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# The importance of unsealed areas in the urban core and periphery for bird diversity in a large central european city

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**Abstract**

Although urbanization poses one of the largest threats for biodiversity, only few studies have so far examined its impact in large Central European cities. Our study aimed at investigating the effects of urbanization on bird diversity using two methods to describe the urban environment. The first measure used the degree of sealing, portion of traffic infrastructure, number of floors of the tallest building at a site scale (100-m radius), and the distance from the city center, while the second one relied on land-cover data at a local scale (1000-m radius). We conducted bird surveys at 761 sites across Hamburg. Bird diversity was assessed as species richness, abundance, and Shannon index. Additionally, evenness was calculated. Both urbanization measures represented a rural-to-urban gradient and were negatively correlated with bird diversity as well as evenness. At the site scale, the degree of sealing had the strongest negative effect on bird diversity followed by the portion of traffic infrastructure and the tallest building. At the local scale, artificial surfaces proved to have the strongest negative effect, while agricultural areas and forests were positively associated with bird diversity. In general, models using the site scale for measuring urbanization showed higher associations with diversity. The results emphasize the importance of unsealed areas in the urban environment and of natural habitats in the periphery for bird diversity in Central European cities with millions of human inhabitants. Considering this for future city planning can help to preserve biodiversity in the urban environment, increase bird diversity in development areas, and thus improve living conditions for people.

**Keywords** Urban ecology · Urban gradient · Land-cover classes · Bird diversity · Germany

## Introduction

An increasing portion of people live in cities (United Nations 2018) which favors urban sprawl as well as densification (Patacchini et al. 2009; Haaland & van den Bosch 2015), and results in urbanization being one of the fastest growing land uses worldwide (United Nations 2019). In contrast, along with climate change, urbanization poses one of the largest threats for biodiversity and wildlife as it is considered one of the main factors for habitat loss and degradation (Grimm et al. 2008; Isaksson 2018).

In order to examine the impact of urbanization on biodiversity, this study uses bird diversity as a bioindicator, since birds are highly mobile animals and are, therefore, able to quickly adapt to changing environment. This makes them ideal for studying fast changing ecological conditions as, for example, in urban environments (Concepción et al. 2015). Additionally, in comparison to other vertebrates, birds can easily be monitored facilitating a dense survey of a large area.

Previous studies reported different responses in different species: Whereas some bird species thrive in the urban environment, more specialized species are not able to adapt to these conditions (McKinney 2002; Leveau 2013). Among the thriving species are generalists, which have adapted to the urban environment and exploit characteristics exclusive to such habitats (Carbó-Ramírez and Zuria 2011; Le Viol et al. 2012). These characteristics include for example the urban heat island, which can favor invasive species and elongate the breeding season for all bird species enabling more breeding attempts per season (Isaksson 2018; Reynolds et

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al. 2019). However, many species are specialized on certain habitat features due to their feeding and nesting traits and lack the ability to survive without them (Evans et al. 2011; Di Pietro et al. 2021). Especially species depending on, for example, closed tree canopies, wetlands, meadows, or other types of cultural landscapes belong to the urban avoiders, which are rarely found within the urban core and vanish from habitats in which urbanization increases (McKinney 2002). As a consequence, urbanization leads to a biotic homogenization of bird communities which are usually composed of few species and often differ immensely from those in a local natural environment (Blair 2001; McKinney 2006; Morelli et al. 2016). However, even well-adapted species often suffer from fewer offspring per breeding attempt in cities in comparison to rural areas caused by a lower quality of available food sources and higher levels of disturbance (Pollock et al. 2017; Reynolds et al. 2019). These factors also negatively affect the number and body mass of offspring in urban bird communities (Liker et al. 2008; Saccavino et al. 2018).

Therefore, numerous previous studies investigated and identified drivers of bird diversity in urban environments (Clergeau et al. 2006; McKinney 2008; Aronson et al. 2014). Studies reported bird diversity being inversely correlated with impervious surfaces and building density, respectively (Chace and Walsh 2006; Beninde et al. 2015), while the portion of green areas (Jokimäki 1999; Tzortzakaki et al. 2018), water bodies (Ferenc et al. 2014b), agricultural areas, especially pastures (Söderström et al. 2001), and woody vegetation (Sandström et al. 2006; Ferenc et al. 2016) increase bird diversity. Additionally, the importance of the size of such habitats is frequently emphasized as there is a species-area relationship in the urban environment resulting in a higher bird diversity in larger habitat patches (Ferenc et al. 2014a). Further on, increasing number of people and traffic are associated with increasing levels of urbanization, resulting in more anthropogenic disturbances and higher levels of stress on birds (Kekkonen 2017). The disturbances include noise, light, and chemical pollution and have been reported to negatively affect birds (Grimm et al. 2008; Isaksson 2018).

As these patterns have been studied, especially, in temperate zones across the world (e.g. Aronson et al. 2014) and most parts of Europe focusing on its western and northern parts (e.g. Clergeau et al. 2006; Evans et al. 2009), general patterns can be expected to return in Hamburg. However, in Central Europe there are only few comparable studies for investigating bird diversity on a rural-to-urban gradient or the role of land-cover classes within large cities (e.g. Meffert and Dziock 2013; Planillo et al. 2021) and none for Hamburg and NW Germany in general. Yet, to further understand the effects of urbanization and in respect to additional structural changes in the future such as the transition to more sustainable energy and traffic, gaining more knowledge of the impacts and drivers of urbanization on bird diversity in large cities will make adequate management actions possible and improve city planning.

Therefore, this study attempts to identify quantitative predictors for bird diversity across Hamburg. However, the explanatory power of these predictors strongly depends on the applied scale. Studies at site scale are able to identify environmental conditions which influence species' access to important resources and nesting sites as well as their exposure to anthropogenic disturbances (McKinney 2008) and represent the high heterogeneity of urban areas (Savard et al. 2000). Using local and larger scales portrays overall distribution patterns in (urban) ecosystems as for example the influence of land use (McKinney 2008). In this respect, the study applies both methods to quantify urbanization. One at a site scale using three variables within a 100-m radius (i.e. degree of sealing, portion of traffic infrastructure, and the number of floors of the highest buildings) which represent the urbanization of a sampling site and can indicate environmental conditions. The site scale approach also includes the distance from the city center as a fourth variable, since it has been successfully used in several previous studies and indicates anthropogenic disturbances as well (Leveau and Leveau 2016; Callaghan et al. 2018; Yang et al. 2020). The second method uses a local scale with land-cover classes for a 1000-m radius around sampling sites to predict the influence of land use on birds. Additionally, covariables (i.e. weather data, location in form of latitude and longitude as well as the time of day and year) were included in the models to assess their influence on bird diversity.

We hypothesized that 1) bird diversity, abundance and evenness are influenced by both site scale (urbanization characteristics) and local scale (land-cover classes). At site scale, diversity parameters and evenness decrease with 2a) higher degrees of sealing, 2b) an increasing portion of traffic infrastructure, and 2c) the number of floors of the highest building, while we expected 2d) an increase in bird diversity and eveness with an increasing distance from the city center. At local scale, we hypothesized that 3a) artificial surfaces have a negative impact on bird diversity, whereas 3b) agricultural areas, 3c) forests and seminatural areas, and 3d) water bodies and wetlands positively influence diversity parameters and evenness.

## Methods

### Study area

The study was conducted in Hamburg (53° 33' N, 59° 36' E), which is the second largest city in Germany with 1.9 million inhabitants (Statistik Nord 2021). The climate is temperate with maritime influences, an average temperature of 9.4 °C, and average precipitation levels of 796 mm (DWD 2021). Hamburg covers an area of 755 km² which consists of a large urban core as well as agricultural areas and forests which are mostly situated in the south (Fig. 1). The city is well vegetated and has numerous urban green spaces. The quarter Neuwerk (7.6 km²) which lies 100 km NW of the city in the North Sea was excluded from the study.

## Site selection

To account for the diversity of the city, sites were distributed over the entire area of Hamburg by overlaying a 1-km² grid using QGIS (version 3.18.1, QGIS Development Team 2021) and counting once in every grid cell when accessible by public roads. Sites were chosen as close to the center of each grid cell as possible to avoid being unconsciously influenced when randomly assigning sampling sites and improve their even distribution. In areas with buildings, crossroads were preferably picked for counting to assure at least three axis of sight and thereby improve comparability to more rural areas where the view is not obstructed by any buildings. Sites were at least 500 m away from each other to avoid duplicate counts (Gregory 2004). In total, 761 sites were visited. They were identified remotely in advance and located by GPS. To account for other variables influencing bird activity such as weather, time of day and year etc., the following system was developed to assure that no additional variables could be associated with the degree of urbanization and therefore influence the results: Every counting day was restricted to one administrative district Which were counted in the same sequence for the entire study period. The counting order of the districts allowed for a high distance between sites on succeeding days. As there are seven districts and two adjacent districts (Eimsbüttel and Hamburg-Nord) were seen as one unit because of their comparably smaller size, one "counting cycle" consisted of six days. To control for time of day differences in bird detectability

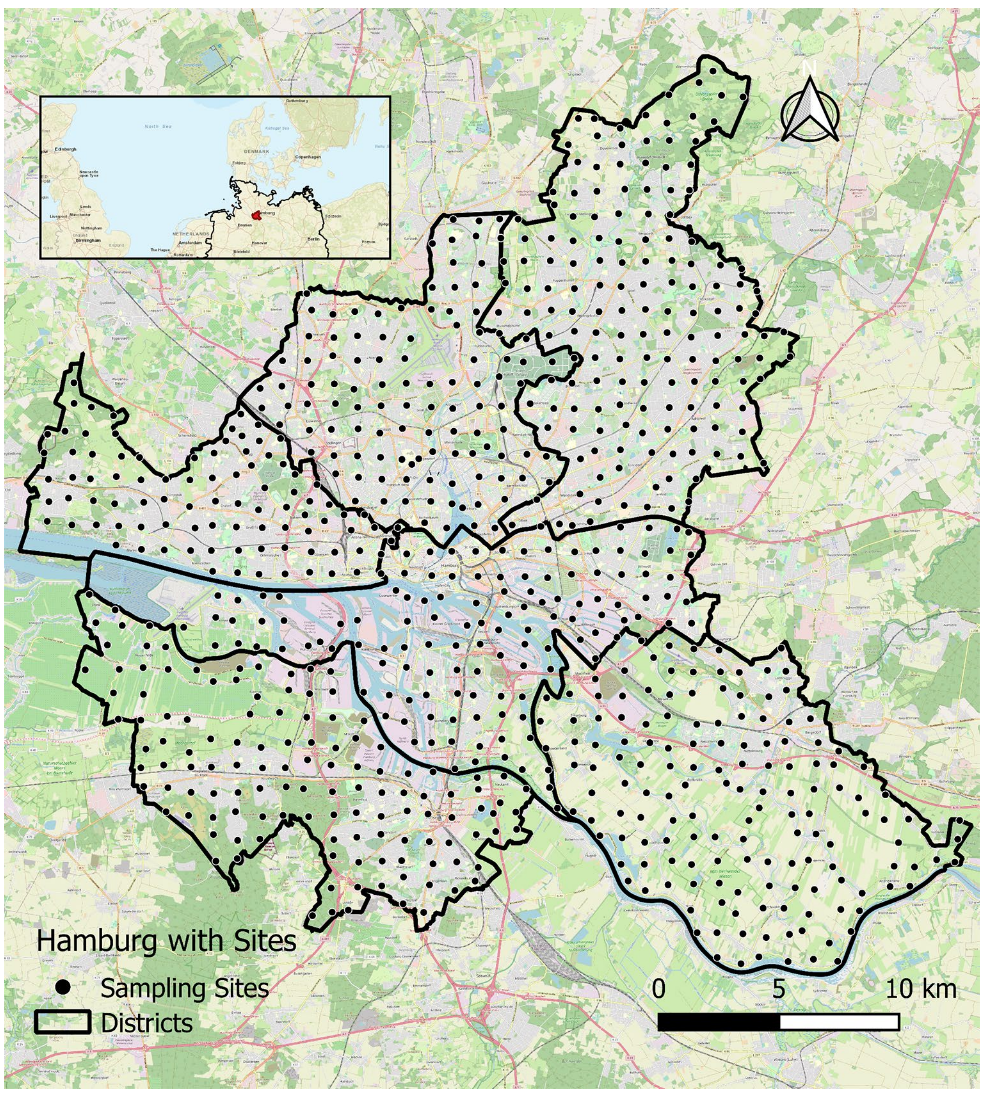


**Fig. 1** Map of Hamburg (Germany) with sampling sites and borders of districts as used for this study. The districts Hamburg-Nord and Eimsbüttel were combinded. The upper left panel shows the geographic location of the study area. Irregularities in the distribution pattern of sampling sites are due to inaccessible areas (e.g. airports, agricultural areas, water bodies, the port). Background map from OpenStreetMap

counts in subsequent cycles were performed on alternating urbanization gradients: In the first cycle, sites started in a highly urban zone and moved to a less urban area throughout the day, whereas the second one was performed on a rural-to-urban gradient.

## Bird survey

Each site was visited ones. On site a point count was performed, during which all birds seen or heard within a 50 m radius and for a fixed 10-min period were recorded (Bibby et al. 2000), since this time interval is considered a good compromise to detect higher species numbers and avoid double counts (Ralph et al. 1995). The 50 m radius was chosen to increase comparability between different sites since auditive detection is limited close to noise sources such as streets. Additionally, differences in visual detectability are reduced when counting in a small radius resulting in a better comparability between open sites such as farmlands and buildings and forests. All counts were carried out by A.H. on 34 days during breeding season (April 12th to June 17th 2021) and over the entire day, however, primarily starting in the early morning. Days with strong winds and high amounts of rain were avoided to minimize the impact of unfavorable weather conditions.

## Additional data collection

Additional data were collected on site including the number of floors of the highest building in a 100-meter buffer zone as well as weather data. Weather data were collected using two methods. Before counting, wind speed and temperature were copied from the website of the Deutscher Wetterdienst (DWD; German Meteorological Service) for the weather station Hamburg Airport which is updated hourly (DWD 2021). In addition, rain intensity and cloud coverage were classified on site into four and three categories, respectively.

## Data analysis

All analyses and statistical tests were performed in R 4.1.0 (R Core Team 2021). All plots were constructed using the R package ggplot2 (Wickham 2016) and all tables were created using the package sjPlot (Lüdecke 2021). Maps were created in QGIS (version 3.18.1, QGIS Development Team 2021). $p<0.05$ was considered as significant and $|r| > 0.7$ was regarded as a strong correlation.

## Weather data

A principal component analysis (PCA) was chosen to minimize the effects of multicollinearity and reduce the number of variables. Since the first principal component only explained 36% of the variance, the first two principal components (PC1W, PC2W) were kept for further analysis as they together explained 64% of the variance (Table 1).

**Table 1** Loadings and summary for the first two principal components for the PCA of weather variables

| | PC1W | PC2W |
|---|---|---|
| Temperature | 0.58 | -0.58 |
| Windspeed | -0.20 | -0.83 |
| Rainfall | -0.64 | -0.28 |
| Cloud coverage | -0.81 | 0.03 |
| Standard deviation | 1.20 | 1.05 |
| Proportion of variance | 0.36 | 0.27 |
| Cumulative proportion | 0.36 | 0.64 |

**Table 2** Loading and summary for the first principal component (PCUrb) for the PCA of urbanization variables

| | PCUrb |
|---|---|
| Sealing | -0.81 |
| Floors of highest building | -0.88 |
| Distance from city center | 0.73 |
| Traffic proportion | -0.15 |
| Standard deviation | 1.51 |
| Proportion of variance | 0.57 |

## Degree of urbanization

In this approach to describe urbanization, building coverage and the portion of traffic infrastructure at a site scale of a 100-m radius were calculated using the raster package (Hijmans 2021) and sealing data (BUKEA 2017) or land-cover data (EEA 2018), respectively, as these are key indicators for urbanization (Bowman and Marzluff 2001; Liker et al. 2008; Szulkin et al. 2020). The number of floors of the highest building was chosen as an additional variable as building height constitutes a proxy for urbanization and can easily be determined on site (Schäfer et al. 2017; Szulkin et al. 2020). Additionally, the distance from the city center (Hamburg's geographical center; Leveau and Leveau 2016) was considered in the study. Since these variables are not independent from one another and therefore correlate, a PCA was conducted to create one urbanization measurement combining the four variables (Elle 2005). The first principal component (PCUrb) explained 56% of the variance and was further on used as a measure for urbanization (Table 2).

## Land-cover types

For the second method to describe urbanization, land-cover data provided by the Urban Atlas Map (EEA 2018) was rasterized in QGIS and imported into R to extract the percentage of land-cover types for each site at a local scale with 1000-m buffer zones. Land-cover types were also calculated within Hamburg's administrative borders to assure the efficiency of site selection in representing Hamburg. Land-cover types were sorted into their five main classes (artificial surfaces, agricultural areas, forests and seminatural areas, water bodies, and wetlands), whereas the last two were treated as one, since wetlands covered less than 0.2% of the study area and both habitat types attract a similar avifauna. Due to intercorrelations, a PCA was conducted for the main classes. The first principal component explained 51% of the variance and was used as the second measure for urbanization (Table 3).

### Bird diversity assessment

Bird diversity was assessed in terms of species richness (number of species, nSp), bird abundance (number of individuals, nInd), and Shannon index for each site. Additionally, evenness was calculated for each site. The three diversity parameters were tested for spatial autocorrelation using the Mantel Test and Moran's I. Statistical significances for both were calculated using Monte Carlo simulations with 999 randomizations. To examine the impact of urbanization on threatened species their occurrence was measured for each site by evaluating either their presence or absence.

### Effect of urbanization on the avifauna

A log-transformation was implemented on the number of individuals (nIndlog) to down-weight the influence of extreme values. The Shannon index and evenness were square-transformed (ShannonSquare, EvennessSquare) to correct left-skewed data distribution. A generalized linear model (GLM) with a Poisson error was carried out for the count data nSp and GLMs with a normal distribution of error were performed on ShannonSquare, EvennessSquare as well as on nIndlog to determine the effects of urbanization on bird diversity and abundance. Additionally, the effect of urbanization on threatened species (Red List for Hamburg's breeding birds; Mitschke 2018) was tested by carrying out GLMs with a binominal error. Due to a high correlation, the effects of the two urbanization measures were calculated in separate models. To test for general patterns and verify that the dataset follows common patterns the time of day, date, longitude, and latitude of sites as well as weather variables (PC1W, PC1W) were used as covariables.

**Table 3** Loading and summary for the first principal component (PCLC) for the PCA of land-cover classes

| | PCLC |
|---|---|
| Agricultural areas | 0.91 |
| Artificial surfaces | -1.00 |
| Forest and seminatural areas | 0.37 |
| Water bodies and wetlands | 0.16 |
| Standard deviation | 1.42 |
| Proportion of variance | 0.51 |

## Results

### Bird survey

Between 1 and 20 bird species were found at each site (average 8.9 species). In total 11,753 individuals representing 119 species (including three hybrids) were recorded in this study. The most common species was the Common Wood Pigeon (*Columba palumbus*, 71.4% of sampling sites), followed by the Great Tit (*Parus major*) which was found on 58.5% of sampling sites and the Common Chiffchaff (*Phylloscopus collybita*) with a frequency of 54.1%. Among the recorded breeding species, 13 are classified as threatened in Germany (Red List categories 3: vulnerable (n = 7), 2: endangered (n = 5), 1: critically endangered (n = 1), 0: extinct (n = 0); Grüneberg et al. 2015) and 20 breeding bird species are threatened in Hamburg (Red List categories 3: vulnerable (n = 8), 2: endangered (n = 7), 1: critically endangered (n = 4), 0: extinct (n = 1); Mitschke 2018; Appendix 1). Species richness, abundance, diversity, and evenness.

There was a significant increase in the number of individuals and species as well as the Shannon index and evenness from the center to the outskirts of the city: both urbanization measures had a highly significant effect on all three diversity measures (Table 4). All variables included in the GLMs had a significant effect on the number of individuals. The only highly significant covariable in all models was the time of the point count, although, weather parameters and the degree of longitude and latitude reached significant importance in some models (Tables 5 and 6). In neither of the two tests for spatial autocorrelation any significant values could be detected.

### Site selection system

The system which was developed for site selection showed to be highly efficient. As it could have been expected, an increasing time of day significantly reduced the recorded bird diversity as well as the detected species and individuals. However, neither the time of day nor the other bird activity determining factors included in the analysis (date and weather) correlate with any of the two urbanization measurements (Table 4). This shows that due to the developed system differences in the diversity measurements can be explained by differences in urbanization rather than any of the covariables.

**Table 4** Correlation coefficients r from a Pearson correlation between all covariables included in the GLMs, diversity parameters and evenness as well as urbanization measures (upper half), as well as between the four original urbanization variables used in the PCA for PCUrb (Building: the number of floors of the highest building, Distance: distance from the city center, Sealing: degree of sealing, Traffic: portion of traffic infrastructure),diversity parameters, evenness and urbanization measures (lower half)

| | Date | Time | Latitude | Longitude | PC1W | PC2W |
|---|---|---|---|---|---|---|
| **nSp** | -0.031 | -0.232 | -0.070 | 0.152 | -0.110 | 0.232 |
| **ShannonSquare** | -0.038 | -0.201 | 0.026 | 0.079 | -0.066 | 0.199 |
| **nIndlog** | -0.139 | -0.152 | -0.150 | 0.173 | -0.149 | 0.208 |
| **EvennessSquare** | -0.034 | -0.178 | 0.076 | 0.039 | -0.042 | 0.172 |
| **PCLC** | 0.049 | 0.049 | -0.323 | 0.171 | 0.064 | 0.060 |
| **PCUrb** | -0.011 | 0.066 | -0.151 | 0.122 | 0.048 | 0.005 |
| | Building | Distance | Sealing | Traffic | PCLC | PCUrb |
| **nSp** | -0.361 | 0.265 | -0.529 | -0.347 | 0.330 | 0.505 |
| **ShannonSquare** | -0.367 | 0.269 | -0.507 | -0.351 | 0.275 | 0.501 |
| **nIndlog** | -0.189 | 0.183 | -0.373 | -0.251 | 0.239 | 0.334 |
| **EvennessSquare** | -0.350 | 0.252 | -0.461 | -0.314 | 0.287 | 0.454 |
| **PCLC** | -0.503 | 0.715 | -0.654 | -0.260 | | 0.726 |
| **PCUrb** | -0.795 | 0.728 | -0.887 | -0.565 | 0.726 | |

## Effect of urbanization on bird diversity, evenness and threatened species

GLMs showed a highly significant increase for all three diversity parameters as well as a higher evenness when PCUrb increased. The degree of sealing, number of floors of the highest building, and the portion of traffic infrastructure were negatively correlated with PCUrb ($r = -0.89$, $r = -0.80$, $r = -0.57$, respectively) while the distance from the city center was positively correlated ($r = 0.73$; Table 4). Therefore, low values of PCUrb can be interpreted as a high degree of urbanization meaning that an increasing urbanization significantly decreases bird diversity and abundance (Fig. 2). The GLM for the occurrence of a threatened species showed a highly significant link between the appearance of a threatened species and PCUrb. With increasing values of PCUrb (and thereby a decreasing degree of urbanization) the odds of recording a threatened species increases (Table 7). Pearson correlations between the variables used for the PCA for PCUrb and the diversity parameters identified the degree of sealing as the most important predictor followed by the number of floors of the highest building, the portion of traffic infrastructure, and the distance from the city center (Table 4).

## Effect of landcover classes on bird diversity, evenness and threatened species

Calculating the land-cover classes on a local scale around each site showed that site selection was highly efficient in representing land-cover distribution in Hamburg ($r = 0.999$, $p < 0.001$). The most frequent land cover was artificial surfaces covering 62.6% of the buffer zones of sampling sites, followed by agricultural areas with 24.6%, forests and seminatural areas with 7.2%, and water bodies and wetlands with 5.6%. Models revealed a highly significant increase for all three diversity parameters as well as a higher evenness when PCLC increased. High values of PCLC represent a high portion of agricultural areas as well as forests and seminatural areas, while low values represent artificial surfaces (Table 3). Thereby, PCLC describes an urbanization gradient and shows that an increasing urbanization significantly decreases bird diversity and abundance. The GLM for the occurrence of a threatened species showed a significant link between the appearance of a threatened species and PCLC. With increasing values of PCLC (and thereby a decreasing degree of urbanization) the odds of recording a threatened species increases (Table 7). Pearson correlations identified artificial surfaces as the most influential land-cover class for all diversity parameters followed by agricultural areas and forests and seminatural areas. Water bodies and wetlands only had an effect on bird abundance (Table 8).

# Discussion

The study examined the influence of the urban environment on bird diversity and highlights the negative impact of urbanization not only on species richness and diversity but also on bird abundance. We found both site scale (site urbanization characteristics) and local scale (land-cover classes) to influence all three diversity measures. Confirming our hypotheses, the degree of sealing, portion of traffic infrastructure, number of floors of the highest building as well as the percentage of artificial surfaces had a negative impact on bird diversity, while it was positively influenced by the distance from the city center, agricultural areas as well as forests and seminatural areas. Contrary to our hypothesis, models showed that water bodies and wetlands had neither influence on bird diversity nor species richness. While there

**Table 5** Results of the final GLMs for the diversity parameters: Shannon index (ShannonSquare), number of individuals (nIndlog), and the number of species (nSp) as well as evenness (EvennessSquare) with the urbanization measure PCUrb and covariables. Significant p-values are represented by bold font

| | nIndlog | | | nSp | | | ShannonSquare | | | EvennessSquare | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Predictors | Estimates | CI | p | Incidence Rate Ratios | CI | p | Estimates | CI | p | Estimates | CI | p |
| **PCUrb** | 0.13 | 0.11–0.16 | **< 0.001** | 1.16 | 1.14–1.18 | **< 0.001** | 0.58 | 0.52–0.65 | **< 0.001** | 0.55 | 0.48–0.62 | **< 0.001** |
| **Time of day** | -0.73 | -1.08 – -0.39 | **< 0.001** | 0.52 | 0.41–0.67 | **< 0.001** | -2.27 | -3.17 – -1.36 | **< 0.001** | -1.96 | -2.91 – -1.01 | **< 0.001** |
| **Date** | 0.00 | -0.01 – -0.00 | **< 0.001** | 1.00 | 1.00–1.00 | 0.580 | 0.00 | -0.01–0.00 | 0.436 | 0.00 | -0.01–0.00 | 0.577 |
| **Longitude** | 0.35 | 0.07–0.63 | **0.014** | 0.94 | 0.78–1.14 | 0.555 | -0.90 | -1.63 – -0.17 | **0.017** | -1.20 | -1.97 – -0.44 | **0.002** |
| **Latitude** | -1.33 | -1.77 – -0.88 | **< 0.001** | 0.66 | 0.49–0.89 | **0.007** | 0.04 | -1.13–1.21 | 0.944 | 1.15 | -0.07–2.38 | 0.064 |
| **PC1W** | -0.06 | -0.09 – -0.03 | **< 0.001** | 0.96 | 0.94–0.98 | **< 0.001** | -0.09 | -0.17 – -0.01 | **0.035** | -0.05 | -0.13–0.04 | 0.290 |
| **PC2W** | 0.04 | 0.00–0.09 | **0.043** | 1.03 | 1.00–1.06 | 0.058 | 0.11 | 0.00–0.22 | **0.044** | 0.10 | -0.02–0.21 | 0.103 |
| Observations | 761 | | | 761 | | | 761 | | | 760 | | |
| $R^2$ | 0.245 | | | 0.496 | | | 0.318 | | | 0.267 | | |

are some contradictions to existing research, the results mainly confirm findings of previous studies (Clergeau et al. 1998; Chace and Walsh 2006; McKinney 2008; Aronson et al. 2014; Beninde et al. 2015) for Hamburg.

## Effect of urbanization and land usage on bird diversity and evenness

Overall, an increase in both urbanization measurements as well as all original urbanization variables which were included in these measurements had a negative effect on bird diversity. In particular, the findings identified the degree of sealing as the most impactful of the original variables on diversity measurements and evenness. Its highly negative effect on bird diversity is consistent with several previous studies (McKinney 2008; Meffert and Dziock 2013; Carvajal-Castro et al. 2019). With an increasing portion of impervious surfaces, birds lose habitable area (Morelli 2021). Species depending on green spaces and tree coverage for breeding suffer from fewer nesting sites (Chace and Walsh 2006; Evans et al. 2009) and areas for foraging are reduced which impacts for example invertebrate abundance (McDonnell and Hahs 2008; Planillo et al. 2021). Alongside a quantitative reduction in habitable areas their quality will decrease as well in urban areas (McKinney 2008). Size as well as structural diversity decreases in green spaces in the urban environment while anthropogenic disturbances increase (Fontana et al. 2011; Paker et al. 2014; Mühlbauer et al. 2021). The increase in anthropogenic disturbances can, among other things, be seen in a higher level of disturbances caused by traffic. Higher portions of traffic infrastructure decrease species richness and abundance caused by increasing noise and pollution levels (Grimm et al. 2008; Isaksson 2018; Amaya-Espinel 2019). Furthermore, building height had a negative impact on bird diversity. Higher buildings usually provide fewer resources in their proximity compared to smaller, detached buildings which are surrounded by a greater cover of vegetation (Leveau 2013) and are often associated with higher pedestrian and car traffic (Leveau and Leveau 2016). These factors are known to negatively affect bird diversity (Fernández-Juricic 2001; Mühlbauer et al. 2021). Additionally, both traffic and high buildings have been reported as major anthropogenic threat through collisions that kill and injure a high number of birds every year (Erritzoe et al. 2003; Loss et al. 2014; Van Doren et al. 2021). The negative impact of sealing, traffic infrastructure and building height is represented as well by the influence on the different types of land use. Accordingly, an increasing portion of artificial surfaces had a highly negative effect on all diversity measurements. In contrast, land-cover types indicating unsealed and seminatural areas such as agricultural areas and forests had a positive effect on bird

**Table 6** Results of the final GLMs for the diversity parameters: Shannon index (ShannonSquare), number of individuals (nIndlog), and the number of species (nSp) as well as evenness (EvennessSquare) with the urbanization measure PCLC and covariables. Significant p-values are represented by bold font

| Predictors | nIndlog | | | nSp | | | ShannonSquare | | | EvennessSquare | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Estimates | CI | p | Incidence Rate Ratios | CI | p | Estimates | CI | p | Estimates | CI | p |
| **PCLC** | 0.07 | 0.05–0.10 | **<0.001** | 1.09 | 1.07–1.11 | **<0.001** | 0.36 | 0.28–0.43 | **<0.001** | 0.34 | 0.26–0.42 | **<0.001** |
| **Time of day** | -0.61 | -0.96 – -0.25 | **0.001** | 0.60 | 0.46–0.77 | **<0.001** | -1.71 | -2.71 – -0.70 | **0.001** | -1.43 | -2.46 – -0.40 | **0.007** |
| **Date** | 0.00 | -0.01 – -0.00 | **<0.001** | 1.00 | 1.00–1.00 | 0.28 | 0.00 | -0.01–0.00 | 0.203 | 0.00 | -0.01–0.00 | 0.305 |
| **Longitude** | 0.67 | 0.39–0.95 | **<0.001** | 1.35 | 1.11–1.63 | **0.002** | 0.51 | -0.27–1.30 | 0.202 | 0.12 | -0.68–0.93 | 0.766 |
| **Latitude** | -1.06 | -1.54 – -0.59 | **<0.001** | 0.86 | 0.63–1.17 | 0.328 | 1.33 | 0.00–2.66 | 0.051 | 2.39 | 1.03–3.75 | **0.001** |
| **PC1W** | -0.06 | -0.09 – -0.02 | **0.001** | 0.96 | 0.94–0.98 | **0.001** | -0.07 | -0.16–0.02 | 0.121 | -0.03 | -0.12–0.06 | 0.522 |
| **PC2W** | 0.04 | 0.00–0.09 | **0.050** | 1.03 | 1.00–1.06 | **0.047** | 0.11 | -0.01–0.24 | 0.071 | 0.09 | -0.03–0.22 | 0.139 |
| Observations | 761 | | | 761 | | | 761 | | | 760 | | |
| $R^2$ | 0.177 | | | 0.320 | | | 0.163 | | | 0.134 | | |

diversity. This is due to an increase in the quantity as well as the quality of habitats and additionally lower disturbance levels (Leveau and Leveau 2016). Both agricultural areas as well as forest constitute foraging and breeding grounds to a variety of species including more specialized ones which increases the overall bird diversity (Sandström et al. 2006; Ferenc et al. 2016). Naturally, these landcover types were found mostly in the periphery, especially the southeast of Hamburg, explaining the significance of longitude and latitude in some models. This is also shown by the correlation of longitude and latitude with both urbanization measurements (Table 4). Sealed surfaces and artificial areas, on the other hand,were characteristic to the urban core. This explains the positive effect of an increasing distance to the city center which has been found in other studies as well (Leveau and Leveau 2016).

These effects also explain the increasing odds for the occurrence of a threatened species with decreasing urbanization. High degrees of the site scale urbanization measurement (PCUrb) have a negative effect on threatened species showing that, especially, these species profit from green areas and seminatural landscapes. Since many of these species are specialized on certain habitats, both agricultural areas and forest with a high structural diversity constitute important breeding and foraging grounds.

While the effects of the previous urbanization variables have been found in several other cities as well. Interestingly, the usually positive effect of water bodies on species richness and diversity in urban environments (Melles et al. 2003; Ferenc et al. 2014b) could not be confirmed for Hamburg. This is due to a distinctive yet highly interesting characteristic of the city of Hamburg; the river Elbe and its usage. The Elbe accounts for a considerable portion of the city's water bodies, however, it does not provide much habitable areas in its immediate surroundings. The appearance of the river is strongly determined by anthropogenic influences which increases towards Hamburg's center. This includes the port, which is the third biggest in Europe and reaches the highest urbanization values on the site scale. Consequently, the port has also been the area with the overall lowest species counts (Fig. 3). Still, the map (Fig. 3) shows high numbers of species for sampling sites close to some water bodies such as the Outer Alster Lake (a lake in the city center). These findings indicate that there might be a positive effect of water bodies for bird diversity and species richness in Hamburg which, however, is counterbalanced by the negative influence of the large port along the river Elbe. Furthermore, overall bird abundance is positively affected by the portion of water bodies indicating its importance for some species (Ferenc et al. 2014b).

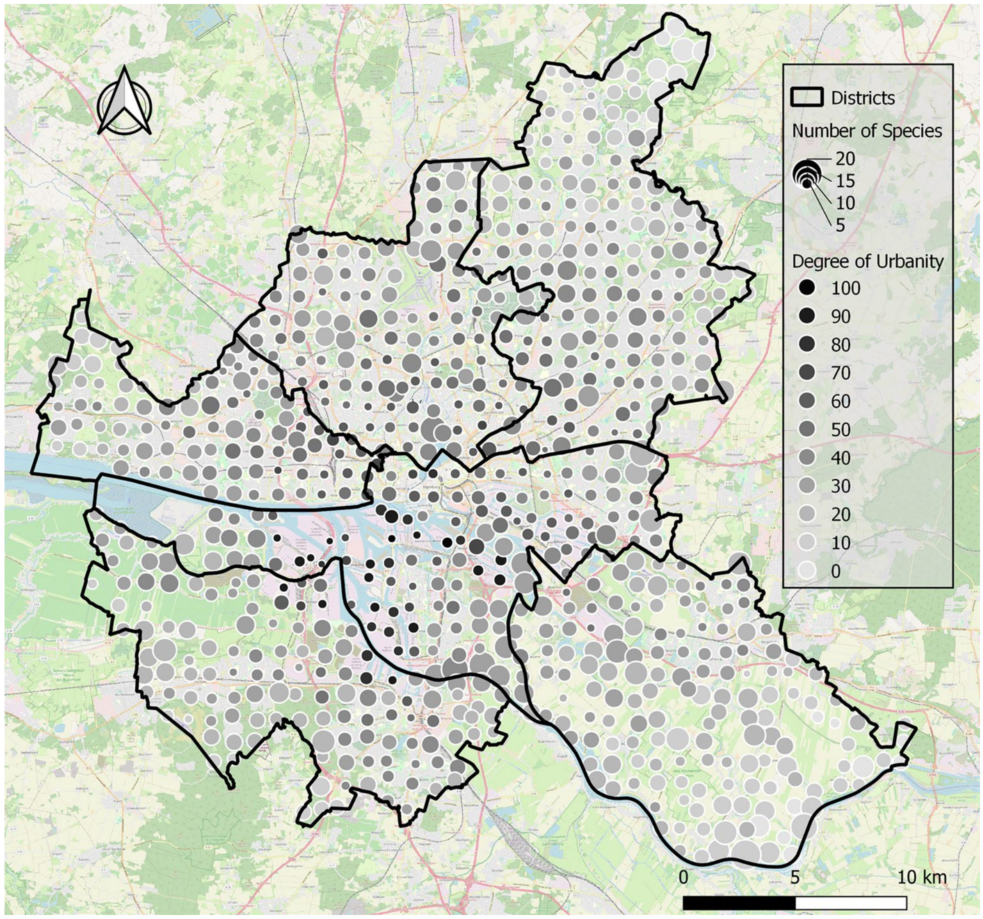


**Fig. 2** Map of Hamburg (Germany) with sampling sites and district borders as used for this study. The number of species (nSp) is displayed by point size of the sampling site. The urbanization gradient is represented by PCUrb, which was inversed and scaled to values between 0 and 100% for illustrative purposes. Background map from OpenStreetMap

**Table 7** Results of the GLMs for the occurrence of a threatened species for both urbanization measurements (PCUrb, PCLC). Significant p-values are represented by bold font

| | Occurence of a threatened species (PCUrb) | | | Occurence of a threatened species (PCLC) | | |
|---|---|---|---|---|---|---|
| Predictors | Odds Ratios | CI | p | Odds Ratios | CI | p |
| **PCUrb** | 1.33 | 1.18–1.51 | **< 0.001** | | | |
| **PCLC** | | | | 1.15 | 1.03–1.29 | **0.015** |
| **Time of day** | 0.68 | 0.14–3.19 | 0.624 | 0.90 | 0.19–4.19 | 0.891 |
| **Date** | 1.00 | 0.99–1.01 | 0.942 | 1.00 | 0.99–1.01 | 0.962 |
| **Longitude** | 18.49 | 5.13–68.62 | **< 0.001** | 34.99 | 10.06–126.07 | **< 0.001** |
| **Latitude** | 0.00 | 0.00–0.02 | **< 0.001** | 0.00 | 0.00–0.03 | **< 0.001** |
| **PC1W** | 0.84 | 0.73–0.97 | **0.018** | 0.85 | 0.74–0.98 | **0.028** |
| **PC2W** | 0.86 | 0.71–1.04 | 0.132 | 0.87 | 0.72–1.05 | 0.147 |
| Observations | 761 | | | 761 | | |
| $R^2$ Tjur | 0.127 | | | 0.107 | | |

**Table 8** Correlation coefficients from Pearson correlations for the diversity parameters as well as evenness and land-cover classes

| | Agricultural areas | Artificial surfaces | Forest and seminatural areas | Water bodies, wetlands |
|---|---|---|---|---|
| **ShannonSquare** | 0.217 | -0.256 | 0.208 | -0.077 |
| **nSp** | 0.302 | -0.333 | 0.143 | 0.025 |
| **nIndlog** | 0.261 | -0.260 | < 0.000 | 0.110 |
| **EvennessSquare** | 0.162 | -0.208 | 0.235 | -0.118 |

## Evaluation of site selection system

The system which was developed for site selection showed to be highly efficient. Neither the time of day nor the other bird activity determining factors included in the analysis (date and weather) correlate with any of the two urbanization measurements. This shows that due to the developed system differences in the diversity measurements can be explained by differences in urbanization rather than any of

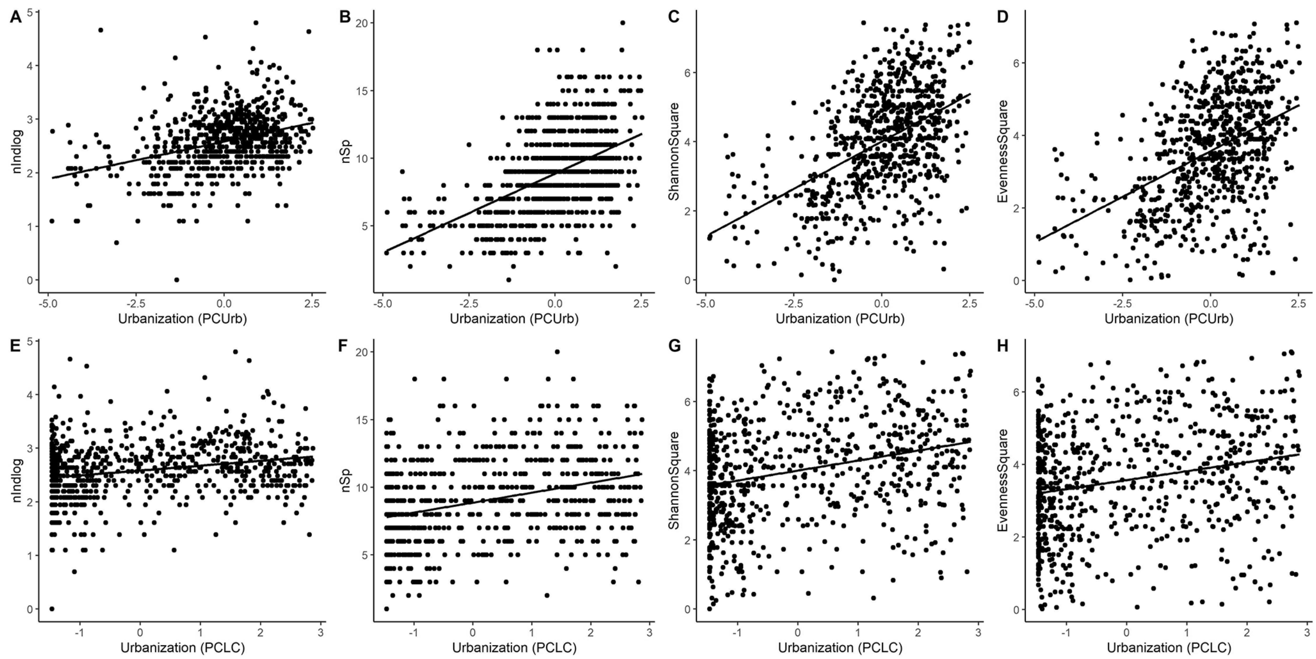


**Fig. 3** Regression plots representing the relationship between the diversity parameters Shannon index (ShannonSquare), number of species (nSp), bird abundance (nIndlog) as well as evenness (EvennessSquare) and the two urbanization measures PCUrb and PCLC. Low values of PCUrb and PCLC represent high degrees of urbanization or a high portion of artificial surfaces, respectively. This figure serves an illustrative purpose only, since Results and Discussion are based on results obtained from GLMs

the covariables. Therefore, adapting this site selection system in other cities for similar studies can help to reduce the impact of confounding variables and improve comparability between studies. Additionally, this approach enables performing counts over the entire day and thereby allows large sampling sizes within a short period of time.

## Evaluation of model and scale differences

Both methods for measuring urbanization proved to be effective in providing a virtual rural-to-urban gradient and differentiating between habitat characteristics. However, the urbanization measure at site scale showed to be superior in comparison to defining the degree of urbanization by land-cover classes at a local scale. The association between diversity parameters as well as evenness and PCUrb showed to be higher and the first principal component captured more of the variance of the original variables. Additionally, the models using PCUrb instead of PCLC had a higher fit, as they explained a higher proportion of variance. While the number of species could be explained well with the chosen variables, models with either measure for urbanization had relatively low $R^2$-values for nIndlog indicating that this diversity parameter has dependencies which have not been considered in this study.

A reason for model differences and partly low fits might be the solely quantitative measurement for both urbanization measures whereas qualitative differences within the chosen variables have not been investigated. Several studies reported that the structure of green spaces (Fontana et al. 2011; Mühlbauer et al. 2021), woody vegetation (Jokimäki 1999; Sandström et al. 2006), and agricultural areas (Fischer et al. 2011; Ekroos et al. 2019) have a strong influence on bird diversity and abundance. This can also explain the differences in the number of species within highly urban areas. Hamburg's urban core is highly sealed, however, differences in the quality of tree coverage are apparent and can often be associated with age of the surrounding buildings. In comparison, development areas usually miss these older vegetation structures and therefore often show a lower bird diversity (Clergeau 1998). Future studies should therefore focus on these factors to confirm their effects for Hamburg and to further understand predictors for bird diversity. Another aspect that was not included in the study is the influence of human activity during point counts, which was reported to have an impact on bird diversity (Fernández-Juricic 2000; Tomasevic & Marzluff 2017).

Another reason for the overall better performance of the models with PCUrb might be the chosen radius. Although birds are highly mobile animals, resources are needed in close proximity to their nesting sites (Mühlbauer et al. 2021). This is shown by all diversity parameters having strong responses to the chosen variables for urbanization at site scale, since they can predict availability of such resources to a certain degree. Especially, the degree of sealing which was the most influential environmental variable influences bird diversity since unsealed areas are important breeding and foraging grounds. Therefore, this variable should be included in future studies if such data is available. The additionally used variables (building height and proportion of traffic infrastructure) support explaining more of the variance of the urban environment as they define the character of the sealed surfaces in the studies radius further. However, adding more variables to the principal component analysis which can characterize the urban environment in more detail might further improve the explained variance of the urbanization measurement and thereby the performance of the models. Still, in addition to the variables at site scale the surrounding matrix in a larger area does impact some species (Jokimäki 1999; Meffert and Dziock 2013) and especially land-cover classes such as agricultural areas attract more mobile species from higher distances (Schifferli 2000). The portion of artificial surfaces, on the other hand, can explain the overall disturbances levels bird are exposed to and can indicate anthropogenic impact in the overall area. Therefore, using land usage can predict bird diversity on a larger scale. Additionally, it could be used to examine more local factors, however, for lower scaled analyses more subdivided data of land uses should be employed. Nevertheless, the results support the suggestion of other studies that differing scales using different variables should be included in further studies to account for the wide variety of factors which influence bird diversity.

## Conclusion and implications

This study provides evidence how increasing levels of urbanization negatively impact bird diversity as well as evenness in Hamburg. Other studies have shown that this result applies to other European cities and is therefore relevant from a city development perspective. Increasing portions of the population living in cities and thereby the increasing requirement for buildings and traffic infrastructure will lead to further densification and urban sprawl. As it is illusive to stop these processes, they have to be considered in future urban planning. Our research suggests that incorporating unsealed areas in new projects and preserving habitable areas in the urban environment will increase or maintain bird diversity, respectively. While future studies for Hamburg will have to examine how these are best structured, their importance is indisputable. Furthermore, green spaces provide a possibility for humans to experience nature and wildlife, which has been shown to have positive effects on human health (Fuller et al. 2007; Methorst et al. 2021). Additionally, the study has emphasized the importance of Hamburg's periphery for bird diversity as they provide habitats to numerous species which cannot be found in the urban core. This pattern is especially distinctive when it comes to endangered breeding bird species from which many depend on green areas and seminatural landscape in the periphery. In contrast, future development projects will destroy large areas of those habitats resulting in predictions of severe population declines for some species in the next decade (Mitschke 2018).

## Appendix 1

List of bird species observed in Hamburg (including three hybrids), conservation status for Germany (Grüneberg et al. 2015) and Hamburg (Mitschke 2018), occupancy in respect to the number of sampling sites at which the species occurred and the percentage of sampling sites occupied. Taxonomy follows the IOC World Bird List (version 11.2; Gill et al. 2021). Conservation Status according to their breeding status: * = least concern, V = near threatened, 3 = vulnerable, 2 = endangered, 1 = critically endangered, 0 = extinct, empty cells = not classified as native breeding birds (includes invasive species, hybrids and passage migrants).

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**Code Availability** Code is available from the corresponding author upon reasonable request.

## Declarations

**Conflicts of interest** The authors have no competing interests to declare that are relevant to the content of this article.

## References

Amaya-Espinel JD, Hostetler M, Henríquez C, Bonacic C (2019) The influence of building density on neotropical bird communities found in small urban parks. Landsc Urban Plan 190:103578. https://doi.org/10.1016/j.landurbplan.2019.05.009

Aronson MFJ, La Sorte FA, Nilon CH, Katti M, Goddard MA, Lepczyk CA, Warren PS, Williams NSG, Cilliers S, Clarkson B, Dobbs C, Dolan R, Hedblom M, Klotz S, Kooijmans JL, Kühn I, MacGregor-Fors I, McDonnell M, Mörtberg U, Pryšek 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. Proc R Soc B 281:20133330. https://doi.org/10.1098/rspb.2013.3330

Beninde J, Veith M, Hochkirch A (2015) Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. Ecol Lett 18:581–592. https://doi.org/10.1111/ele.12427

Bibby CJ, Burgess ND, Hill DA, Mustoe S (2000) Bird census techniques, 2nd edn. Academic Press, London

Blair RB (2001) Creating a homogeneous avifauna. In: Marzluff JM, Bowman R, Donnelly R (eds) Avian ecology and conservation in an urbanizing world. Springer, Boston, MA, pp 459–486. https://doi.org/10.1007/978-1-4615-1531-9_22

Bowman R, Marzluff JM (2001) Integrating avian ecology into emerging paradigms in urban ecology. In: Marzluff JM, Bowman R, Donnelly R (eds) Avian ecology and conservation in an urbanizing world. Springer, Boston, MA, pp 569–578. https://doi.org/10.1007/978-1-4615-1531-9_27

Callaghan CT, Major RE, Lyons MB, Martin JM, Kingsford RT (2018) The effects of local and landscape habitat attributes on bird diversity in urban greenspaces. Ecosph 9:02347. https://doi.org/10.1002/ecs2.2347

Carbó-Ramírez P, Zuria I (2011) The value of small urban greenspaces for birds in a Mexican city. Landsc Urban Plan 100:213–222. https://doi.org/10.1016/j.landurbplan.2010.12.008

Carvajal-Castro JD, Ospina -LAM, Toro-López Y, Pulido -GA, Cabrera-Casas LX, Guerrero-Peláez S, García-Merchán VH, Vargas-Salinas F (2019) Birds vs bricks: patterns of species diversity in response to urbanization in a neotropical Andean city. PLoS ONE 14:0218775. https://doi.org/10.1371/journal.pone.0218775

Chace JF, Walsh JJ (2006) Urban effects on native avifauna: a review. Landsc Urban Plan 74:46–69. https://doi.org/10.1016/j.landurbplan.2004.08.007

Clergeau P, Savard JPL, Mennechez G, Falardeau G (1998) Bird abundance and diversity along an urban-rural gradient: a comparative study between two cities on different continents. Condor 100:413–425. https://doi.org/10.2307/1369707

Clergeau P, Croci S, Jokimäki J, Kaisanlahti-Jokimäki ML, Dinetti M (2006) Avifauna homogenisation by urbanization: analysis at different european latitudes. Biol Conserv 3:336–344. https://doi.org/10.1016/j.biocon.2005.06.035

Concepción ED, Moretti M, Altermatt F, Nobis MP, Obrist MK (2015) Impacts of urbanisation on biodiversity: the role of species mobility, degree of specialisation and spatial scale. Oikos 124:1571–1582. https://doi.org/10.1111/oik.02166

Di Pietro S, Mantoni C, Fattorini S (2020) Influence of urbanization on the avian species-area relationship: insights from the breeding birds of Rome. Urban Ecosyst 24:779–788. https://doi.org/10.1007/s11252-020-01081-4

Ekroos J, Tiainen J, Seimola T, Herzon I (2019) Weak effects of farming practices corresponding to agricultural greening measures on farmland bird diversity in boreal landscapes. Landsc Ecol 34:389–402. https://doi.org/10.1007/s10980-019-00779-x

Elle O (2005) Einführung in die multivariate Statistik für Feldornithologen: Hauptkomponentenanalyse, Diskriminanzanalyse und Clusteranalyse. Vogelwarte 43:19–38

Erritzoe J, Mazgajski TD, Rejt L (2003) Bird casualties on european roads - a review. Acta Ornithol 38:77–93. https://doi.org/10.3161/068.038.0204

Evans KL, Newson SE, Gaston KJ (2009) Habitat influences on urban avian assemblages. Ibis 151:19–39. https://doi.org/10.1111/j.1474-919x.2008.00898.x

Evans KL, Chamberlain DE, Hatchwell BJ, Gregory RD, Gaston KJ (2011) What makes an urban bird? Glob Change Biol 17:32–44. https://doi.org/10.1111/j.13652486.2010.02247.x

Ferenc M, Sedláček O, Fuchs R, Dinetti M, Fraissinet M, Storch D (2014a) Are cities different? Patterns of species richness and beta diversity of urban bird communities and regional species assemblages in Europe. Glob Ecol Biogeogr 23:479–489. https://doi.org/10.1111/geb.12130

Ferenc M, Sedláček O, Fuchs R (2014b) How to improve urban greenspace for woodland birds: site and local-scale determinants of bird species richness. Urban Ecosyst 17:625–640. https://doi.org/10.1007/s11252-013-0328-x

Ferenc M, Sedláček O, Mourková J, Exnerová A, Škopek J, Formánek J, Fuchs R (2016) Disentangling the influences of habitat availability, heterogeneity and spatial position on the species richness and rarity of urban bird communities in a central european city. Urban Ecosyst 19:1265–1281. https://doi.org/10.1007/s11252-016-0558-9

Fernández-Juricic E (2000) Bird community composition patterns in urban parks of Madrid: the role of age, size, and isolation. Ecol Res 15:373–383. https://doi.org/10.1046/j.1440-1703.2000.00358.x

Fernández-Juricic E (2001) Avian spatial segregation at edges and interiors of urban parks in Madrid, Spain. Biodivers Conserv 10:1303–1316. https://doi.org/10.1023/A:1016614625675

Fischer C, Flohre A, Clement LW, Batáry P, Weisser WW, Tscharntke T, Thies C (2011) Mixed effects of landscape structure and farming practice on bird diversity. Agric Ecosyst Enviro 141:119–125. https://doi.org/10.1016/j.agee.2011.02.021

Fontana S, Sattler T, Bontadina F, Moretti M (2011) How to manage the urban green to improve bird diversity and community structure. Landsc Urban Plan 101:278–285. https://doi.org/10.1016/j.landurbplan.2011.02.033

Fuller R, Irvine K, Devine-Wright P, Warren P, Gaston K (2007) Psychological benefits of greenspace increase with biodiversity. Biol Lett 3:390–394. https://doi.org/10.1098/rsbl.2007.0149

Gill F, Donsker D, Rasmussen P (2021) IOC World Bird List (v11.2). https://doi.org/10.14344/IOC.ML.11.2

Gregory RD, Gibbons DW, Donald PF (2004) Bird census and survey techniques. In: Sutherland WJ, Newton I, Green R (eds) Bird ecology and conservation: a handbook of techniques. Oxford University Press, New York, pp 17–55

Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X, Briggs JM (2008) Global change and the ecology of cities. Science 319:756–760. https://doi.org/10.1126/science.1150195

Grüneberg C, Bauer H, Haupt H, Hüppop O, Ryslavy T, Südbeck P (2015) Rote Liste der Brutvögel Deutschlands. Ber Vogelsch 52:19–67. https://www.ogbw.de/images/ogbw/files/other/Grueneberg_et_al_2015_Rote_Liste_Brutvoegel.pdf. Accessed 18 July 2021

Haaland C, van Den Bosch CK (2015) Challenges and strategies for urban green-space planning in cities undergoing densification:

a review. Urban For Urban Green 14:760–771. https://doi.org/10.1016/j.ufug.2015.07.009

Hijmans RJ (2021) raster: Geographic data analysis and modeling. R package version 3.4–13. https://CRAN.R-project.org/package=raster. Accessed 29 Oct 2021

Isaksson C (2018) Impact of urbanization on birds. In: Tietze DT (ed) Bird species. Fascinating life sciences. Springer, Cham, pp 235–257. https://doi.org/10.1007/978-3-319-91689-7_13

Jokimäki J (1999) Occurrence of breeding bird species in urban parks: effects of park structure and broad-scale variables. Urban Ecosyst 3:21–34. https://doi.org/10.1023/a:1009505418327

Kekkonen J (2017) Pollutants in urbanized areas: direct and indirect effects on bird populations. In: Murgui E, Hedblom M (eds) Ecology and conservation of birds in urban environments. Springer, Cham, pp 227–250. https://doi.org/10.1007/978-3-319-43314-1_12

Le Viol I, Jiguet F, Brotons L, Herrando S, Lindström Ã, Pearce-Higgins JW, Reif J, Turnhout CV, Devictor V (2012) More and more generalists: two decades of changes in the european avifauna. Biol Lett 8:780–782. https://doi.org/10.1098/rsbl.2012.0496

Leveau LM (2013) Bird traits in urban-rural gradients: how many functional groups are there? J Ornithol 154:655–662. https://doi.org/10.1007/s10336-012-0928-x

Leveau LM, Leveau CM (2016) Does urbanization affect the seasonal dynamics of bird communities in urban parks? Urban Ecosys 19:631–647. https://doi.org/10.1007/s11252-016-0525-5

Liker A, Papp Z, Bókony V, Lendvai AZ (2008) Lean birds in the city: body size and condition of House Sparrows along the urbanization gradient. J Anim Ecol 77:789–795. https://doi.org/10.1111/j.1365-2656.2008.01402.x

Loss SR, Will T, Loss SS, Marra PP (2014) Bird-building collisions in the United States: estimates of annual mortality and species vulnerability. Condor 116:8–23. https://doi.org/10.1650/CONDOR-13-090.1

Lüdecke D (2021) sjPlot: Data visualization for statistics in social science. R package version 2.8.9, https://CRAN.R-project.org/package=sjPlot. Accessed 29 Oct 2021

McDonnell MJ, Hahs AK (2008) The use of gradient analysis studies in advancing our understanding of the ecology of urbanizing landscapes: current status and future directions. Landsc Ecol 23:1143–1155. https://doi.org/10.1007/s10980-008-9253-4

McKinney ML (2002) Urbanization, biodiversity, and conservation. Bioscience 52:883–890. https://doi.org/10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2

McKinney ML (2006) Urbanization as a major cause of biotic homogenization. Biol Conserv 127:247–260. https://doi.org/10.1016/j.biocon.2005.09.005

McKinney ML (2008) Effects of urbanization on species richness: a review of plants and animals. Urban Ecosyst 11:161–176. https://doi.org/10.1007/s11252-007-0045-4

Meffert PJ, Dziock F (2013) The influence of urbanisation on diversity and trait composition of birds. Landsc Ecol 28:943–957. https://doi.org/10.1007/s10980-013-9867-z

Melles S, Glenn S, Martin K (2003) Urban bird diversity and landscape complexity: species environment associations along a multiscale habitat gradient. Conserv Ecol 7:5. http://www.jstor.org/stable/26271915 Accessed 01 Oct 2021

Methorst J, Bonn A, Marselle M, Böhning-Gaese K, Rehdanz K (2021) Species richness is positively related to mental health-a study for Germany. Landsc Urban Plann 211:104084. https://doi.org/10.1016/j.landurbplan.2021.104084

Mitschke A, Hamburg (2018) https://www.bund-hamburg.de/fileadmin/hamburg/Themen/Voegel/rote-liste-voegel-2018.pdf

Morelli F, Benedetti Y, Ibáñez-Álamo JD, Jokimaki J, Mänd R, Tryjanowski P, Møller AP (2016) Evidence of evolutionary homogenization of bird communities in urban environments across Europe. Glob Ecol Biogeogr 25:1284–1293. https://doi.org/10.1111/geb.12486

Morelli F, Benedetti Y, Ibáñez-Álamo JD, Tryjanowski P, Jokimäki J, Kaisanlahti-Jokimäki ML, Suhonen J, Díaz M, Moller AP, Moravec D, Prosek J, Bussière, Mägi M, Kominos T, Galanaki A, Bukas N, Marko G, Pruscini F, Tonelli M, Jerzak L, Ciebiera O, Reif J (2021) Effects of urbanization on taxonomic, functional and phylogenetic avian diversity in Europe. Sci Total Environ 795:148874. https://doi.org/10.1016/j.scitotenv.2021.148874

Mühlbauer M, Weisser WW, Müller N, Meyer ST (2021) A green design of city squares increases abundance and diversity of birds. Basic App Ecol 56:446–459. https://doi.org/10.1016/j.baae.2021.05.003

Paker Y, Yom-Tov Y, Alon-Mozes T, Barnea A (2014) The effect of plant richness and urban garden structure on bird species richness, diversity and community structure. Landsc Urban Plann 122:186–195. https://doi.org/10.1016/j.landurbplan.2013.10.005

Patacchini E, Zenou Y, Henderson JV, Epple D (2009) Urban sprawl in Europe. Brookings-Wharton Pap Urban Aff 2009:125–149. http://www.jstor.org/stable/25609561 Accessed 12.10.2021

Planillo A, Kramer-Schadt S, Buchholz S, Gras P, von der Lippe M, Radchuk V (2021) Arthropod abundance modulates bird community responses to urbanization. Divers Distrib 27:34–49 https://doi.org/10.1111/ddi.13169

Pollock CJ, Capilla-Lasheras P, McGill RA, Helm B, Dominoni DM (2017) Integrated behavioural and stable isotope data reveal altered diet linked to low breeding success in urban-dwelling blue tits (*Cyanistes caeruleus*). Sci Rep 7:5014. https://doi.org/10.1038/s41598-017-04575-y

R Core Team (2021) R: a language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. https://www.R-project.org/

Ralph CJ, Droege S, Sauer J (1995) Managing and monitoring birds using point counts. US Department of Agriculture, Forest Service, gen tech rep PSW-GTR-149

Reynolds SJ, Ibáñez-Álamo JD, Sumasgutner P, Mainwaring MC (2019) Urbanisation and nest building in birds: a review of threats and opportunities. J Ornithol 160:841–860. https://doi.org/10.1007/s10336-019-01657-8

Saccavino E, Krämer J, Klaus S, Tietze DT (2018) Does urbanization affect wing pointedness in the Blackbird *Turdus merula*? J Ornithol 159:1043–1051. https://doi.org/10.1007/s10336-018-1575-7

Sandström UG, Angelstam P, Mikusinski G (2006) Ecological diversity of birds in relation to the structure of urban green space. Landsc Urban Plan 77:39–53. https://doi.org/10.1016/j.landurbplan.2005.01.004

Savard JPL, Clergeau P, Mennechez G (2000) Biodiversity concepts and urban ecosystems. Landsc Urban Plan 48:131–142. https://doi.org/10.1016/S0169-2046(00)00037-2

Schäfer JE, Janocha MM, Klaus S, Tietze DT (2017) How weather instead of urbanity measures affects song trait variability in three European passerine bird species. Ecol Evol 74:4868–4880. https://doi.org/10.1002/ece3.3032

Schifferli L (2000) Changes in agriculture and the status of birds breeding in European farmland. In: Aebischer NJ, Evans AD, Grice PV, Vickery JA (eds) Ecology and conservation of low and farmland birds. Proceedings of the British Ornithologist's Union conference 1999. British Ornithologist's Union, Tring, pp 17–25

Söderström B, Svensson B, Vessby K, Glimskär A (2001) Plants, insects and birds in semi-natural pastures in relation to local habitat and landscape factors. Biodiv Conserv 10:1839–1863. https://doi.org/10.1023/A:1013153427422

Szulkin M, Garroway C, Corsini M, Kotarba A, Dominoni D (2020) How to quantify urbanization when testing for urban evolution? In: Szulkin M, Munshi-South J, Charmantier A (eds) Urban

evolutionary biology. Oxford University Press, pp 13–35. https://doi.org/10.1093/oso/9780198836841.003.0002
Tomasevic JA, Marzluff JM (2017) Cavity nesting birds along an urban-wildland gradient: is human facilitation structuring the bird community? Urban Ecosyst 20:435–448. https://doi.org/10.1007/s11252-016-0605-6
Tzortzakaki O, Kati V, Kassara C, Tietze DT, Giokas S (2018) Seasonal patterns of urban bird diversity in a Mediterranean coastal city: the positive role of open green spaces. Urban Ecosyst 21:27–39. https://doi.org/10.1007/s11252-017-0695-9
Van Doren BM, Willard DE, Hennen M, Horton KG, Stuber EF, Sheldon D, Sivakumar AH, Wang J, Farnsworth A, Winger BM (2021) Drivers of fatal bird collisions in an urban center. Proc Natl Acad Sci U S A 15:118. https://doi.org/10.1073/pnas.2101666118
Wickham H (2016) ggplot2: elegant graphics for data analysis. Springer-Verlag, New York. https://ggplot2.tidyverse.org. Accessed 29 Oct 2021
Yang X, Tan X, Chen C, Wang Y (2020) The influence of urban park characteristics on bird diversity in Nanjing, China. Avian Res 11:45. https://doi.org/10.1186/s40657-020-00234-5
United Nations (2018) The world's cities in 2018. statistical papers - United Nations (Ser. A), Population and Vital Statistics Report. https://doi.org/10.18356/c93f4dc6-en
DWD - Deutscher Wetterdienst (2021) Wetter und Klima - Deutscher Wetterdienst - Hamburg (Flugh.). https://www.dwd.de/DE/wetter/wetterundklima_vorort/schleswig-holstein_hamburg/hamburg/_node.html. Accessed 29 Oct 2021
QGIS Development Team (2021) QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org. Accessed 05 Oct 2021
EEA - European Environment Agency (2018) Copernicus Land Monitoring Service - Urban Atlas. https://www.eea.europa.eu/data-and-maps/data/copernicus-land-monitoring-service-urban-atlas. Accessed 29 Oct 2021
BUKEA - Behörde für Umwelt, Klima, Energie und Agrarwirtschaft (2017) Versiegelungskarten 1984, 1999, 2012 und 2017. https://www.hamburg.de/boden/135300/versiegelung/. Accessed 29. Oct 2021
Statistik Nord - Statistisches Amt für Hamburg und Schleswig-Holstein (2021) Bevölkerungsstand - Statistikamt Nord. https://www.statistik-nord.de/zahlen-fakten/hamburger-melderegister/bevoelkerungsstand#c6618. Accessed 29 Oct 2021
United Nations (2019) World urbanization prospects 2018: highlights (population studies, 421). United Nations Pubn. https://population.un.org/wup/Publications/Files/WUP2018-Highlights.pdf. Accessed 29 Oct 2021