r = 0.97$) with the number of resident birds (ESM_Fig 1).

Explanatory variables

To investigate the relationship between resident bird species richness (BSR) and potential drivers, we coupled BSR with several explanatory variables, five of which were used as predictors in our analysis (Table 1, ESM_Table 3).

To represent urbanisation, we considered the proportion (%) of impervious surface (IS), which refers to human built-up and settlement extent, and human population density per km^2 (HP). To represent urban habitat conditions, we further considered habitat Shannon metric (HS), presence of cropland (PC), and proportion (%) of tree canopy cover (TC). HS was a positive measure of habitat heterogeneity and referred to compositional variability in Enhanced Vegetation Index (Tuanmu and Jetz 2015); PC was considered to account for the effect due to agricultural area; TC was considered to account for the benefit of the proportion of green cover at the locality.

Alongside these predictors, we considered one covariate in our analysis, native resident bird richness at the regional scale (RB). RB was extracted from the ‘BirdLife international range map’ (BirdLife International 2016) using the area of the specific city. Our dataset included locations which were distributed in different cities. Thus, we included RB to account for the potential confounding effects of distinct regional species pools on locally observed bird richness, possibly owing to different geographic conditions (White and Hurlbert 2010).

Quantified measures of urban predictors vary at different spatial scales, and this variation could underpin different correlations with bird species richness (Concepción et al. 2015; Suarez-Rubio and Krenn 2018). It is known that birds are highly mobile and can be sensitive to varying urban processes present at larger scale extents (Jokimäki and Huhta 1996), though they can respond to urbanisation better at smaller scale extents (Concepción et al. 2015). Thus, we extracted values of the predictor variables around the geographic centroid location of the study localities, each at two scale extents - 1000 and

Fig. 1 The map shows distribution of 57 urban locations across 11 cities of South Asia. The labels ‘1–57’ indicate the unique ID of the studied locations and ‘a–j’ refer to the cites. Bird data of these localities are used in the current assessment and are available in ESM_Table_2

5000 m radius buffer, from available global raster image datasets (Table 1, ESM_Table_3). We considered predictor values at 1000 and 5000 m radius buffer to test their effects at small and large spatial scales. All bird studies selected for this assessment covered $\leq 5 \text{ km}^2$ area, and an average area extent of $0.93 \text{ km}^2 \pm 1.33 \text{ SD}$. Thus, we considered that the

predictors’ value at 5000 m radius were sufficiently large-scale approximations of the predictors for the studied locality. Among all raster image datasets, only two (impervious surface and tree canopy cover) had a spatial resolution of 30 m, whereas most others had a resolution of 1 km (ESM_Table_3). Therefore, we did not consider values of the predictors at the scale extents $< 1000 \text{ m}$ radius.

Raster images were processed in ‘ArcGIS 10.5.1’, and a WGS1984 projection was used. During the selection of raster datasets, we preferred continuous variables over categorical variables if available. For example, for a given locality, we extracted a proportion of impervious surface as a measure of urbanisation, instead of urban/non-urban categories. For each study location and scale extent, we extracted the mean values for all continuous variables and presence-absence for categorical variables.

Statistical analysis

The effect of different predictors on resident bird species richness (response variable) was investigated by fitting linear regression models in a Bayesian framework. Since Bayesian

Table 1 List of predictor variables considered in the model assessment

(A) Predictors [†] (mean values at 1000 m and 5000 m radius buffer scale extent)	
<i>Degree of urbanisation</i>	
1. Proportion of impervious surface (%)	IS
2. Human population density (/km ²)	HP
<i>Urban habitat factors</i>	
3. Habitat Shannon metric	HS
4. Presence of cropland (1/0)	PC
5. Tree canopy cover (%)	TC

Note: [†] A detail explanation, sources and selection processes are available at ESM_Table_3

regression is not based on asymptotic inference, smaller datasets can be analysed without losing much power (Lee and Song 2004; Hox et al. 2012). The model with the highest prediction accuracy was selected for final inference. The analysis described below was applied to the 1000 m and the 5000 m spatial scales alike.

Several of the studied urban localities consisted of a single season survey while others consisted of multiple season surveys over different years. Recorded bird species richness (BSR) at urban locations was positively and linearly correlated with the survey duration, suggesting no cumulative effect of BSR in our dataset (i.e. there was no saturation in the number of observed species over time). Thus, to avoid bias, a ‘bird species richness rate’ was calculated dividing the observed BSR by the survey length (in months). Local BSR rate was then log-10 transformed to approximate normality. The response variable, however, showed issues of right-skewness: thus, for our models, we assumed a skew normal distribution, a generalisation of the normal distribution that allows for non-zero skewness. We started building a global model that included all predictors as additive terms (IS, HP, HS, PC, TC), plus the interaction between HS (habitat Shannon metric) and IS (proportion of impervious surface). The choice of including only the interaction between HS and IS reflects our attempt to keep the model as simple as possible while retaining the most relevant variables. In the model, native resident bird richness at the regional scale (RB) was fitted as a covariate to control for potential confounding effects.

Preliminary analyses suggested that the grouping effect of city (owing to multiple bird records within the same city) was highly non-significant. Thus, no-significant dependence of data points within cities was detected, and the grouping effect of cities was not included in the fitted models. The global model was of the general form:

$$\begin{aligned} \log_{10}(\text{bird richness rate}_i) = & \beta_0 + \beta_1 \cdot IS_i + \beta_2 \cdot HP_i \\ & + \beta_3 \cdot HS_i + \beta_4 \cdot PC_i + \beta_5 \cdot TC_i \\ & + \beta_6 \cdot HS_i \times IS_i + \beta_7 \cdot RB_i \end{aligned}$$

From the global model, 8 simpler models were generated by excluding one or more predictors (Table 2). For all models, β coefficients were estimated running 5000 iterations (including 1000 warm-ups) over 4 chains with a post hoc Markov chain Monte Carlo (MCMC) analysis, using the No-U-Turn Sampler (NUTS) (Hoffman and Gelman 2014). Weakly informative priors (*Cauchy*[0,5]) were defined for β coefficients. Prior to analysis, continuous predictors were standardised to improve the efficiency of MCMC sampling and variance inflation factor (VIF) values were checked in the global model for collinearity issues. To select the model with the highest prediction accuracy, models were compared using leave-one-out cross-validation, a special case of k-fold cross-validation where a single observation in the dataset is selected to validate the model and the remaining

Table 2 Results of the leave-one-out cross validation (LOO) for the selection of the model with the highest prediction accuracy to explain local resident bird species richness at different spatial scales (1000 m and 5000 m), in South-Asian cities. The table reports model structure (predictive variables), LOO values, ELPD values (i.e. the Bayesian LOO estimate of the expected log pointwise predictive density), and delta ELPD (Δ ELPD). Selected models in bold

Model structure	LOO	ELPD	Δ ELPD
<i>1000 m</i>			
~ HS + IS + HS: IS	28.3	−14.2	0.0
~ IS + HP + HS + PC + TC + HS: IS	30.9	−15.5	−1.3
~ HS + PC + TC	32.3	−16.2	−2.0
~ HS	32.6	−16.3	−2.1
~ IS	40.7	−20.3	−6.1
~ TC	41.6	−20.8	−6.6
~ PC	41.9	−20.9	−6.7
~ IS + HP	42.2	−21.1	−6.9
~ HP	43.5	−21.7	−7.5
<i>5000 m</i>			
~ HS + IS + HS: IS	20.3	−10.2	0.0
~ HS	26.6	−13.3	−3.1
~ IS + HP + HS + PC + TC + HS: IS	27.8	−13.9	−3.7
~ HS + PC + TC	32.4	−16.2	−6.0
~ IS	40.6	−20.3	−10.1
~ IS + HP	42.3	−21.1	−10.9
~ HP	43.1	−21.5	−11.3
~ PC	43.7	−21.8	−11.6
~ TC	44.5	−22.2	−12.0

IS Proportion of Impervious surface, *HP* Human population density, *HS* Habitat Shannon metric, *PC* Presence of cropland, *TC* Tree canopy cover

$n - 1$ observations are used to train the model. This procedure is repeated for all observations in the dataset and a measure of predictive accuracy for the n data points taken one at a time is calculated (Vehtari et al. 2017).

Mean point estimates and 95% credible intervals for β coefficients of the selected model were obtained from the simulated values from the joint posterior distribution of the model parameters. The variance explained by the final model (R^2) was calculated following Gelman et al. (2019), as the ratio between the variance of the predicted values and the sum of the variance of the predicted values and the variance of the residuals. The fit of the selected model was assessed through MCMC diagnostics (R-hat estimates and trace plots) posterior-predictive checks and prior sensitivity analysis.

All analyses were conducted with R 3.6.1 (R Core Team 2019) in RStudio 1.2.1335 (RStudio Team 2019). The package ‘brms’ (Bürkner 2017, 2018), a high-level interface to Stan (Carpenter et al. 2017), was used for the MCMC analysis. The package ‘shinystan’ (Gabry 2018) was used for MCMC diagnostics.

Table 3 Model estimates for the effects of ‘proportion of impervious surface (IS)’, ‘habitat Shannon metric (HS)’ (and their interaction) and of the covariate ‘regional scale resident bird species richness (RB)’ on log-10 transformed local resident bird richness rate at different spatial scales (1000 m and 5000 m) in South-Asian cities. The table reports mean estimates of beta coefficients, and lower and upper bounds of 95% credible intervals (i.e. 2.5% and 97.5% quantiles from the joint posterior distribution of model parameters)

Parameter	Mean β	95% Credible Interval	
		2.5% quantile	97.5% quantile
<i>1000 m</i>			
Intercept	0.344	0.261	0.435
IS	0.015	−0.080	0.113
HS	0.019	−0.062	0.108
RB	0.014	−0.099	0.097
IS: HS	0.092	0.020	0.166
<i>5000 m</i>			
Intercept	0.312	0.240	0.395
IS	−0.071	−0.133	−0.007
HS	0.095	0.018	0.178
RB	0.011	−0.082	0.080
IS: HS	0.093	0.011	0.175

Results

The average resident bird species richness (BSR) across all localities was 45 ± 24 SD. A comparison of BSR distribution among the studied localities, using box-and-whisker plot, indicated that higher BSR in low-urban areas and lower BSR in high-urban areas were consistent, whereas BSR varied greatly in intermediate urban areas (ESM_Fig_2). BSR also varied among the studied localities with respect to land-cover type, indicating higher richness in green and waterbody sites (ESM_Fig_3). Urban locations that showed higher-than-average richness were: university campuses, lakes, wetlands and protected / city parks. In contrast, locations with the lowest bird species richness were mostly inner-city urban areas (ESM_Table_2). The selected localities did not differ much in terms of climatic conditions (mean annual temperature of $26^\circ\text{C} \pm 1$ SD), but there was a high variation in terms of urban conditions (mean impervious surface: $51\% \pm 22$ SD; mean human population density: $21596 \text{ ind./km}^2 \pm 19,944$ SD).

Model assessment

The predictors in the global model, at both spatial scales, did not show issues of collinearity (VIF values <3). The leave-one-out cross-validation suggested that the highest prediction accuracy was achieved by the model that included only the interaction between habitat Shannon metric (HS) and proportion of impervious surface (IS), at both spatial scales (Table 2).

For both selected models, no issues of MCMC convergence were detected, as suggested by the trace plots and the values of R-hat (all <1.02 , cf. Brooks and Gelman 1998). Both models predicted the actual response variable well, as suggested by the posterior-predictive checks. The selected priors also did not influence the final estimates. The selected models explained a similar amount of the overall variance in bird species richness (1000 m: 15%; 5000 m: 19%).

For both scale extents, the interaction between HS and IS had a positive effect on local BSR rate (Table 3; Fig. 2). Namely, bird species richness increased with increasing values of HS only at high levels of IS. With low levels of IS, bird species richness maintained fairly stable (and relatively higher) values irrespective of changes in HS. From the posterior distribution of model parameters at the 1000 m scale, the probability that the relationship between BSR rate and the interaction of HS with IS had values greater than zero was 0.99, with evidence ratio [ER] of 157.42 (i.e. this hypothesis was 157 times more likely than its alternative). Similarly, from the posterior distribution of model parameters at the 5000 m scale, the probability that the relationship between BSR rate and the interaction of HS with IS had values greater than zero was 0.99, with evidence ratio [ER] of 69.8. Both values of Evidence Ratio thus support a strong interactive effect between HS and IS on bird species richness rate.

Discussion

Our study provides the first comparative assessment of bird species richness drivers across several urban localities distributed at different cities of South Asian cities and offer insights into the processes underpinning bird species richness in a tropical region, thus partially filling a geographical gap. Our results show that the interaction of imperviousness and habitat heterogeneity is the main driver of bird species richness within South Asian cities, supporting the argument that anthropogenic effects shape bird diversity within cities (Evans et al. 2009; Aronson et al. 2014). The consequence of this driving factor on bird species richness is similar at both smaller and larger spatial scale extents. Since birds require diverse foraging sites at large geographic range, the quantity, quality and structural complexity of the remaining green patches at smaller as well as broader scale extents benefit avian diversity in urban environments. Similar results at smaller and larger spatial scale extents may also indicate to the monotonic urban development that the relationship between increasing human built-up and natural green habitat loss is typical (Liu et al. 2016).

Among all locations, bird species richness was usually higher in less-urbanised areas than in highly urban areas (ESM_Fig_2). Several single-city studies in South Asia identified a similar pattern in bird species richness along the urban-rural gradient, for example in highly urban areas of Kolkata

Fig. 2 Marginal effects of the models at different spatial scales selected to explain variation in local resident bird species richness (BSR) in South Asian cities. The plot shows the effect of ‘habitat Shannon metric (HS)’ on local BSR rate for varying levels of ‘proportion (%) of impervious surface (IS)’, at the spatial scale of 1000 m (a) and 5000 m (b). Darker datapoints indicate increasing values of IS. Dashed, dotted and solid lines respectively refer to the linear fit of bird species richness rate with HS at increasing levels of IS

(Ghose and Santra 2008; Sengupta et al. 2014), Jamshedpur (Verma and Murmu 2015) and Kathmandu (Katuwal et al. 2018). Our investigation further revealed that intermediate urban areas showed large variation in bird species richness. Few such locations with intermediate urbanisation held higher numbers of bird species (ESM_Fig_2), which indicated a likely positive influence of associated high habitat heterogeneity on avian richness in those areas (Evans et al. 2009). Several urban-rural gradient studies highlighted the importance of intermediate urbanisation (i.e. suburban matrix) to promote more complex bird community structure and higher species richness than in highly urban and rural areas (Jokimäki and

Suhonen 1993; Blair 2001; Evans et al. 2007; Faeth et al. 2011). The existing studies also suggest that species richness peaks at intermediate levels of urbanisation (Blair 2001; McKinney 2008; Faeth et al. 2011; Verma and Murmu 2015); however, our assessment failed to confirm this. All our studied locations contained a percentage of impervious surface >0 (ranging from 11 to 96); thus, a complete gradient scenario was not attainable. In turn, our results suggest that the fine-scale influence of different underlying habitat features and their associations are more crucial in shaping bird species richness in urbanised areas compared to the urban-rural gradient that is simple generalisation of complex features of the

urban landscape. The consequence is more likely apparent for highly urban areas within South Asian cities, where imperviousness varies greatly, and the importance of specific habitat features and their interplay are poorly captured by a simple gradient approach (Ghose and Santra 2008; Katuwal et al. 2018; Sengupta et al. 2014).

Our analysis shows that the bird species richness rate in urban localities is positively affected by the interaction between the proportion of impervious surface (human built-up and settlement) and habitat Shannon metric (habitat heterogeneity) (Tables 1, 2; Fig. 2). The positive effect of habitat heterogeneity was strong only when the proportion of human built-up and settlement was very high, at both 1000 m and 5000 m spatial scale extents. In urban localities with a low proportion of built-up areas and limited human settlement, the value of bird species richness was either stable or relatively high, and the influence of habitat heterogeneity on bird species richness was not prominent. This result indicates that the specific habitat factors and their compound relationships are the potential driving factors of bird species richness in urbanised areas (Beninde et al. 2015). One example of such habitat features is urban vegetation structure (i.e., private lawns, small gardens, parks, street trees, riparian vegetation etc.), which can be more diverse in cities than in rural areas (Donnelly and Marzluff 2006). Urban avifauna strongly correlates with habitat factors at local and city scale (van Heezik et al. 2013; Ferenc et al. 2014). Thus, the interface between green habitat diversity and imperviousness might support different feeding guilds of birds by providing diverse foraging sites (Katuwal et al. 2018).

Urban ecologists recognise that higher species richness can exist in cities than in surrounding rural areas and a large variety of species can adapt well to urban life because of increased habitat heterogeneity (de Oliveira et al. 2011; Desrochers et al. 2011). Thus, heterogeneous green spaces (i.e., small habitat patches, a network of corridors) are suggested for the conservation of native birds (Donnelly and Marzluff 2006; Beninde et al. 2015). Increasing urbanisation negatively affects the quantity and quality of native habitat composition (McKinney 2002; Donnelly and Marzluff 2006). The proper management of spatial arrangement and diversity in habitat structure can benefit the overall composition of bird communities (Evans et al. 2009). Our findings are consistent with the data available for several cities of the Northern hemisphere, and they support the beneficial effects of habitat heterogeneity on bird species richness in highly urbanised areas in South Asia as well. Further comparative assessments including cities from different geographic regions are necessary to validate the importance of specific urban features and their association on birds as well as other components of biodiversity.

The interpretation of our results requires some caution. Our richness data was mainly derived from bird checklist inventories extracted from different studies in different cities. Thus, potential differences with respect to, e.g., detection probability or sampling effort cannot be discarded. Furthermore, regional differences may affect local scale bird species richness (McDonnell and Hahs 2009). To minimise bias in our assessment, we accounted for the regional species pool effect as an important covariate of locally observed bird species richness. However, the existence of potential lurking factors accounting for variation in bird species richness rate cannot be excluded. Potential lack of independence in our bird data was accounted for in the preliminary analysis of the city-specific grouping effect. Finally, we did not investigate the composition of avifauna at the urban localities in South Asian cities, which mostly includes generalist species of least conservation concern and species with high adaptability to the altered human environment (Callaghan et al. 2019). Non-native species are poorly documented in cities of this region (Ghose and Santra 2008; Sengupta et al. 2014; Katuwal et al. 2018). In general, higher presence of bird species relates to the presence of native generalist bird species; the presence of rare species is mostly limited to nearby bird refugia (i.e., large green parks, protected gardens, sub-urban matrix and rural areas) (Sengupta et al. 2014; Sorace and Gustin 2017; Katuwal et al. 2018).

Nonetheless, our results contribute to improving the understanding of the bird-habitat relationship in fast-growing urban areas in tropical regions. The bird-habitat relationship may vary among species; however, overall bird diversity appears to be generally driven by the availability of diverse habitat patches within a locality (Evans et al. 2009). When planning new urban development, city planners should therefore focus on the maintenance of compositional variability of habitat in urban neighbourhoods to the greatest extent possible (Evans et al. 2009). We suggest the maximisation of heterogeneity in green habitat composition should be a conservation priority within cities, which is likely to benefit avian diversity in fast urbanising areas.

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Authors' contribution MS designed the study, collected and analysed the data, and wrote the original manuscript. LC performed the statistical analysis, and contributed to writing and revising the manuscript. IS advised throughout the study and contributed to writing and revising the manuscript.

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