




Arthropod abundance modulates bird community responses to urbanization

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Funding information

Bundesministerium für Bildung und Forschung, Grant/Award Number: 01LC1501

Abstract

Aim: We analysed the role of species interactions in wildlife community responses to urbanization. Specifically, we investigated non-trophic associations within a bird community and the role of trophic interactions in the responses of bird species to the urbanization gradient.

Location: City-state of Berlin, Central Europe.

Methods: Arthropod and bird abundances were sampled across the study area and analysed using hierarchical joint species distribution models (JSDMs). Urbanization gradient was defined by environmental predictors reflecting anthropogenic disturbances, for example noise level and human population density, as well as nature-like features, for example tree cover and open green area. Relevant environmental predictors for each group and relevant spatial resolution were selected a priori using AICc. Arthropod abundances were modelled for the bird sampling transects and included as additional predictor variable in the bird community model. In this model, we used abundances and traits of 66 breeding bird species as response variables.

Results: Bird species responses to urbanization were captured by the interaction between invertebrate abundance and environmental predictors. We identified three groups of birds: the urban group (12 species) showed no decrease in abundance along the urbanization gradient and were not related to arthropods abundance; the woodland group (18 species) were positively related to tree cover and arthropod abundance, also in areas with high anthropogenic disturbance; and the nature group (36 species) were positively related to arthropod abundance, but the species abundance decreased sharply with increasing anthropogenic disturbance. All the non-trophic associations found within the bird community were positive.

Main conclusions: Arthropod abundance clearly modulated birds' responses to the urbanization gradient for most species. Especially at moderate levels of anthropogenic disturbance, the abundance of arthropods is key for the occurrence and abundance of bird species in urban areas. To maintain bird diversity in urban green areas, management measures should focus on maintaining and increasing invertebrate abundance.

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KEY WORDS

arthropod abundance, community composition, joint species distribution models, species interactions, urban ecology, urbanization gradient, wildlife diversity

1 | INTRODUCTION

Urban areas are increasing and expanding throughout the world, with an expected 70% of the human population residing in cities by 2050 (United Nations, 2018). Urbanization is one of the most drastic anthropogenic modifications of the natural landscape and habitats (Sala et al., 2000; Shochat et al., 2010), and the sprawl of urban areas results in biotic homogenization across large areas and biodiversity loss (Leveau et al., 2017; McKinney, 2008; Morelli et al., 2016; Sol et al., 2014). Yet, urban areas still host high numbers of wildlife species and even some endangered species (Aronson et al., 2014; Ferenc et al., 2014; Ives et al., 2016). Given the rapid increase in urbanized areas worldwide on the one side and the current biodiversity crisis on the other side, it is crucial to understand how the special conditions provided by cities as novel ecosystems (Kowarik, 2011) affect biodiversity.

Most research investigating the drivers of wildlife biodiversity in cities focused on landscape structure, such as cover of different landscape elements, landscape configuration, habitat connectivity (Aronson et al., 2014; Beninde et al., 2015; Callaghan et al., 2018; Collen et al., 2011; Gagné & Fahrig, 2011), vegetation characteristics (Fontana et al., 2011; Threlfall et al., 2016), anthropogenic disturbance (Beninde et al., 2015; Proppe, Sturdy, & St. Clair, 2013) and microclimatic factors, such as temperature or precipitation (Beninde et al., 2015; Harrison & Winfree, 2015). Often, wildlife community composition is negatively affected by the proportions of impervious surface and increasing noise levels, and positively related to tree cover and green area size (Aronson et al., 2014; Beninde et al., 2015; Callaghan et al., 2018; Camargo Barbosa et al., 2020; Melles, Glen, & Martin, 2003; Sol et al., 2014). Additionally, density of housing area negatively affects bird richness and diversity (Gagné & Fahrig, 2011).

However, the knowledge on how urban environmental drivers shape biodiversity is insufficient, because in addition to climate and habitat, biodiversity is affected by species interactions (HilleRisLambers et al., 2012). Studying these species interactions might be one of the pieces that help us to comprehend the puzzle of biodiversity response to urbanization. Two broad types of species interactions may be distinguished: trophic (i.e. predation) and non-trophic (e.g. competition, facilitation and mutualism) ones (Bronstein, 1994). Species interactions play a crucial role in shaping wildlife communities (Cavieres et al., 2014; Martin et al., 2018; Yodzis, 1981). For example, competition for limited resources modifies the community by favouring a higher abundance of the successful competitors, which will displace other species (Goldshtein et al., 2018; Robertson et al., 2013). Regarding trophic interactions, the ability of some species to exploit food resources under disturbance affects community composition (Galbraith et al., 2015; Planillo et al., 2015; K. E. Plummer et al., 2019). Availability of invertebrate

prey, mainly arthropods, also determines the reproductive success of many bird species inhabiting anthropogenic habitats and shapes the long-term viability of the populations (Peach et al., 2008; Seress et al., 2012, 2018). Therefore, it is essential to consider species interactions in addition to environmental drivers, to gain a complete understanding of urban drivers of biodiversity.

Importantly, species interactions may be modified by urban environmental drivers, as demonstrated by recent studies (Chamberlain et al., 2014; Gelmi-Candusso & Hämäläinen, 2019; Harrison & Winfree, 2015). Environmental factors were previously shown to interact in their effects on biodiversity and ecosystem functioning, for example modifying predator–prey relationships or detritivore species dynamics (Crain et al., 2008; Galic et al., 2017; Garnier et al., 2017; Karakoç et al., 2018). It is therefore likely that urban environmental drivers will be moderated by species interactions in their effects on wildlife community composition in cities. For example, below a certain threshold of prey availability, the diversity of predators is expected to be zero irrespective of suitability and connectivity of the urban landscape. In this context, investigating how urban community composition is shaped by either environmental drivers or species interactions separately will result in an incomplete, if not biased, understanding. Therefore, we studied how both environmental factors and species interactions shape bird community composition in the city-state of Berlin, a metropolitan area in Central Europe.

To which extent species can respond to urban environmental drivers partly depends on their traits. Among them, body mass, migratory status and diet are important traits for bird species occurrence in cities (Evans et al., 2011; Jokimäki et al., 2016). Body mass is positively correlated with urbanization, especially within clades (Callaghan et al., 2019; Croci et al., 2008). Migrant birds are expected to be scarcer in urban areas (Croci et al., 2008; Evans et al., 2011; Jokimäki et al., 2016; Kark et al., 2007), as their shift in phenology to earlier dates is much slower than that in resident species (Chamberlain et al., 2009; Samplonius et al., 2018), and thus, suitable nesting sites might be already occupied by resident species when migrants arrive to the urban area (Jokimäki & Suhonen, 1998). Regarding diet preferences, bird species with narrow diets, for example insectivorous, are expected to decrease and omnivorous species with wider diets are expected to increase with urbanization, as they can take advantage of resources provided by human activities, such as garbage (Callaghan et al., 2019; Croci et al., 2008).

To better understand the complex interactions of urbanization, bird communities and their food resources, here we investigated how bird community composition in the urban area is affected by three aspects: (a) environmental factors reflecting the urbanization gradient, of which we distinguish nature-like variables and anthropogenic disturbance, (b) trophic species interactions as measured

by arthropod abundance and (c) species associations (proxy for non-trophic interactions) within the community. We focus on the bird community and their invertebrate prey (arthropods), both of which were extensively surveyed in citywide regular and standardized monitoring schemes of Berlin (Abraham et al., 2019; Möller et al., 2019; Südbeck et al., 2005). To achieve our goal, we use the modern technique of hierarchical multiresponse models, joint species distribution models (JSDMs), to analyse species responses to environmental conditions while simultaneously accounting for associations between species within the community (Ovaskainen et al., 2017; Pollock et al., 2014; Warton et al., 2015). That is, after removing the effects of environmental covariates, the remaining correlation in the residual variance that is no longer explained by the covariates is termed "species association" (Dormann et al., 2018; Ovaskainen et al., 2017; Warton et al., 2015).

Our main objective is to disentangle the relative importance of environmental conditions and species interactions for bird community composition in urban areas. We predict that: (a) global species abundance will be higher in less urbanized sites with high arthropod abundance; (b) arthropod abundance, as an essential resource, will explain more variability in bird species abundance than the urbanization gradient by itself; (c) species inhabiting sites with high anthropogenic disturbance will use more anthropogenic resources and show lower or no response to arthropod abundance; and (d) resident species with broader diets and larger body mass will displace other species and be more abundant in more urbanized areas.

2 | METHODS

2.1 | Study area

We studied the bird community in the city of Berlin, capital of Germany (52°31' N, 13°24' E). Berlin is the largest city in Germany and constitutes a federal state, with a population of nearly 3.65 million people and an area of 892 km² (Amt für Statistik, 2017). The city is subject to a moderate continental climate, with average precipitation of 568mm and mean annual temperatures from 10.5°C in the city centre to around 8°C in the surrounding forests (Berlin Environmental Atlas, 2018). Berlin is located in a flat terrain at the confluence of the Havel and Spree rivers, and contains a high number of green areas, from highly visited parks to fragments of forests. The built-up area constitutes 48% of the city surface, green and open space occupy 17.6%, forests occupy 17.5%, roads occupy 10.9%, and water bodies occupy 6% (Berlin Environmental Atlas, 2018).

2.2 | Bird community data

We used data on bird species abundance from the Berlin breeding bird monitoring survey in the year 2017, provided by the Berlin

Senate Department for Environment, Transport and Climate Protection (SenUVK). The survey consists of 30 pre-established transects, located within one-km² grids distributed across the city (Figure 1). Grids were previously selected to capture the widest possible range of habitats. To ensure species detection, each transect was visited four times during the bird breeding season from mid-March to mid-June, approximately once per month whenever possible and leaving at least a week between visits (Südbeck et al., 2005). Transects were walked at or shortly after sunrise for 2–4 hr, in days without precipitation or strong winds. All birds seen and heard within the transects were recorded. For a detailed description and information on standards for breeding bird surveys, see Südbeck et al. (2005) and the website of the Swiss Ornithological Institute (<https://www.vogelwarte.ch/de/projekte/monitoring/>). One transect was visited only 3 times and therefore was removed from further analyses.

In the 29 monitoring transects, a total of 97 breeding bird species were recorded. Aquatic species, two non-native species and species that were present in only 2 or less sites were removed to avoid confounding effects and ensure convergence of the statistical model, resulting in 66 species in total (Appendix S1: Table S1.1). As transects differed in length (range: 2.8–6.4 km), we divided each bird species abundance by transect length to obtain an index of relative bird abundance per km (hereafter termed "bird index") that was used as response variable in the analyses.

We selected three traits that are related to wildlife responses to urbanization: body mass, diet and migratory status (Callaghan et al., 2019; Croci et al., 2008; Evans et al., 2011). Body mass values and diet information were obtained from the ELTON database (Wilman et al., 2014). Body mass values were log-transformed to favour linearity. Diet included four categories: invertebrates (species feeding mainly on invertebrates or insectivorous), herbivores (species feeding mainly on plants and seeds), omnivores (species with a mixed diet) and scavengers (species feeding on carcasses and leftovers). Migratory status was assigned following the Checklist of the Birds of Germany (Barthel & Helbig, 2006) (Appendix S1: Table S1.1). We used three categories: "migrant" for species that breed in Germany and winter in other countries, "resident" for species that spend the whole year in Germany and "partial-migrant" for species with mixed behaviour, in which some of the individuals are migrant and others are resident.

2.3 | Arthropod community data

In 2017, 42 sampling sites for arthropods were established randomly across grasslands in the city of Berlin, representing the whole gradient of urbanization (covering ranges: 0%–94% impervious surface; 0–64 inhabitants/ha, human population density; 0%–100% open green area; and 0%–82% tree cover). Three groups of arthropods were sampled: carabid beetles, spiders and grasshoppers.

Carabids and spiders were sampled by pitfall traps (Brown & Matthews, 2016; Hill et al., 2005). We used a nested design

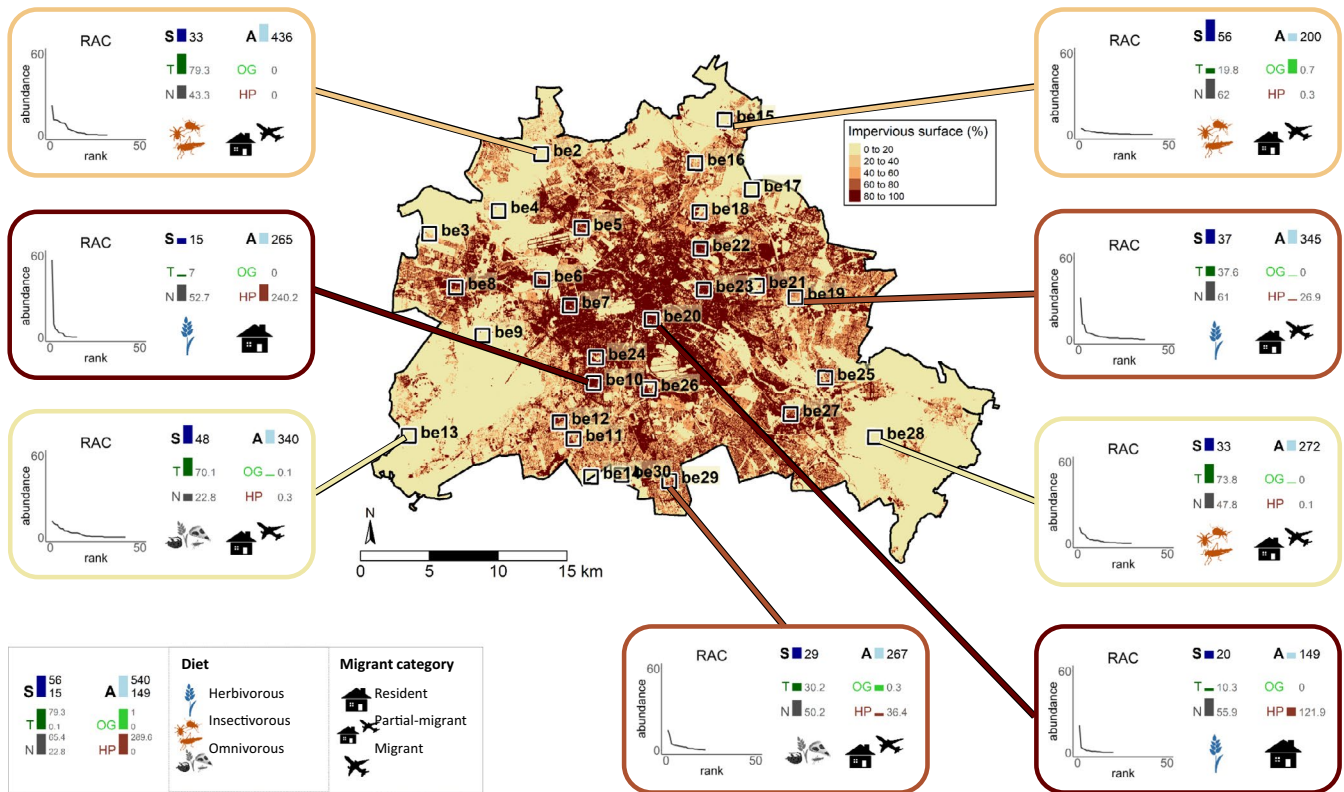


FIGURE 1 Location of the one-km² grid cells containing bird sampling transects in Berlin. Examples of data from 8 transects along a gradient of anthropogenic disturbance (human population density and noise levels) are included; RAC: rank–abundance curve; S: species richness; A: total abundance; T: tree cover percentage; OG: proportion of open green area; N: noise level (dBA); HP: human population density. Additionally, community-weighted most abundant trait values are shown. Trait symbols and the full range of values (found in all sites) for the variables can be found in the bottom left of the figure

(Boetzel et al., 2018), with four pitfall traps in each sampling site in a square with a distance of 6 m to each other. Pitfall traps consisted of plastic cups (10 cm diameter and 16.0 cm depth) filled with a 1% formalin–detergent solution. A grid was placed on each pitfall trap to keep organic material outside of the traps. Sampling took place in 2017 from May to July and from September to October, and pitfall traps were emptied every four weeks. Both taxa were sorted and afterwards preserved in ethanol. Standard keys were used for identification of adult carabid beetles (Müller-Motzfeld, 2006) and spiders (Almqvist, 2005, 2006; Roberts, 1987, 1998). Grasshopper data were collected using a box quadrat (ground area of 2 m² and gauze-covered sides of 0.8 m height)(Gardiner et al., 2005), haphazardly set up 10 times per site in August 2017. All individuals found inside the box quadrat were identified to be species using keys provided by Bellman (2006), counted and afterwards released.

The field sampling identified a total of 104 carabid species, 20 grasshopper species and 182 spider species. Prior to the statistical analyses, rare species, defined as those present in less than 5% of the sites, were removed from the dataset to avoid convergence problems. The final datasets contained 73 carabid species, 18 grasshopper species and 112 spider species (Appendix S1: Table S1.2). We

used the number of individuals of each species as a relative abundance index.

2.4 | Environmental data

We selected variables relevant to the distribution of wildlife species in urban areas, as identified by other studies (Batáry et al., 2018; Beninde et al., 2015; Ferenc et al., 2014). We divided our environmental variables into two groups: variables related to natural conditions (e.g. tree cover and open green area) and variables related to anthropogenic disturbance in the urban areas (e.g. noise level) (Table 1). All environmental layers were rasterized at 20 x 20 m resolution, but their importance was tested at a 100 m, 500 m, 1 km and 5 km scale using a moving window approach (further information in Appendix S2: Figures S2.1 and S2.2).

2.5 | Data analysis

We modelled urban bird community response to environmental drivers and arthropod abundance, the species associations within

TABLE 1 Environmental variables considered for the hierarchical joint species distribution models. Variables are categorized into two groups (“anthropogenic disturbance” and “nature-like”) that will be used for variable selection (see Methods)

Variable (units)	Abbr.	Description	Year	Source
Anthropogenic disturbance				
Impervious surface (%)	imperv	Sealed surfaces related to human constructions: roads, buildings, concrete surfaces, etc.	2015	1
Human population density (number of inhabitants in raster cell)	pop	Number of people living in the defined area	2015	2
Artificial light (relative brightness, unitless)	light	Relative luminosity for different city areas during the night	2013	3
Noise (dBA)	noise	Noise level	2012	2
Nature-like				
Distance to water (m)	dist.water	Distance to the closest water body (lake or river)	2015	2
Open green area (%)	o.green	Grasslands and other non-forested green areas, such as wastelands and road verges	2015	1
Temperature summer day (°C)	temp.day	Average temperature measured at 14:00 hr during summer days.	2016	2
Temperature summer night (°C)	temp.night	Average temperature measured at 22:00 hr during summer nights.	2016	2
Tree cover (%)	tree	Trees or forested areas, including parks and trees in the streets	2015	1

Note: Abbr: abbreviation; Year: refers to the original year the data were taken; Source: source of the GIS data.

1. European Union, Copernicus Land Monitoring Service, 2018; <http://land.copernicus.eu/pan-european/high-resolution-layers/>

2. Berlin Environmental Atlas, 2018 (https://www.stadtentwicklung.berlin.de/geoinformation/fis-broker/index_en.shtml)

3. Image and data processing by NOAA's National Geophysical Data Center. DMSP data collected by US Air Force Weather Agency, 2018 (ngdc.dmsp@noaa.gov)

the bird community and species traits using a joint species distribution model (JSDM) in a hierarchical Bayesian framework (Ovaskainen et al., 2017; Tikhonov et al., 2019). Community composition was studied by using the relative abundance of each species as response variables for all the models (for modelling details, see below).

Our modelling workflow consisted of the following steps (Figure 2): as JSDM fitting is computationally demanding, precluding fitting all possible models, we first selected the optimal spatial resolution and the relevant environmental variables for the JSDMs. Variables and their spatial resolution were selected using Akaike's information criterion for small sample sizes (AICc) in multiresponse models, after testing for multicollinearity (see Appendix S3: Figure S3.3, Tables S3.3 and S3.4). Second, for each arthropod group (carabids, spiders and grasshoppers), we ran a JSDM with the respective arthropod abundances as model responses and the environmental variables selected in the previous step as predictors. These models were used to estimate arthropod abundance in the bird transects, because invertebrate sampling plots and bird transects were not spatially overlapping. We predicted arthropod abundance in the area of the transects, which was then used as a covariate in the bird community model (see below).

Last, we ran the hierarchical JSDM for the bird community with the bird index values (relative abundances) and species trait values as model responses, and environmental variables selected in the first

step and total arthropod abundance obtained in the second step as predictors.

The final environmental variables retained for the JSDM of each community (Appendix S3) were as follows:

- Carabids model: *imperv*, *dist.water* and *temp.day*, all at 100 m scale.
- Grasshoppers model: *imperv* at 100 m scale and *o.green* at 500 m scale.
- Spiders model: *imperv*, *noise*, *temp.day* and *o.green*, all at 100 m scale.
- Birds model: *pop*, *noise*, *tree*, and *o.green*, all at 100 m scale.

2.5.1 | Modelling and extrapolating arthropod communities

For each arthropod group, we ran a hierarchical JSDM in a Bayesian framework, using as response variables the abundance of each species within the respective arthropod group (carabids, spiders and grasshoppers). We included the previously selected environmental variables as explanatory variables (see above), a spatially explicit random effect with the location of each sampling site to control for spatial effects, and used Poisson error distribution with a log-link function.

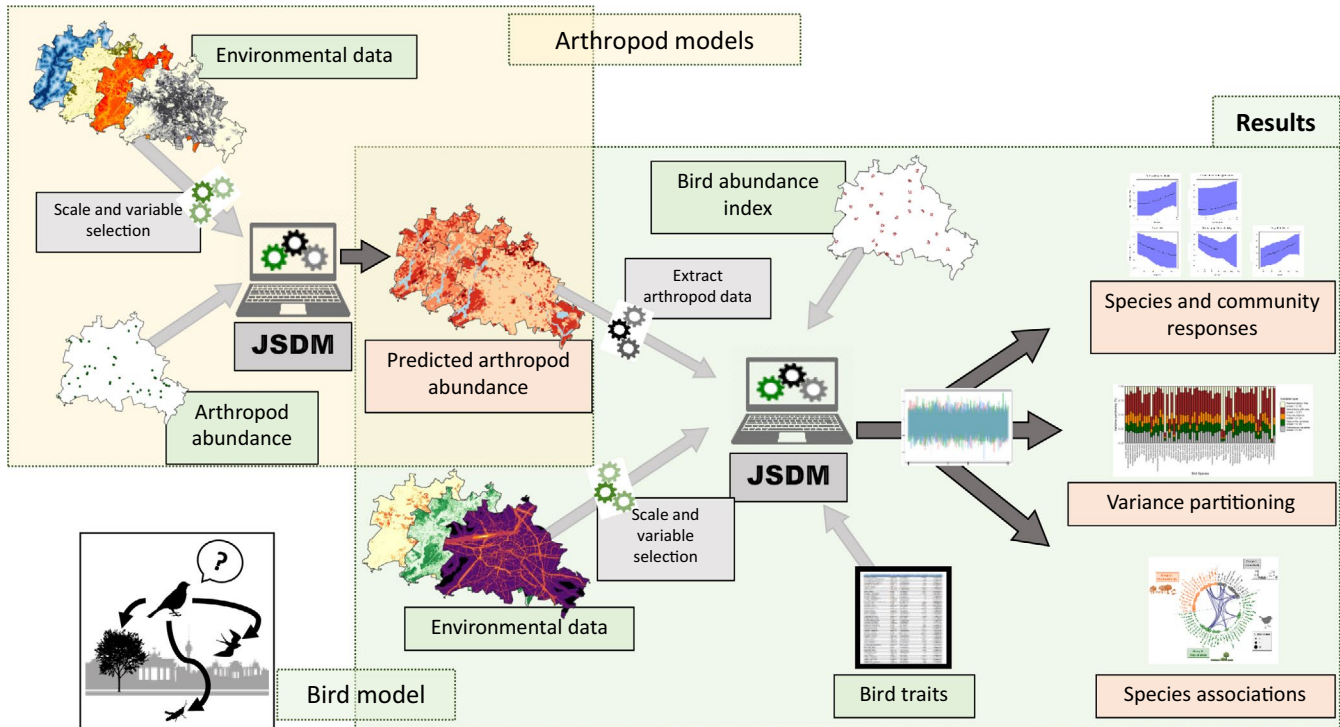


FIGURE 2 Representation of the modelling workflow followed in this study to disentangle effects of environment and trophic interactions, as well as explore species associations (lower left pictogram). The workflow has been divided into three sections: arthropod community models (JSDMs; left square), bird community model (JSDM; central-right square), which is used to derive the final results (right). Green boxes and light grey arrows represent input data in the models. Orange boxes and dark grey arrows represent outputs of the statistical models. Grey boxes represent relevant modelling steps

We ran three chains of 780,000 iterations with a burn-in of the first 30,000 iterations and a thinning rate of 50 to avoid autocorrelation within the chains, retaining 45,000 ($3 \times 15,000$) samples for further analyses. Model convergence was assessed using trace plots and Gelman–Rubin convergence parameter (Gelman & Rubin 1992).

After checking that all the assumptions were met, we obtained the explanatory power of the models for each invertebrate group using the R^2 value, computed based on the correlation of observed versus predicted values. We evaluated two R^2 values for each model: the species R^2 value, as an average value across species abundances, and the site R^2 value, as the average value across sites for the summed abundance of all the species. In our case, the site R^2 value gives information about how accurate the model prediction will be in each site for the full arthropod community, that is, how accurate the prediction will be in the bird transects. All the explanatory power values were relatively high (Species $R^2_{\text{carabids}} = 0.71$; $R^2_{\text{grasshoppers}} = 0.6$; $R^2_{\text{spiders}} = 0.72$; Site $R^2_{\text{carabids}} = 0.94$; $R^2_{\text{grasshoppers}} = 0.92$; $R^2_{\text{spiders}} = 0.95$); thus, we confidently used these JSDM for extrapolating arthropod abundance to the bird monitoring transects creating raster maps with a resolution of 100 m, which was the best scale for predicting arthropod abundances. Then, we averaged the predicted values per arthropod group of all the raster cells overlapping the bird transects. Finally, total arthropod abundance was calculated as the sum of the predicted abundances of the three arthropod groups at the bird transects.

2.5.2 | Modelling the bird community

We modelled bird community using a hierarchical JSDM in a Bayesian framework (Ovaskainen et al., 2017) that models each of the observed species accounting for the potential associations among them and provides results for individual species and the global community, as the sum of the species responses. We used two different types of response variables: each bird species relative abundance index (bird index) and species traits. The explanatory variables were the selected environmental variables (Table S3.4) and total predicted arthropod abundance in each transect. We did not use the different arthropod groups as separate covariates because their relative abundances were highly correlated (spiders–grasshopper: Pearson's $r = .927$; spiders–carabids: $r = .917$; and grasshoppers–carabids: $r = .924$). Finally, the spatial locations of the bird monitoring transects were included as spatially explicit random effect to account for a potential spatial structure in the data (Appendix S4: Table S4.5).

We ran three chains of 780,000 iterations with a burn-in of the first 30,000 iterations and a thinning rate of 50 to reach model convergence, retaining 45,000 ($3 \times 15,000$) samples for further analyses. Model convergence was assessed using chain trace plots and the Gelman–Rubin statistic (Gelman & Rubin 1992). We calculated the 95% and the 75% posterior credible intervals (CI) for all the parameters. Following other publications (Mata et al., 2014; Ribeiro et al., 2018), we considered that 95% CI not overlapping zero showed a strong effect and that 75% CI not overlapping zero were enough to

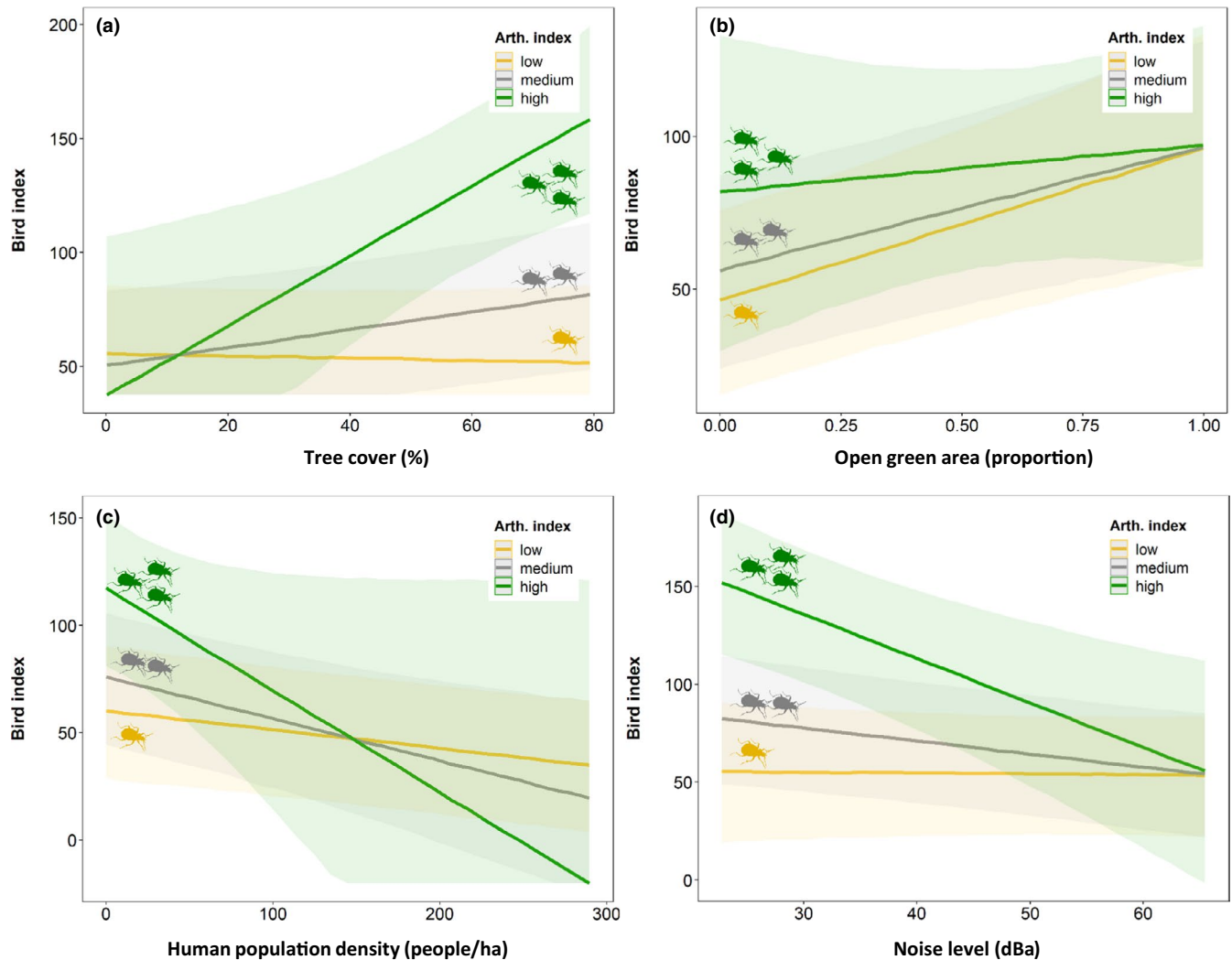


FIGURE 3 Effects of arthropod abundance and environmental variables reflecting urbanization gradient on bird index values (relative bird abundance per km, see Methods). To show the interaction, plots were obtained by predicting model results at three levels of Arthropod abundance (*Arth. index*): low = minimum value of arthropod abundance in bird transects; medium = average value of arthropod abundance; max = maximum value of arthropod abundance in bird transects. Shaded area corresponds to the 75% CIs

show the existence of an effect. Consequently, we considered that when the 75% CI overlapped zero, the support from the data was weak to demonstrate an effect.

We examined the individual species responses to search for common trends and patterns. By carefully considering the negative, positive or lack of response of each species to each of the environmental variables, and whether this response was modulated by the arthropod abundance, we defined species groups with similar response patterns to the urbanization gradient.

We grouped the explanatory variables into four groups (Table 1), nature-like, anthropogenic disturbance, arthropod abundance and the (statistical) interaction between arthropod abundance and environmental variables, and assessed the importance of each group through variance partitioning analysis (Ovaskainen et al., 2017; Tikhonov et al., 2019).

Analyses were done in R v 3.5.2 (R Core Team, 2019). Multiresponse models for variable selection were run with

package “mvabund” (Wang et al., 2012). The JSDM was run using package “Hmsc” (Tikhonov et al., 2019). Bayesian model evaluation was done with “coda” (Plummer et al., 2006) and “MCMCVis” (Youngflesh, 2018) packages.

3 | RESULTS

We analysed data from 66 breeding bird species found in Berlin. On average, we found 29.70 species per transect (range: 15–47 species per transect) and a mean prevalence across species of circa 40% of the sites. Twelve out of 66 species had a prevalence of at least 80%, and five species were present in all the sites: common wood pigeon (*Columba palumbus*), European blue tit (*Parus caeruleus*), great tit (*Parus major*), common starling (*Sturnus vulgaris*) and common blackbird (*Turdus merula*). Carrion crow (*Corvus corone*) and Eurasian blackcap (*Sylvia atricapilla*) were recorded in 28 out of 29 sites. The

house sparrow (*Passer domesticus*) was recorded at 24 sites. Five of these species presented values higher than 15 individuals per km: common wood pigeon, European blue tit, great tit, common blackbird and house sparrow. The other species with a 100% prevalence, the common starling, had an average relative abundance of 11.4 individuals per km.

In general, species with higher prevalence also presented higher relative abundance (see bird index) per site. Taking into account only the sites with species presence, the average value of the bird index was 2.07 individuals per km (range: 0.29 (common kestrel, *Falco tinnunculus*)-24.21 (*Passer domesticus*) individuals per km).

Total bird abundance, that is the sum of the relative abundance of all species, declined with increasing anthropogenic disturbance (noise and human population density), while increased with nature-like variables (tree cover and proportion of open green area) and arthropod abundance (Appendix S5: Figure S5.2). The results remained qualitatively the same if we used species richness instead of total abundance (Appendix S5: Figure S5.3).

Bird relative abundance was highly impacted by arthropod abundance, which modulated the community response to environmental variables (Figure 3). As a general response, relative bird abundance was higher in areas with higher arthropod abundance, especially in areas with high tree cover (Figure 3a). When arthropod abundance was low, the relative abundance of birds was negligibly influenced by anthropogenic disturbance variables (human population and noise levels) and tree cover. When arthropod abundance was high, relative bird abundance decreased sharply with increasing anthropogenic disturbance (Figure 3c,d).

Our hierarchical JSDM revealed idiosyncratic responses of the abundance of each individual species to the environmental variables and arthropod abundance and their statistical interaction (Appendix S6: Figures S6.4, S6.5, S6.6 and S6.7). Responses were species-specific, but some general trends emerge that allow to classify species into three groups, based on the similarity of their responses to all the variables reflecting the urbanization gradient. Group 1, the urban group, was characterized by no or positive response to increasing anthropogenic disturbance levels and a very weak effect of nature-like variables (credible intervals overlapping zero). This group was formed by 12 species, including the carrion crow, the house sparrow and the common blackbird. Species from this group occurred on average in 20 out of 29 monitoring transects and had an average bird index value of 4.38 individuals/km. Group 2, the woodland group, was strongly affected by tree cover and arthropod abundance (credible intervals not overlapping zero), whereas noise had a negative effect and the effect of human population density was not as pronounced. Species in this group kept larger populations with high arthropod abundance over the full urbanization gradient. This group was formed by 18 species, including the great tit, the Eurasian blue tit and the Eurasian wren (*Troglodytes troglodytes*). Species from group 2, woodland group, occurred on average in 16.6 monitoring transects and had an average bird index value of 2.32 individuals/km. Group 3, the nature group, was characterized by a negative effect of anthropogenic disturbance (noise levels

and/or human population density) and positive response towards nature-like variables (tree cover or open green area). This last group was formed by the remaining 36 species and included species such as the skylark (*Alauda arvensis*), the nightingale (*Luscinia megarhynchos*) and the yellowhammer (*Emberiza citrinella*). Species from group 3, nature group, occurred on average in 9 monitoring transects and had an average bird index value of 1.1 individuals/km.

When extrapolating the responses to the area of the whole city, spatial patterns became apparent, with species from group 2, woodland group, showing a distribution pattern very similar to that of the whole community (Figure 4; for environmental variables maps, see Appendix S2: Figures S2.1 and S2.2).

The variance partitioning analysis of the explanatory variable groups in the JSDM showed that the variable interactions with arthropod abundance explained almost 40% of the variance (Figure 5). Regarding the other groups, variance partitioning is not straightforward to interpret because of the different group sizes; "nature-like variables" and "disturbance variables" are each represented by two variables, while "arthropod abundance" is represented by one variable, and the (statistical) "interactions with arthropod abundance" are four variables. Arthropod abundance as single effect additionally explained on average 13% of the variation, as much as either nature-like (14%) or disturbance variables (16%). Taking that into account, we can confidently say that arthropod abundance and its statistical interactions with environmental variables were most important for bird community composition.

The analyses based on trait values showed fewer clear responses, although some potential trends are worth mentioning (Appendix S7: Figure S7.8). Regarding diet, species feeding on invertebrates showed a positive trend in relation to arthropod abundance and tree cover and negative trend in relation to noise. No trend in species body mass was apparent. Regarding migratory status, the most pronounced responses were observed for partial migrants, which were negatively affected by noise and positively affected by arthropod abundance and tree cover. No trend was identified in body mass.

The associations among bird species within the community identified in the residual variance of the JSDM were all positive (Figure 6). These non-trophic associations occur mainly among bird species with high prevalence in more urbanized areas (group 1, urban group). Some positive associations were also found among species belonging to different response groups, which could point to facilitation or neutral co-occurrence between those species. No competitive interactions resulting in spatial exclusion were found, as shown by the lack of negative associations.

4 | DISCUSSION

Our results highlight the key role of trophic species interactions in wildlife community composition under anthropogenic disturbance. Arthropod abundance was the main variable driving bird community response across the urbanization gradient, and it modulated the effect of anthropogenic disturbance on bird

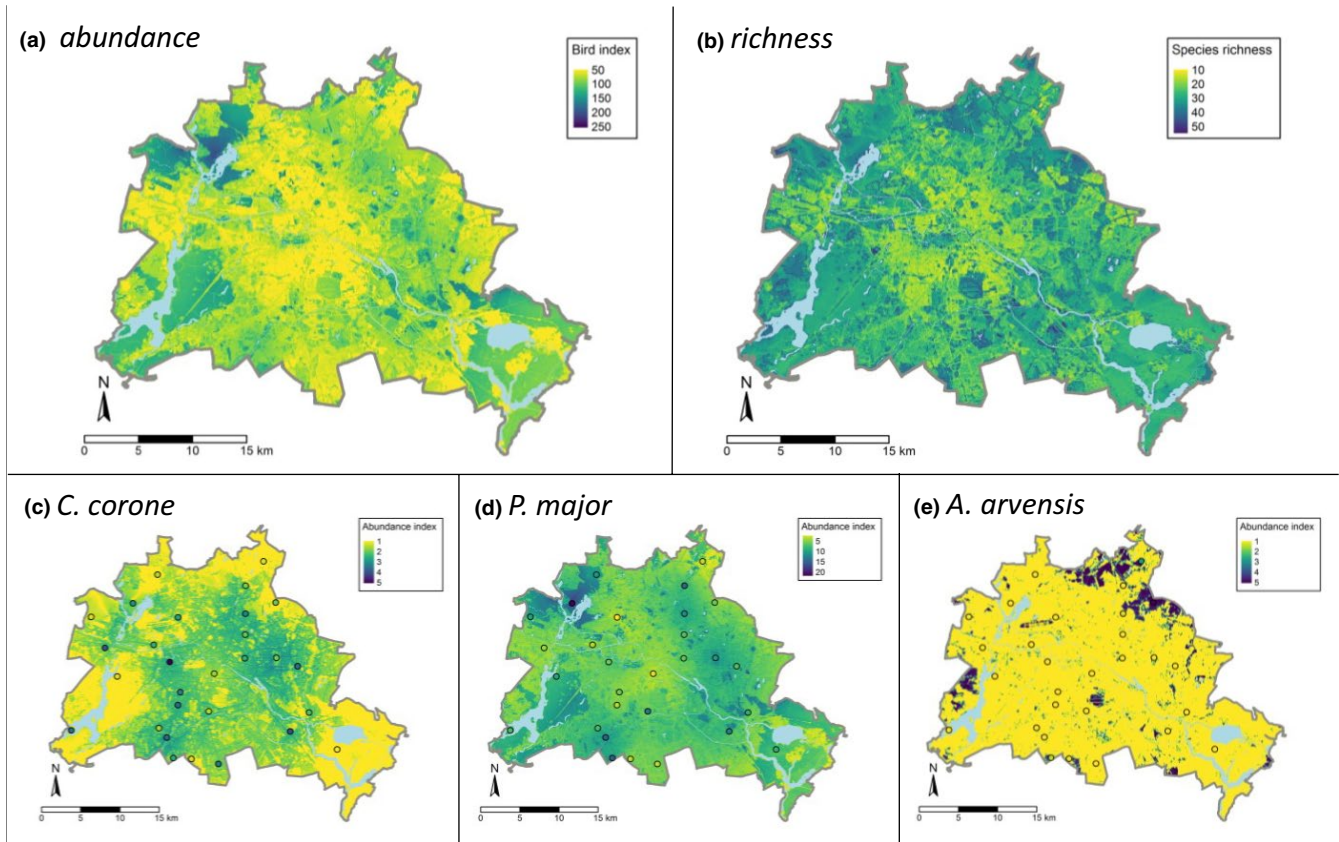


FIGURE 4 Prediction maps of total bird abundance (a), bird species richness (b) and abundance of representatives from the identified three groups reflecting general bird responses to urbanization. The examples used for each group are as follows: carrion crow (*Corvus corone*) from group 1: urban group (c); great tit (*Parus major*) from group 2: woodland group (d); and Eurasian skylark (*Alauda arvensis*) from group 3: nature group (e)

species abundance, hence bird community composition. This is a novel finding, as most studies still focus on environmental variables and neglect biotic interactions (Batáry et al., 2018; Beninde et al., 2015; Callaghan et al., 2018).

As a general pattern, both total bird abundance and species richness were higher in low disturbance areas and decreased towards more urbanized areas. Arthropod abundance increased bird abundance in low to moderately disturbed areas, but had little influence on species inhabiting the most urbanized areas. This variable was also the most important factor explaining bird abundance variance along the urbanization gradient (Figure 5). Although some species have diets that rely mainly on plants or seeds, invertebrates are an important resource during breeding season for many birds (Peach et al., 2008; Seress et al., 2012). Therefore, arthropod abundance represents a key resource that allows bird diversity to increase in less urbanized areas. Above certain disturbance thresholds, our results show that only a few bird species can tolerate the anthropogenic disturbance and overall bird community abundance clearly decreases. A meta-study on urban biodiversity patterns showed no clear overall trend of bird abundance in response to urbanization as both negative and positive trends were detected in a similar amount of studies (Faeth et al., 2011). Our results demonstrate that failing to explicitly consider prey

availability may result in different relations of bird abundance with the urbanization gradient.

Additionally, our analyses of species traits showed that anthropogenic disturbance negatively affected species feeding on invertebrates and partial-migrant species, as corroborated by previous studies, although no clear response was found for fully migrant species (Crocì et al., 2008; Evans et al., 2011; Kark et al., 2007).

We identified three groups of birds regarding their responses to the urbanization gradient (Figure 6). We believe our groups 1, 2 and 3 (birds of urban, woodland and natural areas) resemble and support the classification of wildlife species into urban exploiters, urban adapters and urban avoiders, respectively (Blair, 1996; McKinney, 2002; Shochat et al., 2006). The urban species, or urban exploiters, persisted at high abundance under high disturbance levels. These species, in agreement with other studies (Callaghan et al., 2019; Crocì et al., 2008; Kark et al., 2007), are small- to medium-sized, have mainly scavenging or omnivorous diets and are resident species (Appendix S1: Table S1.1). Species in our dataset that were classified as scavengers belong mainly to generalist and opportunistic species and, therefore, they are expected to adjust more easily to urban conditions (Callaghan et al., 2019), due to bold behaviour and the ability to profit from anthropogenic resources (Evans et al., 2011; Greggor et al., 2016;

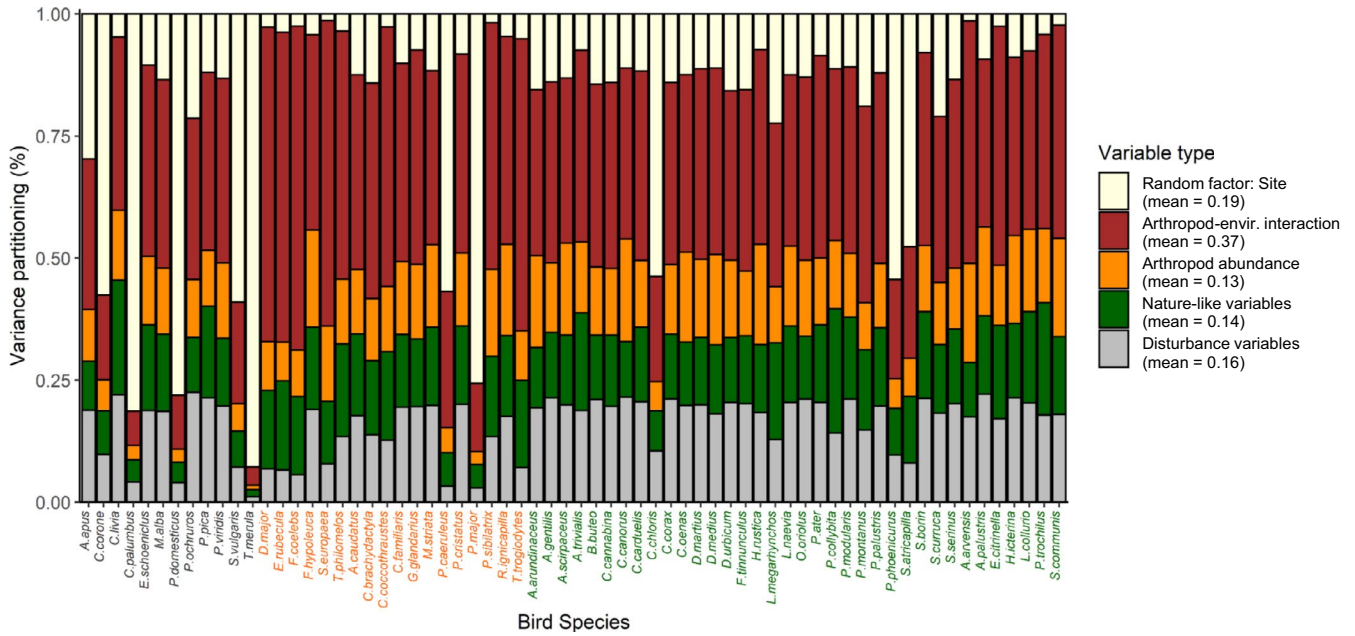


FIGURE 5 Results of the variance partitioning analysis. Variables were grouped in four groups: (anthropogenic) disturbance variables, nature-like variables, arthropod abundance and the interactions between arthropod abundance and the environmental variables (Arthropod-envir. interaction). The variance explained by the spatial location of the sites (random factor) is also shown. Species names are colour-coded based on the group they were classified: urban birds (grey), woodland birds (orange) and natural areas birds (green)

Jokimäki et al., 2016). Interestingly, this pattern is parallel to that identified for mammals, where the most opportunistic mesocarnivores can colonize the urban areas (Bateman & Fleming, 2012; Gras et al., 2018).

Group 2, woodland species, or urban adapters, drove the general pattern of community composition in the city. Although group 2 did not consist of the most widespread or abundant species, the species of this group were relatively abundant (2.32 individuals/km), widely distributed and had strong responses to the urbanization gradient (Appendix S6). These species can cope with urban disturbance, at least to some degree, as long as their habitat requirements are fulfilled. Our study was conducted in Berlin, which is characterized by a high abundance of trees, including big parks and woodland remnants in the city centre. However, all open areas in the centre are heavily used by humans. In this context, only bird species related to trees that can find branches or holes high enough to avoid direct human disturbance could thrive in urban areas.

Group 3, nature group consisting of urban avoiders, was formed mainly by species associated with open habitats, such as the skylark (*Alauda arvensis*) (Del Hoyo, Elliot, & Sargata, 2004). Although some of these species could perhaps increase their abundance in disturbed areas, open habitats in an urban context are usually exposed to direct contact with humans and pets (unpublished data), which might drive bird species away from more populated areas.

An interesting finding of our study is the inclusion of the house sparrow in the group of urban birds, which means a lack of relationship with arthropod abundance. Although its presence in the cities cannot directly be interpreted as adjustment, sparrows are declining across Europe and identifying the conditions under which the

species survives is of vital importance for its conservation (BirdLife International, 2018). In our study area, some big areas with low anthropogenic disturbance still persist near the city centre, and we hypothesize that the availability of these quiet areas next to areas with high anthropogenic resources might mitigate the negative effects of areas with high disturbance, thus allowing the species to persist in the city. Another interesting species that is usually sensitive is the nightingale, which also appears at high abundances in areas with low disturbance and high arthropod abundance, highlighting again the key role of prey abundance for bird diversity.

There is some evidence for the highest species abundance at intermediate urbanization levels (Batáry et al., 2018), an effect that conforms with the intermediate disturbance hypothesis (Chace & Walsh, 2006; Connell, 1978; Hacker & Gaines, 1997; Marzluff, 2017; McKinney, 2008). In this context, the findings of how the size of green areas in cities affects bird abundance or diversity are sometimes contradictorily discussed. Larger green areas in urban context are expected to have low disturbance and higher bird diversity, but some results show small green patches with a diversity that is comparable or higher than that of the big areas (Callaghan et al., 2018; Matthies et al., 2017), which sometimes has been related to the intermediate levels of disturbance in such small areas. Our findings suggest that high biodiversity at intermediate urbanization levels or differences in bird abundance between green areas of similar size may be due to missing influential variables in the analyses (Fox, 2013). If we included arthropod abundance or a similar measure of prey availability in the analyses, for the same relative prey abundance, larger green areas should contain higher bird diversity. However, if there is a difference in prey abundance, we would expect small green areas

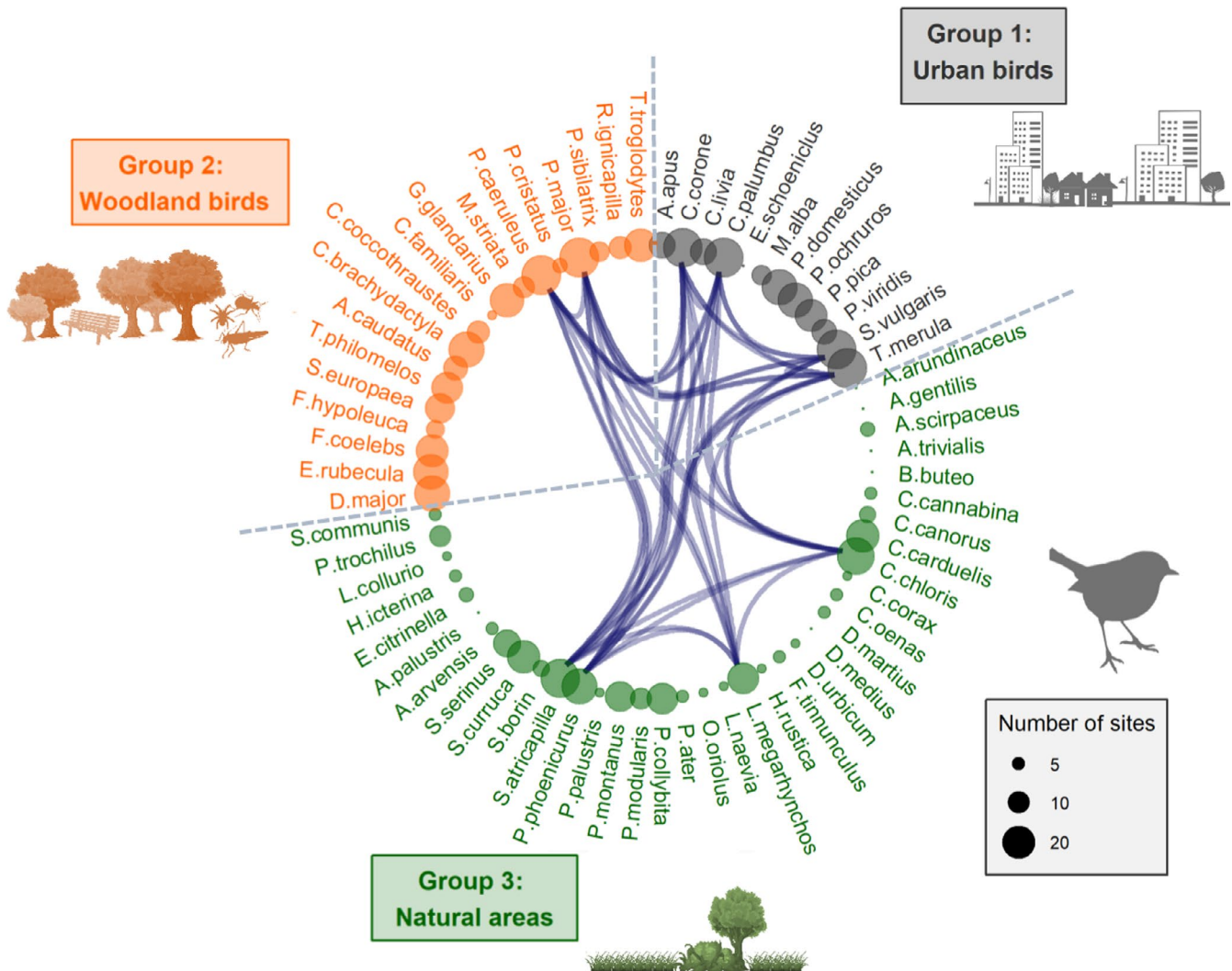


FIGURE 6 Associations among bird species in urban areas identified by the JSDM, whose 95 CI did not overlap zero. All associations were positive. Species have been categorized based on their response group (see results). The size of the dot represents the number of sites where the species was recorded (total 29 sites)

with high prey abundance to support higher bird diversity than large green areas with low prey abundance. Indeed, failing to consider prey availability in the analyses may result in the apparent support of the intermediate disturbance hypothesis.

Regarding the non-trophic interactions, we found only positive associations among bird species. From a statistical point of view, the associations or co-occurrence patterns detected by the JSDM might refer either to real biotic interactions or represent a shared species response to a missing covariate in the analysis (Abrego et al., 2017; Dormann et al., 2018; Warton et al., 2015). In our case, all the positively interacting species detected by our model were present at least at 20 sites (except the nightingale, recorded in 19 sites). This result points to species that can cope well with the urban disturbances and, probably, are benefiting from anthropogenic resources. We speculate that the presence of important resources for urban birds, such as feeders or artificial nesting sites in highly urbanized areas (personal observation)(Kark et al., 2007; Plummer et al., 2019), might explain this pattern for most of the species.

We did not find any negative association among bird species. Community responses to disturbance are scale-dependent (Chase et al., 2018), and some responses might be detectable only when using broad spatial scales (Planillo et al., 2015). While competitive interactions may influence species responses to urbanization at broad scales (Martin et al., 2018), we focused on the community inhabiting the city. Another possible explanation for the lack of competitive interactions is the potential stress caused by anthropogenic disturbance (Beaugeard et al., 2019; Strasser & Heath, 2013). It has been shown that communities under stress are characterized by positive rather than negative interactions (Callaway et al., 2002; He et al., 2013).

Our results are also subject to some caveats. We used data on ground-dwelling arthropods as a proxy for arthropod diversity. The survey of canopy-dwelling arthropods would be interesting in further studies. Our data come from observations under field conditions, and as such, they are correlational. However, we firmly believe that the responses we found in the data are

reliable, as the identified responses are coherent with other studies (Aronson et al., 2014; Beninde et al., 2015; Callaghan et al., 2018; Sol et al., 2014). Caution is also needed when inferring whether a species is successful in a disturbed environment. Although some species thrive in disturbed environments (Prange et al., 2003; Rebolo-Ifrán et al., 2017; Sol et al., 2017; Stracey & Robinson, 2012), abundance is not a synonym of a successful population (Mumme et al., 2000; Strasser & Heath, 2013) and we cannot assess whether the high abundances of some species are related to long-term population viability. Disturbed areas sometimes become ecological traps for wildlife species (Hale & Swearer, 2017; Hollander et al., 2011; Lepczyk et al., 2017; Stillfried et al., 2017). Therefore, our study refers only to the observed abundance and cannot be extrapolated to population viability.

We conclude that high invertebrate prey abundance (here included as arthropod abundance) is a key variable for bird community composition in urban areas, and high levels of prey abundance can counteract, to some degree, negative effects of anthropogenic disturbance. In the last 30 years, insect abundance has declined by up to 70% (Hallmann et al., 2017), coupled with a insectivorous bird populations in Europe declining by 13% in abundance, and bird populations in the United States show a decrease of 30% in abundance since the last decades of last century (Bowler et al., 2019; Rosenberg et al., 2019). Against this background, our results have crucial implications for sustainable urban planning if we want to avoid a “silent spring” (Carson, 2002) in cities. Keeping areas with high prey abundance in the city will help maintaining bird diversity and thus decrease the homogenization process that urbanized areas currently undergo (Evans et al., 2018; Ferenc et al., 2014; McKinney, 2006). In order to preserve bird biodiversity in urban areas, native and diverse arthropod communities should be encouraged in green spaces. Additionally, a healthy bird community will help in the biotic control of insect pests, preventing damage to vegetation. We suggest some management actions: increase invertebrate abundance in urban parks through the installation or maintenance of structures for arthropod survival by an appropriate habitat management, for example extensive or reduced mowing, leave dead wood and stones, walls as nesting substrates, preserve wastelands and decrease or avoid the use of pesticides; increase the habitat diversity for birds by providing both forested (including dead wood) and open green areas in urban parks; and decrease anthropogenic disturbance, such as noise or human density in some designated core areas to allow the regeneration of sensitive species.

ACKNOWLEDGEMENTS

Dr. Conny Landgraf and Dr. Sarah Kiefer provided very useful help acquiring the bird data and communicating with the Berlin Senate Department for Environment, Transport and Climate Protection. We are thankful to Johannes Schwarz who coordinated and provided the bird data, and to all the volunteers who collected and identified invertebrate species in Berlin grasslands. The work was funded by the German Federal Ministry of Education and Research BMBF within the Collaborative Project “Bridging in Biodiversity Science—BIBS”

(funding number 01LC1501). Open access funding enabled and organized by ProjektDEAL.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ddi.13169>.

DATA AVAILABILITY STATEMENT

Data used in this study are provided in the Supplementary Material files.

BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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