



# Are the same factors determining biodiversity in cities across different regions? Comparing drivers of urban bird richness patterns in Southern Asia vs. Western Europe

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## Abstract

According to general urban ecological understanding, bird species richness declines in highly urban areas due to the increasing extent of built-up areas, and decreasing proportions of green areas. However, this hypothesis is mainly based on studies conducted in cities located in the Global North and rarely in the Global South. We aimed to assess whether existing conceptual understandings of drivers of bird species richness patterns within cities are similar across different regions, specifically Southern Asia (in the Global South) vs. Western Europe (in the Global North). Using avian occurrence data drawn from GBIF (gbif.org), we estimated resident bird species richness in 943 selected grid cells (each cell corresponding to approximately 1 km<sup>2</sup> area) distributed in 24 cities, 13 in Southern Asia and 11 in Western Europe. We applied generalised linear mixed models to relate resident bird richness with different explanatory variables of gradients of urbanisation, habitat and climatic factors using the selected grid cells as sampling units. Our results showed that bird richness declined with increasing human built-up and settlement extent (imperviousness) in both regions, but this relationship was stronger in Southern Asia compared to Western Europe. Bird richness also sharply declined in urban areas located far from inland waterbodies, but only in Southern Asia. Our findings suggest that high imperviousness drives bird richness decline, but this process appears to be more pronounced in regions where rapid urbanisation is ongoing. Urban planning integrating green spaces throughout cities is crucial in Southern Asia, as it is in Western Europe, to benefit both people and biodiversity.

**Keywords** Urbanisation · Species diversity · Global South · Global North

## Introduction

Urbanisation is considered an opportunity to accelerate economic development for human well-being. Accordingly, the proportion of the global urban population is currently higher than the rural population and will continue to rise in cities (Elmqvist et al. 2013; Zhang 2016). This transition from rural to urban areas goes along with increasing built-up and settlement extent, driving loss in natural areas (McDonald

et al. 2013). As a result, urbanisation is profoundly altering biodiversity at local and regional scales (Grimm et al. 2008; Faeth et al. 2012; Lepczyk 2017). The dominant drivers of species diversity within cities are anthropogenic (Aronson et al. 2014). In particular, increasing built-up extents and decreasing amounts of green space have been identified as major correlates of species loss in cities (Carvajal-Castro et al. 2019; Gagné and Fahrig 2011; Marcacci et al. 2021; Silva et al. 2015). This pattern, however, is mainly based on studies conducted in developed countries of the Global North (e.g., in North America, Europe, Australia) (Faeth et al. 2011; Aronson et al. 2014). Since cities differ globally in (bio-)geographic setting and socioeconomic status (Grimm et al. 2008; McIntyre 2014; Nilon 2014), a debate exists in urban ecology about whether the same general drivers shape species diversity patterns within cities worldwide (Geschke et al. 2018).

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There are remarkable differences in the urbanisation process worldwide. In the Global North, this process has come to a halt, while urbanisation in the developing countries of the Global South is proceeding at an unprecedented rate (Seto et al. 2013; Zhang 2016). It can be expected that this rapid urban growth will lead to a considerable loss of habitats and species diversity in the cities of the Global South in the future (Reynolds et al. 2021; Seto et al. 2013). Many Global North ecologists traditionally used a gradient approach to investigate species diversity patterns from low to highly urbanised areas. Different concepts such as intermediate disturbance (Connell 1978), local scale productivity (Mittelbach et al. 2001) and competition (Menge and Sutherland 1987) suggested a hump-shaped relationship between diversity and urbanisation (Faeth et al. 2012). These concepts incorporated the notion that urbanisation alters species occurrence patterns within cities in a non-linear fashion. Species richness generally declines from low to highly urban areas because large built-up extents cause fragmentation and a loss in connectivity in important habitat patches such as green areas (parks, gardens, and trees) and waterbodies (Faeth et al. 2011; McKinney 2008; Sandström et al. 2006). As built-up extent increases, only species with broader ecological niche adapt well to urban settings and become predominantly abundant at both temporal and spatial scale. In highly productive urban areas (e.g., parks, gardens), high species abundance is largely owing to urban exploiters, although species richness may decline (Shochat et al. 2010; Faeth et al. 2012). On the contrary, species richness can improve in intermediate urban areas because a heterogeneous habitat structure that integrates suburban green features in proximity promotes the coexistence of different species (owing to a confluence in species turnover process) (Faeth et al. 2012). It is thus commonly suggested to increase the amount of and variety within green habitat spaces to compensate the negative effect of human built-up and settlement extent on biodiversity in highly urbanised areas (Faeth et al. 2012; Sultana et al. 2020). Nevertheless, built-up extents and habitat availability that usually drive species diversity patterns vary among cities in the Global South vs. Global North.

Moreover, it is expected that rapid urban growth leads to pronounced inequality in socioeconomic status in the Global South cities (Shatkin 2007; UN-Habitat 2020), which ultimately affects land-use practices and, thus, biodiversity (Melles 2005). Urban neighbourhoods with higher socioeconomic status host more vegetation and complex habitat structures that support more species; this has been described as the ‘luxury effect’ in several studies from the Global North (Leong et al., 2018; Strohbach et al. 2009). Also for the Global South, recent studies confirmed such a luxury effect (Chamberlain et al., 2019) and showed adverse

effects of poverty on bird diversity (Sultana et al. 2022). Therefore, understanding the general driving factors of species diversity patterns among cities under different levels of urbanisation in the Global South versus those in the Global North will strengthen the foundation of urban ecology and biodiversity conservation across continents (Faeth et al. 2011; Shackleton et al. 2021; United Nations 2014).

We focused to compare driving factors of bird species richness (as a proxy to biodiversity) across urban areas of different regions, Western Europe (in the Global North) and Southern Asia (in the Global South). Birds are one of the most surveyed taxa in urban ecology, and bird richness has been used to indicate and monitor overall biodiversity status by numerous studies (Bibby 1999; Strohbach et al. 2009; Harrison et al. 2014). Moreover, consistent bird data is easily attainable from avian checklists and online platforms (Speed et al. 2018; Sultana and Storch 2021; Tye et al. 2017). Thus, focusing on birds covers one of the main downfalls in research: the availability of data to fill the knowledge gaps across different geographic regions. Western Europe (WE) can be considered as a proxy for the Global North, where drivers of urban bird diversity patterns are well-understood by existing research, and Southern Asia (SA) as a proxy for the Global South, which is poorly covered in urban ecology. These regions are different in terms of urbanisation processes and socio-economic aspects. WE is an economically developed region, and a large proportion of the population (70–100%) already lives in urban areas (UN-Habitat 2020). In the course of industrialisation, this region experienced massive economic and demographic transitions in recent centuries, which ultimately led to extensive urbanisation. Nevertheless, in contrast to the Global South, urbanisation progressed relatively slowly and was strictly controlled (Kunzmann and Wegener 1991; Zhang 2016). Today, Western European urban planners increasingly adopt green concepts (e.g., eco-city toward sustainable urbanism) (Bibri 2020) to improve habitat quality for both human well-being and biodiversity. In contrast, the historically grown urban centres of SA are currently expanding rapidly and uncontrollably (UN-Habitat 2020). Moreover, unlike WE cities, SA cities are struggling with rapidly growing human population, poverty and low quality of habitation (Ellis and Roberts 2016).

Among European cities, great similarities in bird species occurrences and community structure have been found. This “avian homogenization” is attributed to the loss of specialists and raise of generalists in the course of the long European history of urbanisation (Clergeau et al. 2006; Ferenc et al. 2014; Morelli et al. 2016). There is indication that the historic declining trend in urban bird populations in European countries might have currently levelled off (e.g., in Germany; Kamp et al. 2021). While WE with its long

history of urbanisation, has already lost much of its avian diversity in the past, Southern Asian cities still host a rich avian diversity (Grimmett et al. 2011), which however is threatened by the recent, rapidly progressing urbanisation process. Given the differences in timing, speed, patterns and quality of urbanisation, urban biodiversity conservation in the Global South is lacking a scientific basis. It is unclear if the same general drivers of urban biodiversity reported from the Global North also hold in cities of developing countries of SA.

In this paper, we aimed to understand if the general drivers of urban biodiversity patterns are consistent across different regions of the globe. Based on conceptual understanding from the Global Norths, we hypothesised that bird species richness would decline in relation to an increasing proportion of imperviousness (i.e., human built-up extent), and it would improve in the presence of available habitat patches. Namely, we expected bird richness to increase with increasing levels of local habitat heterogeneity and in proximity to urban green areas and waterbodies. Further, due to the differences in urbanisation processes and socioeconomic patterns, we hypothesised that the influence of different drivers on bird species richness in urban localities would interface differently in WE vs. SA cities. We assumed that bird richness would vary more significantly from lowly to highly urban areas in SA than in WE. Specifically, the negative effect of built-up extent on bird richness would be higher in highly urban areas of cities of SA, since the rapid urbanisation process is recent and biodiversity loss is ongoing.

## Methods

### Bird richness data

We collected readily available digital bird observation records from GBIF (Global Biodiversity Information Facility; gbif.org) for the last 2 decades (2000–2020) in several cities of Southern Asia (GBIF 2020a) and Western Europe (GBIF 2020b, 2021). Avian records have good coverage in comparison to all other taxa within the currently available digital databases (Chandler et al. 2017; Freeman and Peterson 2019). In fact, the coverage of digital species occurrence records is better in human developed sites than the rural areas (Petersen et al. 2021; Speed et al. 2018), and these data are suitable for investigating species diversity patterns in urban sites (Sultana and Storch 2021).

We selected bird observation records in 24 cities – 13 cities in 7 countries of Southern Asia (SA) and 11 cities in 6 countries of Western Europe (WE) for our assessment (Fig. 1). Our preliminary selection of sites included well-known cities from each region. The number of selected

cities per countries differ; a single city was chosen from small countries and multiple cities from large countries (e.g., one city in Nepal and 5 cities in India from SA). The selection was also based on the ranking after human population of the cities (i.e., with > 10,000), and our visual inspection of data availability on the GBIF database site for the city. During data collection from all selected cities, we checked for geospatial issues and did not consider locations with invalid coordinates, geodetic data, or imprecise coordinates. For our assessment, we considered only the records of native resident bird species at the city scale extent, which we filtered following BirdLife International's species range maps (BirdLife International and Handbook of the Birds of the World 2018).

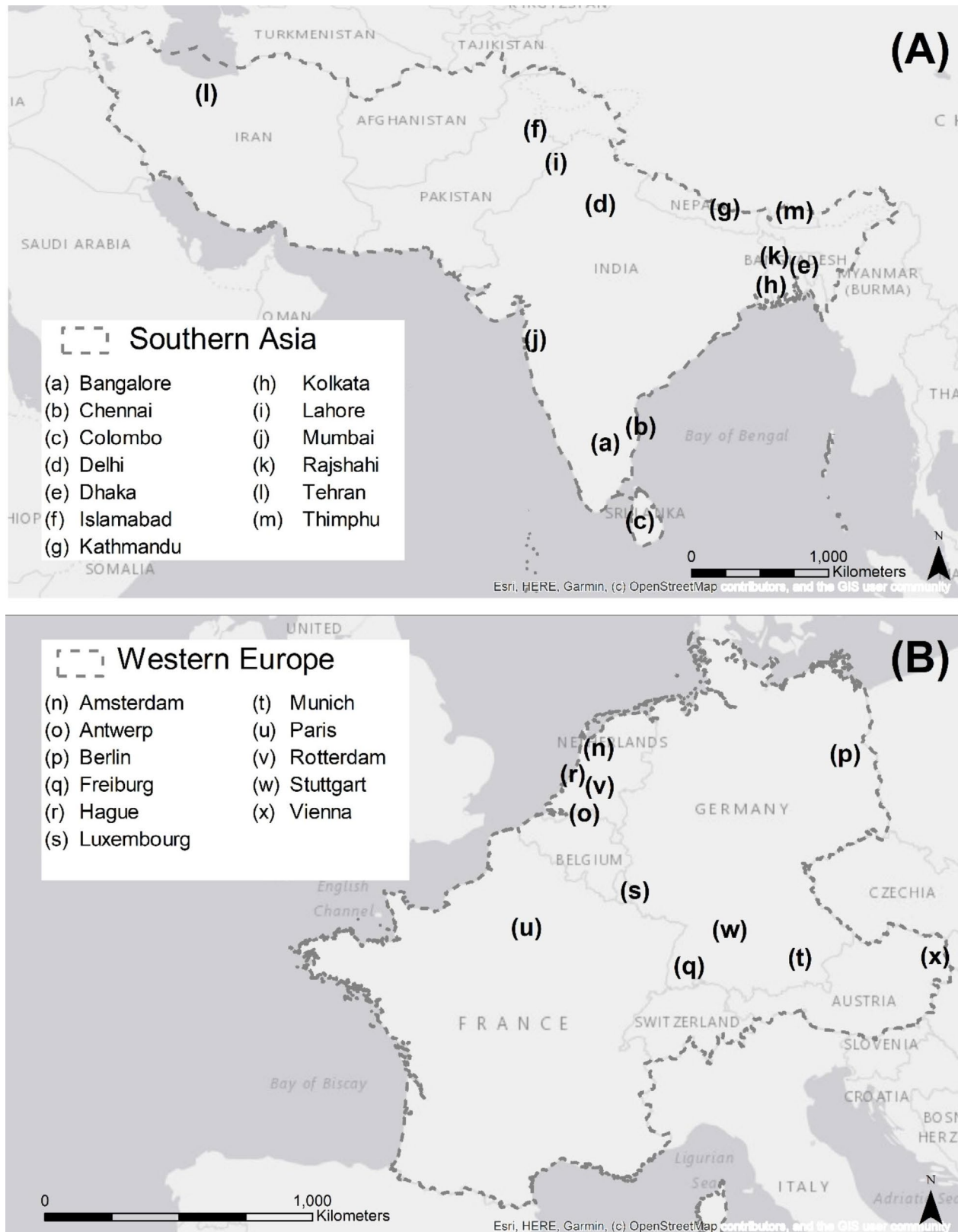
We spatially joined all occurrence records of resident birds at the grid cells of cities in ArcMap version 10.8.1, using the projection Geographic Coordinate System WGS84. Grid cell spatial resolution was near 0.00833 degree which corresponded to approximate 1 km<sup>2</sup> area. We excluded the grid cells that represented predominantly forest and agricultural land cover located far from built-up areas. Only the urban grid cells that consisted of impervious surface 1–100% were considered.

Next, for our analysis, we selected the grid cells from each city where inventory completeness estimate was > 0.50 and frequency of bird species occurrences records was > 50. Inventory completeness at each grid cell was measured following the formula - observed species richness ( $S_{obs}$ ) / expected true species richness ( $S_{exp}$ ; Chao<sup>2</sup> estimate is used) (Freeman and Peterson 2019; Sousa-Baena et al. 2014). We considered the selected grid cells as well-surveyed urban sites with satisfactory avian observation records and hereafter, suitable for further analysis (Sultana and Storch 2021). At each selected well-surveyed grid cell site, we estimated resident bird species richness (i.e., the number of species) for our major assessment.

### Explanatory variables

We explored the relationship of resident bird species richness with different explanatory variables at the grid cell extent (i.e., 1km<sup>2</sup> sampling unit), among which 10 were selected for the statistical analysis. We used readily available different raster image datasets and OpenStreetMap datasets to extract values of our explanatory variables. Source references of the explanatory variables data are available in ESM\_Table\_1.

To represent the gradient of urbanisation, we considered human population density and impervious surface (%) which refers to the proportion of built-up areas and settlement extent. We preferred continuous values over



**Fig. 1** The map shows location of selected cities in Southern Asia (A) and Western Europe (B) considered to investigate driving factors of bird species richness along different gradients of urbanisation

categorical values and took continuous measure of urbanisation, instead of high-medium-low urban categories.

Amount and proximity of different habitat patches and their variations are suggested as important predictors of bird diversity in cities (Callaghan et al. 2018; Yang et al. 2020) and local scale habitat features have been found to be more related to avian diversity than landscape scale habitat features (Callaghan et al. 2018). To represent habitat conditions, we thus also explored the total proportion and proximity of different habitat patches (i.e., urban green areas, inland waterbodies, agricultural areas, coastlines), and habitat heterogeneity at the grid cell unit (ESM\_Table\_1). Most of our selected grid cell units (89–99%) were in proximity (i.e., < 5 km) to urban green areas, inland waterbodies and agricultural areas, but located far away (i.e., > 5 km) from coastlines. We, thus, only considered the proportion of green area (i.e., sum of total area of urban parks, gardens, cemetery, forest, nature reserves; m<sup>2</sup>), inland waterbody area (i.e., sum of total area of major waterways, rivers, lakes, ponds, canals; m<sup>2</sup>) and agricultural area (i.e., percentage of cropland extent) at the grid cell unit as the general local habitat drivers of bird species richness during our statistical analysis (ESM\_Table\_1). We also considered the proximity as distances (km) from grid cell centre to the nearest edge of green, inland waterbody and agricultural areas (ESM\_Table\_1). Additionally, we considered habitat Shannon metric as a positive measure of habitat heterogeneity (Tuanmu and Jetz 2015).

Our data was distributed in multiple cities of two different geographic regions. Thus, we also considered average annual temperature and average annual precipitation to account for distinct climatic conditions which possibly influence varying species pools among cities (White and Hurlbert 2009).

### Sampling effort

Species occurrence data of GBIF is collected mostly in a non-systematic manner by local observers. Preliminary data exploration indicated the occurrence of a saturation effect of the ‘number of sampling event days’ (i.e., total number of days of bird observation) and of the ‘number of observers’ (i.e., total number of individual observers who contributed with bird observation) on the estimates of bird species richness at the sampling units. We, thus, considered these two variables as covariates to account for variability in sampling effort at the selected grid cell’s unit.

### Statistical analysis

All analyses were conducted with R v. 4.0.4 (R Core Team 2020) in RStudio v. 1.3.1056 (RStudio Team 2020). To

investigate the potential drivers of bird species richness, grid cells were considered as our basic sampling units. We started by fitting a global model where bird species richness was set as a count response variable; region was set as a predictor in interaction with: green area, inland waterbody area, agricultural area, distance to green area, distance to agricultural area, distance to inland waterbody (all log<sub>10</sub>-transformed, due to data skewness; before transformation, for each variable half of the smallest non-zero value was added to all values, to avoid zeros), temperature, precipitation, human population density and the interaction between impervious surface and habitat Shannon metric. City was fitted as a random intercept to account for repeated sampling within each city. All explanatory variables were standardized prior to fitting the global model. Additionally, the number of sampling event days and the number of observers were included in the model as offsets to account for sampling effort, and fitted with a natural cubic spline function with 2 degrees of freedom to account for potential saturation effect.

The global model was fitted with the package “glmmTMB” (Brook et al. 2017) assuming a negative binomial conditional distribution, which proved a better fit than a Poisson distribution in exploratory analyses. The global model therefore was of the form:

$$\text{Bird species richness}_{ij} \sim \text{NB}(\mu_{ij}, k).$$

$$E[\text{Bird species richness}_{ij}] = \mu_{ij}.$$

$$\text{Var}[\text{Bird species richness}_{ij}] = \mu_{ij} + k \times \mu_{ij}^2$$

$$\begin{aligned} \text{Log}(\mu_{ij}) = & (\text{impervious surface}_{ij} + \text{habitat Shannon metric}_{ij} + \text{human population density}_{ij} + \log_{10}(\text{green area}_{ij}) \\ & + \log_{10}(\text{agricultural area}_{ij}) + \log_{10}(\text{waterbody area}_{ij}) \\ & + \log_{10}(\text{distance to green area}_{ij}) + \log_{10}(\text{distance to agricultural area}_{ij}) \\ & + \log_{10}(\text{distance to inland waterbody}_{ij}) + \text{temperature}_{ij} + \text{precipitation}_{ij}) \times \text{Region}_{ij} \\ & + \log(\text{number of sampling event days}_{ij}^2) + \log(\text{number of observers}_{ij}^2) + \text{City}_{ij}. \end{aligned}$$

where  $E(\text{Bird species richness}_{ij})$  defined the expected mean value of bird species richness data for sampling event  $i$  at city  $j$ , as a function of the explanatory variables, controlling for sampling effort (number of sampling days and of observers) and including a random intercept for each city  $j$ . Region was a dichotomous variable with two levels, SA and WE.

We checked for collinearity issues among explanatory variables by means of the Pearson correlation coefficient (absence of collinearity was set at values < |0.7|, Dormann et al. 2013) and for adequacy of residual distribution using the quantile residual approach (Dunn and Smyth 2008) implemented in the package “DHARMa” (Hartig 2020).

From this initial model, we compared models using the Akaike’s Information Criterion (AIC) with the package “buildmer” (Voeten 2021) to find an



appropriately-parsimonious model. More specifically, the function “buildglmmTMB” first finds the largest possible regression model that will converge and then performs step-wise elimination, based on the change in AIC (Matuschek et al. 2017).

Once the final model was obtained, the parameter estimates were inspected with the package “parameters” (Lüdecke et al. 2020a) and the marginal and conditional  $R^2$  values (Nakagawa and Schielzeth 2012) extracted using the package “performance” (Lüdecke et al. 2020b). Marginal effects were plotted with the package “visreg” (Breheny and Burchett 2017).

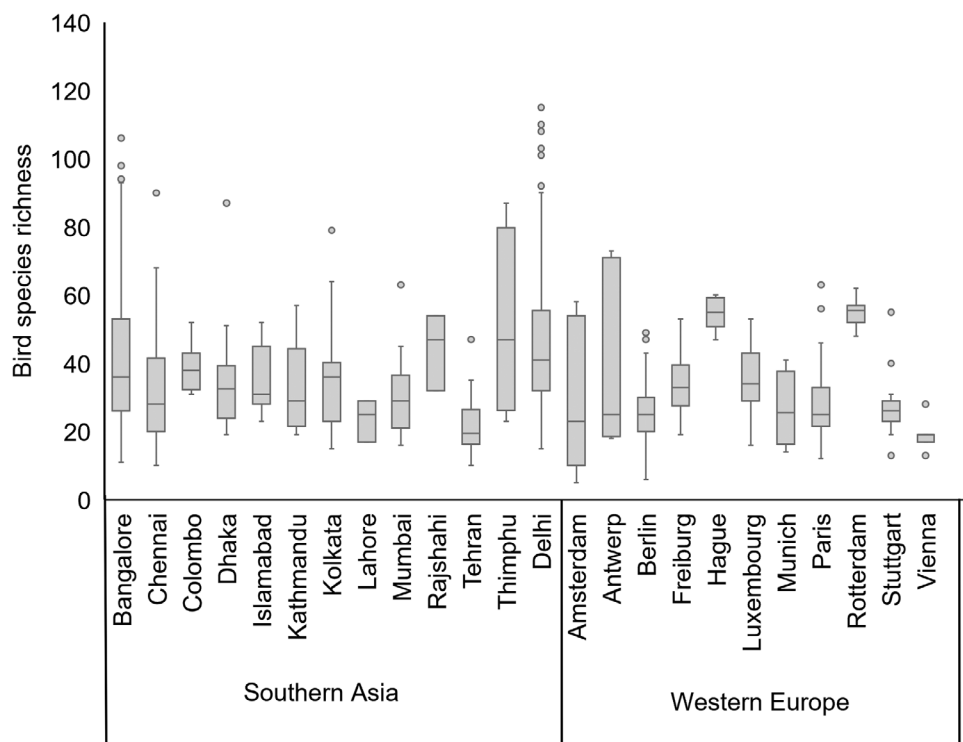
## Results

A total of 798,892 observation records of resident bird species was obtained at 943 selected grid cell sites distributed across 24 cities of Southern Asia (SA) and Western Europe (WE). The selected grid cell sites varied greatly between SA and WE, in relation to the status of human population density (SA mean  $12,653 \pm 1,2748$  SD; WE mean  $5,762 \pm 6,715$  SD) and human development index (SA mean  $0.55 \pm 0.1$  SD; WE mean  $0.81 \pm 0.02$  SD) (i.e., value extracted from gridded global datasets for Gross Domestic Product and Human Development Index; Kummur et al. 2017; ESM\_Table\_1). From the obtained bird observation records we found a total occurrence of 97 species in WE cities and of 425 species in SA cities. In turn, this indicated presence probability of

approximately 48% of regional scale resident bird species across WE cities and approximately 38% of that across SA cities (i.e., compared with species range maps at the regional scale; BirdLife International and Handbook of the Birds of the World 2018). However, the average resident bird species richness observed at the grid cell sites varied among cities in both SA (mean  $39 \pm 19$  SD) and in WE (mean  $29 \pm 12$  SD) (Fig. 2). In both regions, the majority of the observed bird species were listed as least concern for conservation.

The global model did not show issues of collinearity, or issues of residual distribution, thereby suggesting no major violations of model assumptions. The final model included as explanatory variables the two-way interaction between impervious surface and Region, and the two-way interaction between distance to inland waterbody (i.e., one proxy variable of green habitat patches) and Region, and the quadratic effect of sampling effort. Table 1 shows the estimates for each of the terms included in the model. The two-way interactions had positive effects on bird species richness (Table 1; Figs. 3 and 4), and the sampling effort showed a saturation effect (Table 1; Fig. 5). Specifically, bird species richness declined with increasing percentage of imperviousness (i.e., from low to highly built-up areas) in both SA and WE. However, the declining curve was sharper in SA than in WE. The effect of proportions of different green habitat patches and distance to green area and agricultural area were not retained in the final model. The final model had a conditional  $R^2$  of 60% and a marginal  $R^2$  value of 52%.

**Fig. 2** A box and whisker plot showing resident bird species richness (per 1 km<sup>2</sup> grid cell units) observed at the selected grid cell sites among cities of Southern Asia and Western Europe. The plot shows a comparison of median value and inter-quartile range of the observed bird number in each selected city



**Table 1** Parameter estimates of the model selected via stepwise selection based on change in AIC values. For each parameter, the table reports the beta estimate and the lower (LCL) and upper (UCL) bounds of the 95% confidence intervals

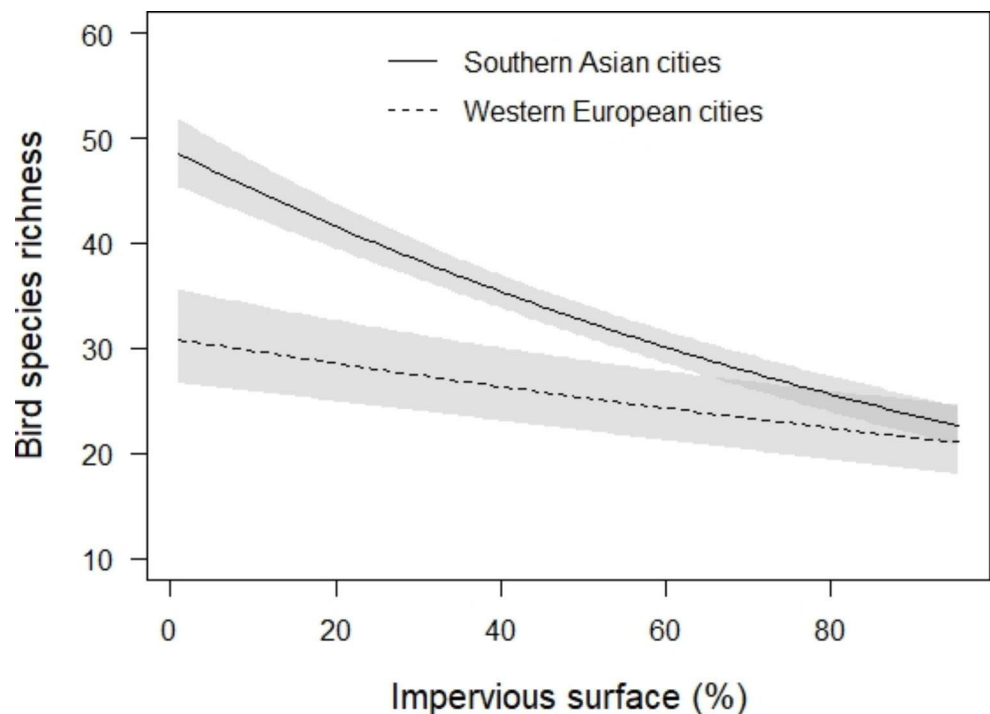
Term	Estimate	LCL	UCL
Intercept	3.192	3.049	3.337
Impervious surface	-0.176	-0.203	-0.148
Log10(distance to inland waterbody)	-0.142	-0.172	-0.113
Region [Western Europe]	-0.302	-0.428	-0.175
Log(Number of observers)	0.491	0.339	0.642
Log(Number of observers <sup>2</sup> )	0.559	0.399	0.718
Log(Number of sampling event days)	0.899	0.631	1.168
Log(Number of sampling event days <sup>2</sup> )	1.248	1.109	1.387
Log10(distance to inland water body) : Region [Western Europe]	0.185	0.136	0.235
Impervious surface : Region [Western Europe]	0.088	0.045	0.131

## Discussion

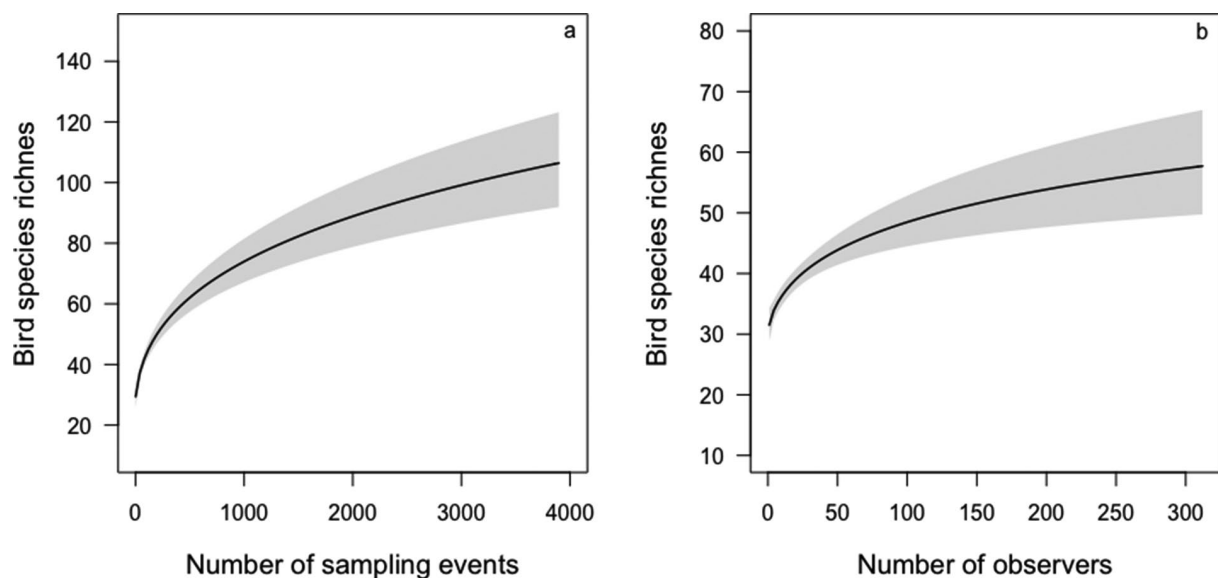
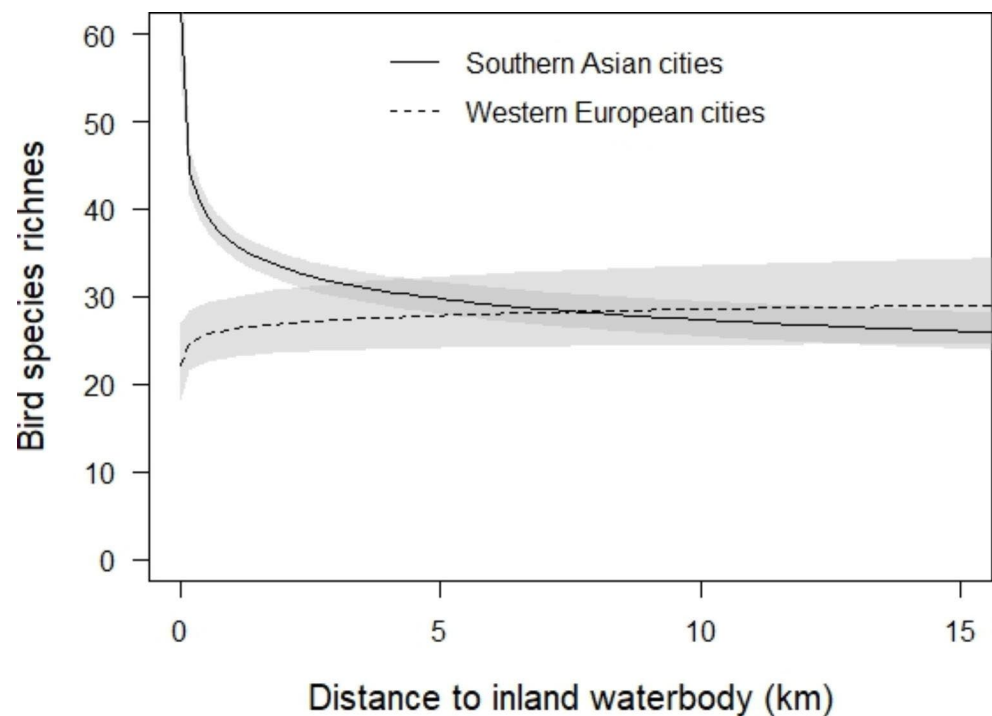
Our results showed a decline in resident bird species richness associated with an increasing level of imperviousness (i.e., in highly built-up areas) within cities. This effect is consistent in cities in both the Global North and the Global South. Our findings agree with existing studies that report reduced bird richness in highly built-up sites with high imperviousness (Carvajal-Castro et al. 2019; Gagné and Fahrige 2011; Marcacci et al. 2021; Silva et al. 2015).

However, we observed that the decrease in resident bird species richness from lowly to highly built-up areas is likely steeper in Southern Asia (SA) than in Western Europe (WE) (Fig. 3).

SA is geographically one of the most biodiversity rich regions and home to 13% of the World's birds (Grimmett et al. 2011). Thus, resident bird richness in lowly built-up areas of SA was naturally much higher owing to the higher regional species pool compared to that of WE (Fig. 3). It indicates to higher structural diversity of natural or semi-natural patches in low urban sites within SA cities. In contrast, in highly built-up areas, bird species richness was fairly comparable across SA and WE cities, which indicate to the avian homogenisation due to urbanisation across continents. In fact, it indicates to a greater decline in species variety with increasing urbanisation within SA cities compared to that in WE. This consequence of bird decline in highly urban areas of SA is expected (Sengupta et al. 2014; Katuwal et al. 2018; Marcacci et al. 2021), since many cities already reported huge reductions in the amount of urban green patches, e.g., less than 15% vegetation stands in Bangalore (Ramachandra et al. 2017), only 8% tree cover remains in Dhaka (Byomkesh et al. 2012), and only 5% green cover was reported in Kolkata (Mondal 2013). Our best predicted model did not infer presence of such green patches as the major driver of resident bird richness within cities, which might be due to our consideration of green areas collectively (i.e., do not account for different types and diversity in patches). However, a fast urbanisation (through increasing human settlement and built-up areas) is currently

**Fig. 3** Marginal effect of impervious surface on bird species richness (per 1km<sup>2</sup> grid cell units) in South Asian cities (continuous line) and Western European cities (dashed line). The graph shows the mean expected value keeping the other variables in the model at their median value. The shaded area shows 95% confidence intervals

**Fig. 4** Marginal effect of distance to inland water bodies on bird species richness (per 1 km<sup>2</sup> grid cell units) in Southern Asian cities (continuous line) and Western European cities (dashed line). The graph shows the mean expected value keeping the other variables in the model at their median value. The shaded area shows 95% confidence intervals



**Fig. 5** Marginal effect of sampling efforts (a: number of sampling events; b: number of observers) on bird species richness (per 1 km<sup>2</sup> grid cell units). The graphs show the mean expected value keeping the

other variables in the model at their median value. The shaded area shows 95% confidence intervals

ongoing in many parts of SA, which is causing an enormous loss of green patches and degradation of remnant habitats, ultimately leading to greater bird decline and potentially triggering more pronounced ‘extinction debt’ effect (Dri et al. 2021; Tilman et al. 1994) in urban areas within SA cities.

In WE cities, the relatively lower trend in bird richness decline might be because of homogenisation and decline in avifaunal variety across urban gradients (Clergeau et al. 2006; Ferenc et al. 2014; Morelli et al. 2016)

which is presumably happened due to urbanisation during the 18th–20th century. Moreover, there is also a historical trend in parallel loss of suitable habitat for birds in natural or semi-natural non-urban areas in Europe, due to industrialised agricultural intensification (Donald et al. 2001). It is reported that a significant decline in common breeding birds and in farmland species has already occurred during the last century (Butchart et al. 2010; EEA 2021), and the declining trend in avian population in human settlement



areas has probably reached a stable condition in many European countries, e.g., since ca. 2003 in Germany (Kamp et al. 2021). Our data thus might show relatively lower contrast in resident bird richness from low to highly urban areas in WE cities, since it comes from bird observation records in the 21st century. As such, the actual scenario of bird diversity loss in highly urban areas within WE cities, which likely took place in the past, might not be notable in relation to recent urbanisation.

Alongside the intensity of urbanisation, we observed a sharp decline in bird species richness in areas which are located far away from inland waterbodies, but only in SA. It supports the existing concept that local habitat features play an important role in shaping species diversity across urban areas (Evans et al. 2009; Lepczyk et al. 2017b). SA is home to an extensive network of large rivers, canals, lakes and many wetlands flowing throughout most of its area (Babel and Wahid 2008) which support numerous waterbirds. An increasing trend in waterbirds decline was found relatively higher in Asia than any other regions due to the loss of aquatic features (Li et al. 2009; BirdLife International 2017). Urbanisation is one of the major threat to the shrinkage of waterbodies (Li et al. 2009) and loss of connectivity within in many cities of SA, such as in Bangalore (Ramachandra et al. 2017), Dhaka (Sultana et al. 2009), Kolkata (Li et al. 2016). Our finding highlights the degradation and loss of connectivity among ecologically important habitat areas like waterbody features within cities that contributed to resident bird richness decline in SA cities.

We observed that most of the birds documented across our selected cities in both SA and WE were listed as “least concern” (iucnredlist.org), which reconfirms that most bird species found in urban centres globally are generalists (Callaghan et al. 2019). Geographically, greater resident bird diversity is present in SA than in WE. Though this, the percentage of regional scale richness that potentially can occur throughout cities in WE was higher than in SA. Existing Global North studies also stated that several bird species (e.g., *Passer domesticus*, *Parus major*, *Corvus corone*) with greater flexibility in resource use and high dispersal ability have evolutionarily adapted to urban settings in many Western cities (Møller 2009; Shochat et al. 2010; Faeth et al. 2012). This might indicate the presence of somewhat better habitat conditions in highly urban areas of WE cities providing better opportunities for sustaining local resident birds than that in SA cities. This variation, in turn, supports the influence of varying socioeconomic status on species diversity across urban neighbourhoods in developed vs. developing regions.

On average, the human development index (HDI) was higher in our selected WE cities than SA cities. HDI measures not only aspects of wealth, but also human well-being

as a proxy for a decent standard of healthy living in a given area (Kummu et al. 2018). So, it clearly reflects on higher socioeconomic status in WE (than in SA) that can benefit species richness mediated through better habitat conditions. In WE, quality of habitat is usually maintained not only by city authorities but also by local citizens. Citizens with high socio-economic status normally own their houses and transform the surrounding landscape with more greenery; consequently, bird richness benefits from greater level of vegetation cover and better plant diversity (Hedblom et al. 2017). Consequently, lower bird diversity might also relates to inequal human socioeconomic condition (Melles 2005), which is relatively extreme in SA. Our assessment, however, cannot pinpoint the exact socio-economic factors that play role in shaping such effect. Our statistical analysis excluded socio-economic variables (e.g., Human development index; see ESM\_Table\_1) because of higher correlation with urbanisation-related factors and climatic variables.

It should be noted that we focused only on resident bird species richness, as one of the proxies to overall biodiversity, which appears to be generally driven by level of imperviousness and near proximity of ecologically important habitat features such as inland waterbodies. There might be several other disturbance factors that affect bird richness across cities such as artificial light (Dominoni 2017), anthropogenic noise (Carral-Murrieta et al. 2020), air pollution (Sanderfoot and Holloway 2017), heavy metals and organic pollutants (Kekkonen 2017), disease transmission (Riley et al. 2014). Future studies focusing on the influence of these factors in Global South vs. Global North would advance the current understanding. Further, we did not investigate bird community composition and did not explicitly assess species-specific relationships with urbanisation. Thus, our paper does not provide insights on avifaunal homogenisation and cannot confirm whether birds with certain traits are experiencing particularly steep declines in urban areas. Our study also lacks a full spectrum on the consequences of urbanisation on bird species in each individual city selected from SA and WE. As an example, we observed highest average bird species number in Rotterdam and Hague (Fig. 2) within WE region, possibly due to their proximity to the coast and the presence of numerous seabird species. Using data from all cities, we could not explore the importance of this effect during our preliminary assessment, since most of our sampling grid units were located far from the coast.

Moreover, our data comes from readily available GBIF bird observation records, which were collected mostly by amateur citizens, often in a non-standardised way and rarely through planned surveys. Such data are collected largely from opportunistic surveys and are biased toward higher sampling intensity of certain species, greater sampling effort near observers' residences, in urban as opposed to rural

areas (Freeman and Peterson 2019; Petersen et al. 2021). However, digitally available species observation data have better coverage in cities and thus can be suitable in urban ecological research because of their easy accessibility (Sultana and Storch 2021). Nevertheless, all of the potential sampling related biases can be challenging to identify. During our assessment, we attempted to minimise such bias by considering the saturation effects of sampling effect factors in the model analysis. We also considered potential lack of independence in our bird data by considering city-specific grouping effect in our statistical model analysis.

WE is largely an urbanised region from the Global North consisting of many “green cities” like Berlin, Freiburg, Paris, Vienna, which are recognised as models of sustainable development globally. Under the European Union action programme for the environment, WE countries are committed to protecting nature and restoring and maintaining biodiversity since 1973 (EU 2019). Here, environmental and nature protection actions are currently well-integrated in urban planning, with green urbanism and infrastructure practices being implemented in several WE cities (Beatley et al. 2000; Lachmund 2013w and Antalovsky 2018). Such well-integrated urban planning improves the quality of green spaces for both people and biodiversity (Nilon et al. 2017). We emphasise that similar urban planning, by laws and regulations, is now crucial in SA countries, since it is predicted that 96% of the future urbanisation will occur in fast growing regions of the Global South such as Southern Asia (UN-Habitat 2020). Here, an ambitious focus on restoration of degraded green areas, waterbodies and connectivity within them, and on compensation of nest sites will help to address bird diversity declines within cities. The observed trend in bird richness decline in highly urban areas of SA cities is recent and still ongoing, but it may become even worse in the future (i.e., considering extinction debt) compared to the Western European cities if proper conservation actions are not taken urgently.

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**Authors' contributions** MS and IS designed the study. MS prepared the data, contributed in the analysis and wrote the manuscript. LC conducted the statistical analysis, contributed during writing and revising

the manuscript. IS guided throughout the study and contributed during revising the manuscript.

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**Data Availability** Data and the analysis script used in this paper can be found at this link: [https://osf.io/p6kmq/?view\\_only=a73dba608c8c4114ab354ff1577ff0b](https://osf.io/p6kmq/?view_only=a73dba608c8c4114ab354ff1577ff0b).

**Code Availability** None to declare.

## Declarations

**Conflict of interest** None to declare.

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