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# Habitat preferences of two sparrow species are modified by abundances of other birds in an urban environment

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## Abstract

Every species has certain habitat requirements, which may be altered by interactions with other co-occurring species. These interactions are mostly ignored in predictive models trying to identify key habitat variables correlated with species population abundance/occurrence. We investigated how the structure of the urban landscape, food resources, potential competitors, predators, and interaction between these factors influence the abundance of house sparrow *Passer domesticus* and the tree sparrow *P. montanus* in sixty 25 ha plots distributed randomly across residential areas of the city of Poznań (Poland). The abundance of the house sparrow was positively correlated with the abundance of pigeons but negatively correlated with human-related food resources. There were significant interaction terms between abundances of other urban species and habitat variables in statistical models. For example, the abundance of house sparrow was negatively correlated with the abundance of corvids and tree sparrows but only when food resources were low. The abundance of tree sparrows positively correlated with density of streets and the distance from the city center. The abundance of this species positively correlated with the abundance of corvids when food resources were low but negatively correlated at low covers of green area. Our study indicates that associations between food resources, habitat covers, and the relative abundance of two sparrow species are altered by the abundance of other urban species. Competition, niche separation and social facilitation may be responsible for these interactive effects. Thus, biotic

interactions should be included not only as an additive effect but also as an interaction term between abundance and habitat variables in statistical models predicting species abundance and occurrence.

Species distribution models combine observations of species presence or abundance with environmental data in order to develop predictive estimates about species distribution and abundance (Kosicki and Chylarecki 2013). The main explanatory variables are habitat features, land covers, or landscape characteristics (Baker et al. 2014; Kosicki et al. 2015). However, there are several aspects that can affect the predictive performance species distribution models. For example, species traits and the presence of associated or avoided species may cause differential responses to the processes that control their distribution (Campomizzi et al. 2008; Kissling et al. 2011; Morelli and Tryjanowski 2015 ). Indeed, recent works showed that the inclusion of biotic interactions (abundance of other species) in models increase their predictive performance (Campomizzi et al. 2008; Rödder and Lötters 2010, Morelli and Tryjanowski 2015). However, most of these models assume additive effects of all studied variables and thus do not consider the interaction between variables. This may lead to flaws in models. To explain this, let us consider a hypothetical situation in which two species compete for a key resource. The resource positively affects the population densities of two species. When resources are limited the stronger competitor should negatively affect the population size of weaker competitor. However, when resources are abundant, the population sizes of both weak and strong competitors may be positively correlated. In other words, it is not enough to include the abundance of competitors, predators or social facilitators as a substitute for biotic interaction in predictive models. These biotic interactions will change with different values of environmental variables (generally called resources). In statistical meaning they should be modeled as interaction terms between the abundance of species that are indicators of biotic relations with environmental variables. This approach is unfortunately very rare (Heikkinen et al. 2007).

Most models predicting species occurrence or abundance that include biotic interaction were built for agricultural ecosystems (Morelli and Tryjanowski 2015), wetlands (Baker et al. 2014), or forests (Heikkinen et al. 2007). Analyses that include biotic interactions are very rare for urban areas (Przybylska et al. 2012). Towns and cities are nowadays the most rapidly developing areas in the world, and they have a profound effect on wildlife (Tomiałojć 1976; Luniak 1983; Marzluff et al. 2001, Lin et al. 2008; Evans et al. 2010). In urban landscapes, the presence and density of animal populations is limited by the availability of suitable habitats, human disturbance, collisions with vehicles, and behavioural shyness (Górski and Antczak 1999; Fernández-Juricic and Jokimäki 2001; Randler 2003; Chace and Walsh 2006; Ditchkoff et al. 2006; Wang et al. 2009; Møller 2010). However, little is known about how different urban colonizers respond to the structural complexity of an urban landscape and to resources and population densities of other species (Marzluff et al. 2001; Skórka et al. 2006; Devictor et al. 2007). An urban environment often offers a release from predators and provides abundant resources, such as man-made food and nest sites (Jokimäki and Suhonen 1998; Marzluff et al. 2001; Jokimäki and Kaisanlathi-Jokimäki 2003; Fuller et al. 2008; Robb et al. 2008). Theoretical models (Anderies et al. 2007) and empirical data

have shown that competition for these resources may be strong, but it remains unclear how this affects the population densities of urban birds (Sol et al. 1998; Shochat 2004; Wysocki and Walasz 2004; Shochat et al. 2010). Niche theory predicts that inter-specific competition may be strong when species are ecologically similar and have similar habitat requirements (Giller 1984; Robertson 1995). In such a scenario, competition should lead to a negative relationship between the population densities of two species and to their spatial segregation (Bengtsson 1989). Body size is regarded as a good indicator of competitive abilities (Alatalo and Moreno 1987; Jonart et al. 2007), thus in a community of species utilizing similar resources the successful species (the most abundant one) are those characterized by larger body size. Therefore, the population density of a larger species may negatively affect the density of smaller ones.

We choose the house sparrow *Passer domesticus* and the tree sparrow *P. montanus*, very similar species in terms of body size and diet and common species, as a demonstration case to investigate these issues. There is a potential competitive relationship between the house sparrow and tree sparrow (Summers-Smith 1994; Vepsäläinen et al. 2005), but there have been no studies on the effects of possible interactions between the two species on their relative abundances (Summers-Smith 1994; Vepsäläinen et al. 2005). Both species are directly associated with a human altered environment (Luniak 1983; Anderson 1984, 2006). In Europe, these species inhabit villages, towns and cities, and they build nests in holes in buildings and nest boxes (Møller et al. 2012). However, the house sparrow is considered a typical town dweller, while the tree sparrow is believed to rely more on natural resources, for example it often breeds in tree holes (Pinowski 1966, 1967; Shaw et al. 2008; Kuczyński and Chylarecki 2012). In recent years, the population size of house sparrows in Poland and other European countries has decreased both in towns and farmlands, but the population size of tree sparrow is stable or even increasing (Chamberlain et al. 2007; Kuczyński and Chylarecki 2012). Despite the often high abundance of both species, there are still relatively few studies on their spatial ecology. Existing data are old, mainly from times when both species were seen as farmland pests (Pinowski and Kendeigh 1977; Cordero 1993). Since both species have a similar body size and utilize similar resources (food, nesting habitat, and sites), one may expect a negative relationship between their relative abundances. Thus, the effect of resources on their population abundance may depend on the abundance of a counterpart species, which, in statistical formula, implies a significant interaction between the effect of the environmental variable and abundance of the potential competitor. Adding to this, the abundance of pigeons (e.g., *Columba livia*) and corvids (e.g., *Pica pica*) often varies across towns in Europe (Fontana et al. 2011) and these species have a diet and habitat overlapping with both sparrow species (Holland et al., 2006). Pigeons and corvids are much larger species thus, they are potentially stronger competitors to sparrows and their population abundances should negatively affect the sparrow population size (Summers-Smith 2003). Pigeons and corvids may prevent access to food (sparrows usually wait at the edge of a foraging flock) and also access to water left in paddles

and containers (authors' unpublished observations). Additionally, corvids are known as predators of nests, fledglings, and even adult sparrows (Pinowski 1966; Pinowski et al. 1994).

The aim of this article is to investigate the effects of habitat structural complexity, number of potential food resources, and the abundance of different species within an urban environment on the abundance and distribution of house- and tree sparrows. Specifically, we tested following predictions

The abundance of both sparrow species is positively related to shelter, the abundance of human-related food resources and plot covers of tall buildings and lawns which are breeding and foraging sites, respectively.

The abundances of both species should be negatively correlated with road densities because collisions with cars are one of the most important mortality factor in sparrows (Erritzoe et al. 2003).

If biotic interactions (e.g., competition) between two species exist then it is expected that the effect of environmental variables on the abundance of one species should depend on the relative abundance of other sparrow species. Also, abundances of both species should be negatively correlated; however, the negative correlation should be the strongest at low level of resources (breeding habitat, food).

If there are biotic interactions between sparrows and corvids as well as pigeons, then the effect of environmental variables on the abundances of sparrows should vary depending on the abundance of corvids and pigeons. Also, abundances of both sparrows should be negatively correlated with the abundance of these larger potential competitors. However, again, the negative correlation should be strongest at a low level of resources.

## Materials and Methods

### Study area

The study was conducted in Poznań (52°17'34"–52°30'27"N, 16°44'08"–17°04'28"E), in western Poland (Figure 1) in 2010. Poznań is one of the largest Polish cities with 556 thousand inhabitants and covers an area of $261.3 \, km^2$ (population density 2,123 people per $km^2$). The altitude ranges from 60 m to 157 m a.s.l. The climate of Poznań is a humid continental climate with relatively cold winters and fairly hot summers (mean temperature in the coldest month, December, is –0.2 °C and in the hottest, June, 17.4 °C). Annual rainfall is about 500 mm (Anonymous 2003).

### Bird counts

To estimate the relative abundances of both sparrows, we selected sixty $0.5 \, km \times 0.5 \, km$ (25 ha) plots within the residential areas of the city. The house sparrow does not occur in habitats other than human settlements. The tree sparrow also occurs mostly in residential areas. As we aimed to gain information about the interactions between the two species, the inclusion of other habitats (e.g., arable fields) would have produced meaningless results. Residential areas are also the dominating land cover in the city of Poznań. Plots were chosen by a random selection of geographical coordinates of points that were upper-left corners of the square plots. The mean distance between the borders of the nearest plots was 1050 m (minimal was 122 m, maximal was 2745 m). The selection was performed with Quantum 1.7 GIS software. Sparrows were surveyed in June. This period covers the peak of reproduction of these species (Pinowski 1965, 1968). Three counts were done in each plot at approximately 10-day intervals. Each visit to each plot lasted 1 h. Counts were made during favorable weather conditions (without
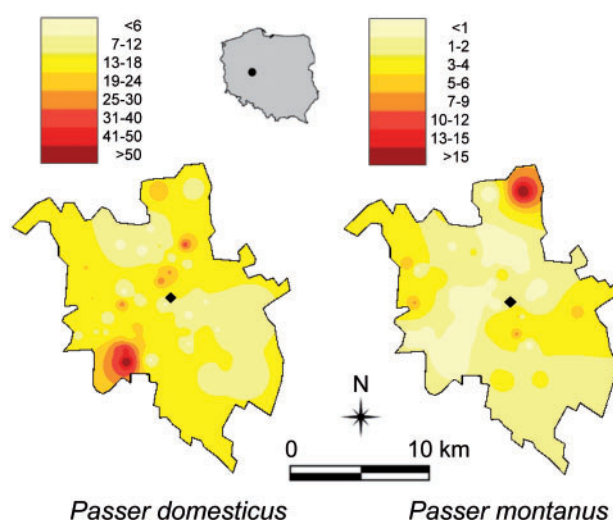


**Figure 1.** The interpolated abundance (number of individuals per 25 ha plot) of house and tree sparrows in residential areas within the administrative boundaries of Poznań. The interpolation was performed with an inverse distance method in Quantum GIS software. The black diamond indicates the historical centre of the city.

rain and heavy wind). Observers walked in plots (one observer per plot) to cover the entire area visually and aurally. All birds seen within plots were counted. We counted all seen birds because these sparrow species are social and it appeared difficult to assess their number based on hearing only. When a sparrow was seen or heard, we scanned by binoculars all buildings (including roofs and windowsills), trees and shrubs to count the number of individuals. We also visited all sites where birds foraged. Observers did not count birds that were suspected to be already noted. Because many sparrows breed in inaccessible lofts we were unable to establish the exact number of breeding pairs and our analysis was based on the mean number of individuals noted during three surveys. Mean number was strongly positively correlated with maximal numbers (house sparrow: $r = 0.981$, $P < 0.001$, tree sparrow $r = 0.956$, $P < 0.001$) and minimal numbers (house sparrow: $r = 0.939$, $P < 0.001$, tree sparrow $r = 0.916$, $P < 0.001$).

### Explanatory variables

The following explanatory variables potentially affecting the relative abundance of sparrows were measured in each plot (see Table 1 for an overview of the variables including mean values and standard errors).

Abundance of pigeons. We recorded three species: the feral pigeon *Columba livia* (average abundance ± *SE* was 13.6 ± 1.74 individuals per 10 ha), the common wood pigeon *Columba palumbus* (0.8 individual ± 0.10 per 10 ha) and the collared dove *Sterptopelia decaocto* (1.2 ± 0.15 individuals per 10 ha) in the same plots where sparrows were counted. The mean total number of all individuals of these species recorded in a plot was later used in analyses as the proxy of their abundance. We decided to pool abundances of these species because their diet overlaps with the diet of sparrows (Holland et al. 2006) and all are larger and thus potentially stronger competitors than sparrows. Analysis with the most abundant species only—the feral pigeon—produced similar results (Tables S1–S2 in Supplementary material).

The abundance of corvids. Two species were recorded, the magpie *Pica pica* (1.4 ± 0.24 individuals per 10 ha) and the hooded crow

**Table 1.** Mean values ($\pm$ *SE*) of variables investigated in the studied plots ($n = 60$) in residential areas of Poznań

| Variable code | Explanation | Mean | SE | Min–Max |
|---|---|---|---|---|
| HouseSpar | Population abundance (individuals per 10 ha) | 14.5 | 1.3 | 0–62.7 |
| TreeSpar | Population abundance (individuals per 10 ha | 1.8 | 0.4 | 0–17.6 |
| Corvids | Population abundance (individuals per 10 ha) of corvids (*Pica pica* and *Corvus cornix*) | 1.6 | 0.2 | 0–10.9 |
| Pigeons | Population abundance (individuals per 10 ha) of all pigeon species (*Streptopelia decaocto*, *Columba palumbus* and *Columba livia domestica*) | 15.7 | 1.7 | 0.5–54.0 |
| FoodRes | Sum of all food resources (waste bins, restaurants, groceries, feeding sites | 32.9 | 4.9 | 0–197 |
| StreetDen | Density of streets (m per 10 ha) | 1346 | 45 | 515–1970 |
| HedgDen | Density of hedgerows (m per 10 ha) | 173 | 15 | 0–485 |
| GreenArea | Percentage of the plot covered by green area (parks, lawns, fallows) | 22.9 | 2.1 | 0–63 |
| HighBuild | Percentage of the plot covered by tall buildings | 28.6 | 3.4 | 0–89 |
| CityCentr | Distance of the plot from the city centre (km) | 4.5 | 0.3 | 0.1–9.3 |

*Corvus cornix* (0.1 ± 05 individuals per 10 ha) during sparrow counts. These two species are commonly seen foraging with sparrows and are also predators both of adult sparrows and their broods.

The availability of human-related food resources. We counted all sites where birds fed (based on direct observations of people feeding birds and left food remains), the number of litter-bins (of any type) and the number of grocery stores and fast-food restaurants. The number of food resources was a sum of these elements (Table 1). When litter-bins occurred in groups (e.g., in refuse heaps) each litter-bin was treated as a separate unit. We originally intended to use each category as a separate variable but their numbers were highly positively correlated (all $r > 0.700$).

The density of streets (metres per 10 ha, Table 1). Traffic may influence mortality of sparrows through collisions with vehicles (Erritzoe et al. 2003).

The density of hedgerows (m per 10 ha, Table 1). A hedgerow was defined as a line of closely spaced shrubs below 4 m high. We expected a positive association between densities of sparrows and hedgerows because the latter may be a shelter for both species.

The percentage cover of green space (Table 1). Green space was defined as all the parks, squares, lawns, and fallows within residential areas. As they provide foraging habitat with natural food resources for sparrows, we expected positive correlation between green cover and the abundance of both sparrows.

The percentage cover of tall buildings (of over four floors) in the plot (Table 1). We expected a positive association between this variable and the abundance of sparrows because more people live in tall buildings, therefore more additional nesting sites and food (e.g., on windowsills or just thrown out the window) for both sparrow species is expected in such areas.

We also noted the percentage cover of low-rise buildings up to four floors (e.g., family houses), but since this variable was highly negatively correlated with the cover of tall buildings ($r = -0.795$, $P < 0.001$), only the latter was used in analyses. It was a dominating type of residential area, specific for the urban environment.

Distance of the plot to the city centre (taken as the historical central square in the Old City district; Table 1, Figure 1). This variable represents the urbanization gradient, and we expected a negative association of this the variables with the abundances of house sparrow (increasing abundances towards the city centre) and a positive

association (decreasing abundances towards the city center) with the tree sparrow, which is a less urbanized species.

Variables 1–3 were recorded directly in the plots. Variables 4–8 were determined from aerial photos supported by field data and calculated in Quantum 1.7 GIS software. Our dependent variables were the relative abundance of house sparrows and tree sparrows calculated as the mean number of individuals per 25 ha plot from the three surveys.

## Statistical analysis

The first analytical goal was to estimate the detection probability of both species within plots using the approach proposed by MacKenzie et al. (2002). The detection probability was modeled using a generalized linear model with a logit-link function in Presence 4.0 software (Hines 2006). We modeled two scenarios: a detection probability, which was the same among surveys $p(.)$, and a survey-specific detection probability of individuals $p(t)$. However, the estimated proportion of plots occupied did not differ substantially from our naive estimates of occupied plots without correction for detectability. Also, detection probabilities were high (see results). Therefore, it was not necessary to consider imperfect detectability in our statistical analyses (Cozzi et al. 2008).

We used Moran's I correlograms (Legendre 1993) to describe the spatial aggregation in densities and occupancy of both species. The spatial autocorrelation value at a given distance class indicates how predictable (positively or negatively) population density or occupancy is at a given point of the sampling framework. Autocorrelation using Moran's index typically varies between $-1$ and 1, with non-significant values close to zero. To test the significance of the autocorrelation, we estimated $P$-values based on 500 Monte Carlo simulations. As we found statistically significant autocorrelation (see results), we used inverse distance weighted interpolation (Shepard 1968) implemented in QGIS 1.7 to visualize abundances of both sparrows in Poznań city. This interpolation method assumes that plots that are close to one another are more alike than those that are farther apart. This interpolation method uses the abundance recorded in the surrounding plots and those abundances recorded closest to the prediction location have more influence on the predicted value than do those farther away.

We used model selection procedures based on information theory (Burnham and Anderson 2002) to identify factors affecting the

relative abundance of both species in Poznań. For each sparrow species, we built a generalized linear model with a negative binomial error variance and log-link function for a dependent variable. As explanatory independent variables we used variables 1–8 presented above. Moreover, we included interaction terms:

abundance of other sparrow species × density of food resources,
abundance of other sparrow species × density of hedgerows,
abundance of other sparrow species × cover of green spaces,
abundance of other sparrow species × cover of high buildings,
abundance of corvids × density of food resources,
abundance of corvids × density of hedgerows,
abundance of corvids × cover of green spaces,
abundance of corvids × cover of high buildings,
abundance of pigeons × density of food resources,
abundance of pigeons × density of hedgerows,
abundance of pigoens × cover of green spaces, and
abundance of pigeons × cover of high buildings.

Akaike information criterion corrected for a small sample size (AICc) was used to identify the most parsimonious model from each candidate set. To take spatial autocorrelation into account, we applied the approach proposed by Diniz-Filho et al. (2008). We fixed a spatial variable which was obligatorily present in all models to eliminate spatial autocorrelation in the residuals. The fixed spatial variable was defined as an autoregressive term given by $\rho WY$ where W was the connectivity matrix, Y the response variable and $\rho$ the autoregressive coefficient (Dormann et al. 2007). Finally, we ranked all possible model combinations according to their ΔAICc values and used models with the lowest AICc together with associated weight values (the probability that a given model is the best) as those best describing the data. We considered models with ΔAICc lower than 2 as equally well supported (Burnham and Anderson 2002). We used model averaging for estimates of function slopes of parameters of interest (Burnham and Anderson 2002). For averaging, we used models with weights which had ΔAICc values lower than four (Burnham and Anderson 2002).

We used square root transformation (for human-related food resources, hedgerow density, cover of green area, cover of tall buildings and abundances of two sparrows, corvids, and pigeons) to reduce the effects of outlier observations (Quinn and Keough 2002). Moreover, in all regression models, variables were standardized (with mean = 0 and standard deviation = 1) to allow a direct comparison of beta (slope) estimates. There was no collinearity between the explanatory variables ($r < 0.5$ for every pair; Mertler and Vannatta 2002).

Moran's statistics and spatial autocovariates were computed in SAM 4.0 statistical software (Rangel et al. 2010). The model selection procedure was performed in the MuMIn library (Bartoń 2014 ) in R (R Core Developmental Team 2015). All estimates of statistical parameters (means, betas) are quoted with standard errors (SE) and 95% confidence intervals (CI). We considered that the slopes of the regression function to be significant if their 95% CI did not overlap with zero.

## Results

The detection probability of house sparrows in a plot was near perfect (0.99 ± 0.01), and the model with a constant survey-specific detection probability had almost the same support (AICc = 35.28, weight = 0.51) as the model with a constant detection probability (AICc = 35.97, weight = 0.49). The detection probability of tree sparrows in a plot was also high (0.80 ± 0.04), and the model with a
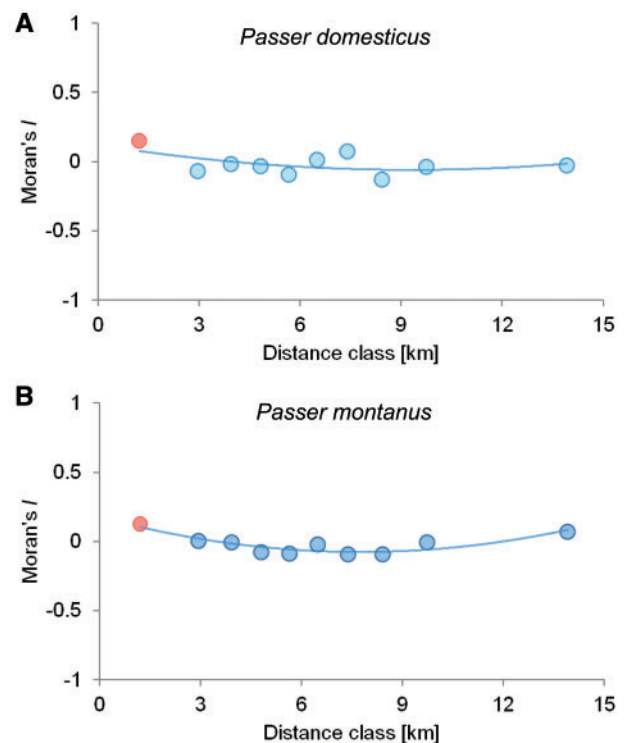


**Figure 2**. Spatial autocorrelogram (Moran's I) for (a) abundance of house sparrows and (b) abundance of tree sparrows in 60 plots in Poznań. Red circles indicate spatial autocorrelations significant at $\alpha < 0.05$.

constant detection probability had slightly better support (AICc = 196.56, weight = 0.55) than the model with survey-specific detection probability (AICc = 198.00, weight = 0.45). The relative abundance of house sparrows was higher than that of tree sparrows ($t = 12.851$, $df = 110$, $P < 0.001$, Table 1). We found statistically significant positive spatial autocorrelation of both house sparrow and tree sparrow population abundance at a distance up to 2 km (Figure 2).

Model selection based on Akaike's criterion showed that six models were equally good and explained on average 35% of the variation in the relative abundance of house sparrows (Table 2). Examination of slope estimates and their standard errors showed that the abundance of house sparrow was positively correlated with pigeon population abundance, but it was negatively related to anthropogenic food resources (Table 3). However, there were significant interaction terms among the best models (Tables 2 and 3). Corvids and tree sparrows negatively correlated with abundances of house sparrows but only when food resources were low (Tables 2 and 3, Figure 3). Also, the abundance of tree sparrows negatively correlated with that of house sparrows when cover of tall buildings was high (Tables 2 and 3, Figure 3). Contrarily, the relative abundance of pigeons positively correlated with that of house sparrows in plots with high and moderate cover of tall buildings but not with the cover of low buildings (Tables 2 and 3, Figure 3).

Model selection based on Akaike's criterion showed that 10 models were equally good and explained 23% of the variation in the relative abundance of tree sparrows on average (Table 2). Examination of function slopes and their standard errors revealed that the abundance of tree sparrow positively correlated with distance from the city centre and the density of streets; however, there were statistically significant interaction terms in the

**Table 2.** Best models explaining the relative abundance of house sparrows and tree sparrows in 60 plots in Poznań

| Model | $R^2$ | logLik | AICc | delta | $w$ |
| --- | --- | --- | --- | --- | --- |
| **House Sparrow** | | | | | |
| Corvids + HighBuild + FoodRes + Pigeons + TreeSpar + Corvids × FoodRes + HighBuild × Pigeons + HighBuild × TreeSpa + FoodRes × TreeSpar | 0.38 | −242.7 | 516.03 | 0 | 0.13 |
| Corvids + HighBuild + FoodRes + Pigeons + TreeSpar + Corvids × FoodRes + HighBuild × TreeSpa + FoodRes × TreeSpar | 0.36 | −244.72 | 516.95 | 0.92 | 0.08 |
| Corvids + HighBuild + FoodRes + Pigeons + TreeSpar + Corvids × FoodRes + HighBuild × Pigeons + HighBuild × TreeSpa + FoodRes × Pigeons + FoodRes × TreeSpar | 0.37 | −241.56 | 517.02 | 0.99 | 0.08 |
| Corvids + FoodRes + Pigeons + Corvids × FoodRes | 0.30 | −250.62 | 517.4 | 1.36 | 0.06 |
| Corvids + HighBuild + FoodRes + Pigeons + TreeSpar + Corvids × HighBuild + Corvids × FoodRes + HighBuild × Pigeons + HighBuild × TreeSpa + FoodRes × TreeSpar | 0.34 | −241.74 | 517.4 | 1.37 | 0.06 |
| Corvids + HighBuild + FoodRes + Pigeons + StreetDen + TreeSpar + Corvids × FoodRes + HighBuild × Pigeons + HighBuild × TreeSpa + FoodRes × TreeSpar | 0.35 | −241.84 | 517.59 | 1.56 | 0.06 |
| **TreeSparrow** | | | | | |
| Corvids + FoodRes + HedgDen + HouseSpar + Pigeons + StreetDen + Corvids × FoodRes + HedgDen × Pigeons | 0.23 | −136.23 | 303.1 | 0 | 0.07 |
| Corvids + GreenArea + CityCentr + HedgDen + HouseSpar + Pigeons + StreetDen + Corvids × GreenArea+ Corvids × FoodRes + HedgDen × Pigeons | 0.24 | −133.01 | 303.35 | 0.25 | 0.06 |
| Corvids + GreenArea + CityCentr + FoodRes + HedgDen + Pigeons + StreetDen + Corvids × GreenArea + Corvids × FoodRes + HedgDen × Pigeons | 0.23 | −134.79 | 303.49 | 0.38 | 0.06 |
| Corvids+GreenArea + CityCentr + FoodRes + HedgDen + HouseSpar + Pigeons + StreetDen + Corvids × GreenArea + Corvids × FoodRes × HouseSpar + HedgDen × Pigeons | 0.25 | −131.4 | 303.72 | 0.61 | 0.05 |
| Corvids + GreenArea + CityCentr + FoodRes + HedgDen + HouseSpar + Pigeons + StreetDen + Corvids × FoodRes + HedgDen × Pigeons | 0.21 | −134.97 | 303.85 | 0.75 | 0.05 |
| Corvids + CityCentr + FoodRes + HedgDen + Pigeons + Street + Corvids × FoodRes + HedgDen × Pigeons | 0.22 | −138.2 | 303.91 | 0.8 | 0.05 |
| Corvids + CityCentr + FoodRes + HedgDen + HouseSpar + Pigeons + StreetDen+ Corvids × FoodRes + FoodRes × HouseSpar + HedgDen × Pigeons | 0.23 | −135.13 | 304.18 | 1.07 | 0.04 |
| Corvids + HighBuild + FoodRes + HedgDen + HouseSpar + Pigeons + StreetDen + Corvids × FoodRes + HedgDen × Pigeons | 0.21 | −136.89 | 304.42 | 1.31 | 0.04 |
| Corvids + GreenArea + CityCentr + FoodRes + HedgDen + Pigeons + StreetDen + Corvids × FoodRes + HedgDen × Pigeons | 0.22 | −136.89 | 304.42 | 1.32 | 0.04 |
| Corvids + GreenArea + CityCentr + FoodRes + HedgDen + HouseSpar + Pigeons + StreetDen + Corvids × FoodRes + FoodRes × HouseSpar + HedgDen × Pigeons | 0.23 | −133.79 | 304.91 | 1.8 | 0.03 |

For explanation of the variable codes: see Table 1.

**Table 3.** Factors affecting the abundance of house sparrow and tree sparrow in Poznań

| Effect | Estimate | SE | Z | P |
|---|---|---|---|---|
| **House Sparrow** | | | | |
| Intercept | 3.369 | 0.093 | 36.323 | **<0.001** |
| Corvids | 0.057 | 0.079 | 0.714 | 0.475 |
| FoodRes | −0.313 | 0.106 | 2.949 | **0.003** |
| HighBuild | −0.124 | 0.104 | 1.196 | 0.232 |
| Pigeons | 0.338 | 0.090 | 3.74 | **0.000** |
| TreeSpar | −0.131 | 0.077 | 1.699 | 0.089 |
| SpatialAutocovariate | 0.351 | 0.070 | 5.024 | **<0.001** |
| StreetDen | 0.085 | 0.075 | 1.145 | 0.252 |
| FoodRes × Corvids | 0.304 | 0.087 | 3.499 | **0.000** |
| HighBuil × Pigeons | 0.201 | 0.098 | 2.045 | **0.041** |
| HighBuil × TreeSpar | −0.238 | 0.084 | 2.819 | **0.005** |
| TreeSpar × FoodRes | 0.321 | 0.111 | 2.882 | **0.004** |
| FoodRes × Pigeons | −0.129 | 0.077 | 1.687 | 0.092 |
| HighBuild × Corvids | −0.124 | 0.102 | 1.211 | 0.226 |
| **Tree Sparrow** | | | | |
| Intercept | 1.029 | 0.172 | 5.971 | **<0.001** |
| Corvids | 0.288 | 0.213 | 1.354 | 0.176 |
| CityCentr | 0.650 | 0.259 | 2.51 | **0.012** |
| FoodRes | −0.298 | 0.267 | 1.117 | 0.264 |
| GreenArea | 0.288 | 0.178 | 1.622 | 0.105 |
| HedgDen | −0.411 | 0.218 | 1.884 | 0.060 |
| HighBuild | −0.330 | 0.326 | 1.014 | 0.311 |
| HouseSpar | −0.331 | 0.249 | 1.331 | 0.183 |
| Pigeons | 0.374 | 0.229 | 1.631 | 0.103 |
| SpatialAutocovariate | −0.039 | 0.153 | 0.255 | 0.799 |
| StreetDen | 0.787 | 0.200 | 3.939 | **<0.001** |
| Corvids × FoodRes | −0.935 | 0.273 | 3.425 | **0.001** |
| HedgDen × Pigeons | −0.552 | 0.198 | 2.785 | **0.005** |
| Corvids × GreenArea | 0.307 | 0.153 | 2.009 | **0.045** |
| FoodRes × HouseSpar | 0.399 | 0.222 | 1.796 | 0.072 |

Averaged parameters are presented. Statistical significance of estimates in the last two columns. Statistically significant relationships are emboldened. For further explanations see Tables 1 and 2.

best models (Tables 2 and 3). These interactions indicated that the abundance of corvids positively correlated with abundances of tree sparrows when food resources were low (Tables 2 and 3, Figure 4). However, corvids negatively correlated with tree sparrows when the cover of green areas was low but positively correlated with tree sparrows if the cover was moderate or high (Tables 2 and 3, Figure 4). The abundance of pigeons positively correlated with the abundance of tree sparrows when hedgerow density was low but negatively correlated with the abundances of tree sparrows when the hedgerows grew more densely in plots (Tables 2 and 3, Figure 4).

## Discussion

We showed that relative abundances of both sparrows were correlated with several environmental variables. However, the effect of these environmental variables was altered by variables describing biotic relations as indicated by statistically significant interaction terms in the best models. The biological meaning of these statistical interaction terms is that abundances of different species may affect others, but the strength and direction of these relationships changes with varying values of environmental variables. These findings indicate that species distribution/abundance models should include not
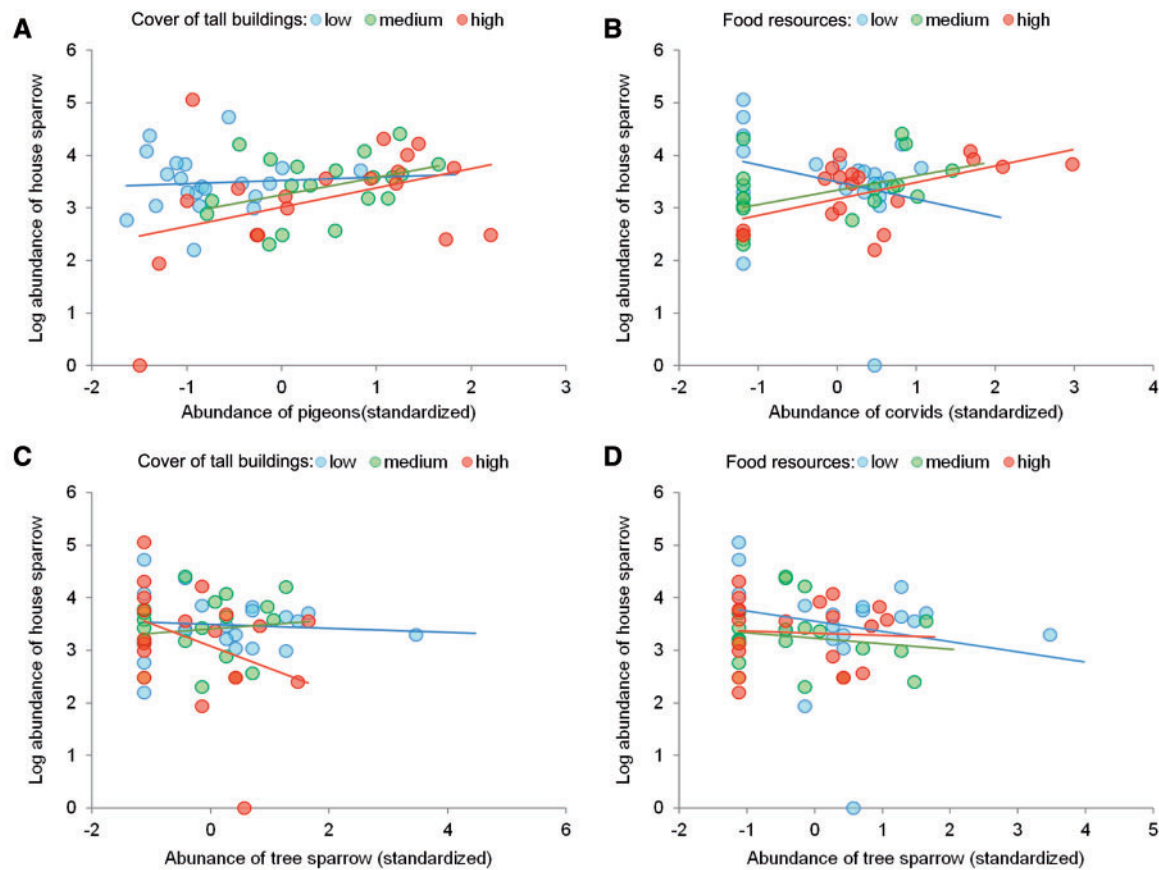
only the abundance of other species (predators, competitors) as the additive effect (modelled as a covariate) together with habitat variables (e.g., Przybylska et al. 2012; Baker et al. 2014; Morelli and Tryjanowski 2015) but also include interaction terms among these types of variables. Inspection of the function slopes of interaction terms indicated that function slopes of biotic variables (species abundances) often had opposite signs across levels of environmental variables.

### Biotic interactions versus environmental variables

A statistically significant effect was found for the number of human-related food resources that was negatively correlated with the abundance of house sparrows. This result contradicts our expectations. Usually, the availability of such food attracts a number of species, which congregate in such places (Belant 1997; Jerzak 2001 Chace and Walsh 2006; Skórka et al. 2009; Maciusik et al. 2010). The negative effect of human-related food resources indicates that during the breeding period sparrows may use more natural food sources (e.g., invertebrates, weeds), whose importance for nestlings is known (Pinowski and Kendeigh 1977). It is also possible that human-related food resources were correlated with a confounding variable that was not included in this study. For example, anthropogenic food resources may attract some potential predators of sparrows such as feral cats. They may hunt sparrows and also affect their abundance by the non-lethal effect of fear (Lima 1998; Turner and Bateson 2000; Krauze-Gryz et al. 2013).

Moreover, it must be noted that the association between the abundance of the two sparrow species and food resources was altered by the abundance of corvids. The abundance of corvids negatively correlated with abundances of house sparrows but this relationship was positive if the level of food resources was higher. In our opinion, this may be evidence for competition between these species. Corvids are known to forage intensively on human-related resources (Kristan et al. 2004; Lenda et al. 2012). When resources are rare corvids may outcompete house sparrows or hunt their chicks or adults (Pinowski 1966; Pinowski et al. 1994). However, when human-related resources are abundant a positive correlation between corvids and house sparrows may emerge. Corvids are known for aggressive mobbing behaviour towards aerial and ground predators such as Eurasian sparrowhawks *Accipiter nisus* and feral cats. These predators may negatively affect sparrow populations (Biaduń 2006; Bell et al. 2010), and mobbing and vigilance behaviors are the most efficient when the abundance of birds is high (Krams et al. 2009). As opposed to house sparrows, the association between abundances of corvids and tree sparrows was positive when food resources were low. It is possible that, if human-related food sources are low, corvids may seek natural food and tree sparrows may use this public information (Danchin et al. 2004), which, in turn may increase their abundance.

Direction of the relationship between tree sparrows and corvid abundance varied also depending on the cover of green areas. We found that the abundance of tree sparrows was negatively correlated with that of corvids when the cover of green areas was low. This supports the above explanations, that tree sparrows depend on more natural habitats in an urban environment. Tree sparrows may find natural food resources (e.g., weed seeds) in green areas (Pinowski and Kendeigh 1977), and people often visit such places and frequently feed birds, mostly corvids (Kristan et al. 2004). This, of course, is a tentative explanation that should be studied in detailed observational and experimental study.

**Figure 3.** The effect of the abundance of other species on the abundance (number of individuals in 25 ha plot) of house sparrows modified by environmental variables: (A) the interaction between the abundance of pigeons and the cover of tall buildings, (B) the interaction between the abundance of corvids and food resources, (C) the interaction between the abundance of tree sparrow and the cover of tall buildings, (D) the interaction the between abundance of tree sparrows and food resources. The environmental (continuous) variables were divided into categorical variables with the levels: low (blue circles and fitted line), medium (green circles and fitted line) and high (red circles and fitted line) . Each level contained 20 cases.

Contrary to expectations, the abundance of house sparrows was positively correlated with the abundance of pigeons indicating some kind of social facilitation between these birds. It is an interesting result because pigeons are much larger species than house sparrows and often forage in flocks which allow them to monopolize food resources. Body size is also one of the major indicators of competitive ability in animals (Alatalo and Moreno 1987; Jonart et al. 2007). However, smaller species, if abundant enough, are able to resist larger species or avoid competition (Quintana and Yorio 1998). Moreover, smaller species may be more efficient foragers (scramble competition, Lima et al. 1999). It is possible that house sparrows may directly benefit from the presence of pigeon flocks as social information on scattered food resources. We also observed sparrows foraging on the ground within flocks of feral pigeons and collared doves and, although some aggressive encounters were noted, the food items taken by the sparrows were smaller than those eaten by the pigeons (authors' unpublished data). It is also likely that smaller sparrows may benefit from the social behaviour of pigeons in terms of the improved vigilance of predators (Lima 1995). However, the above explanations seem to be relevant only when the cover of tall buildings is high. Tall buildings are a usual breeding habitat for feral pigeons—the most abundant species included in the variable "pigeons" in this study (Mizera 1988; Jokimäki and Suhonen 1998; Buijs and van Wijnen 2001; Przybylska et al. 2012). When the cover of tall buildings was low, the estimate of function slope indicated no

or negative associations between pigeons and house sparrow and tree sparrow, respectively.

The association between pigeons and tree sparrows also depended on the density of hedgerows. If the density of hedgerows was low, the abundance of tree sparrows increased with the abundance of pigeons, but it decreased if hedgerows became more densely distributed. Hedgerows may provide food resources for many species, including sparrows, and shelter from predators in an urban environment (Deckers et al. 2004; Biaduń 2006). However, pigeons also frequently seek food along hedgerows (Przybylska et al. 2012). Thus, at a higher density of hedgerows, pigeons probably use them as a foraging site and perhaps negatively affect tree sparrows. This should be investigated in more detail in further study.

## Possible interactions between house sparrow and tree sparrows

The abundance of house sparrows was higher than the abundance of tree sparrows what may reflect the different time of colonization of the urban environment in Europe by these species (Møller et al. 2012). The abundances of house sparrows and tree sparrows were also spatially structured with significant positive spatial autocorrelation recorded in our study area. They were positively autocorrelated up to a distance of 1.5–2 km. This distance is short and corresponds to low dispersal abilities observed in these species
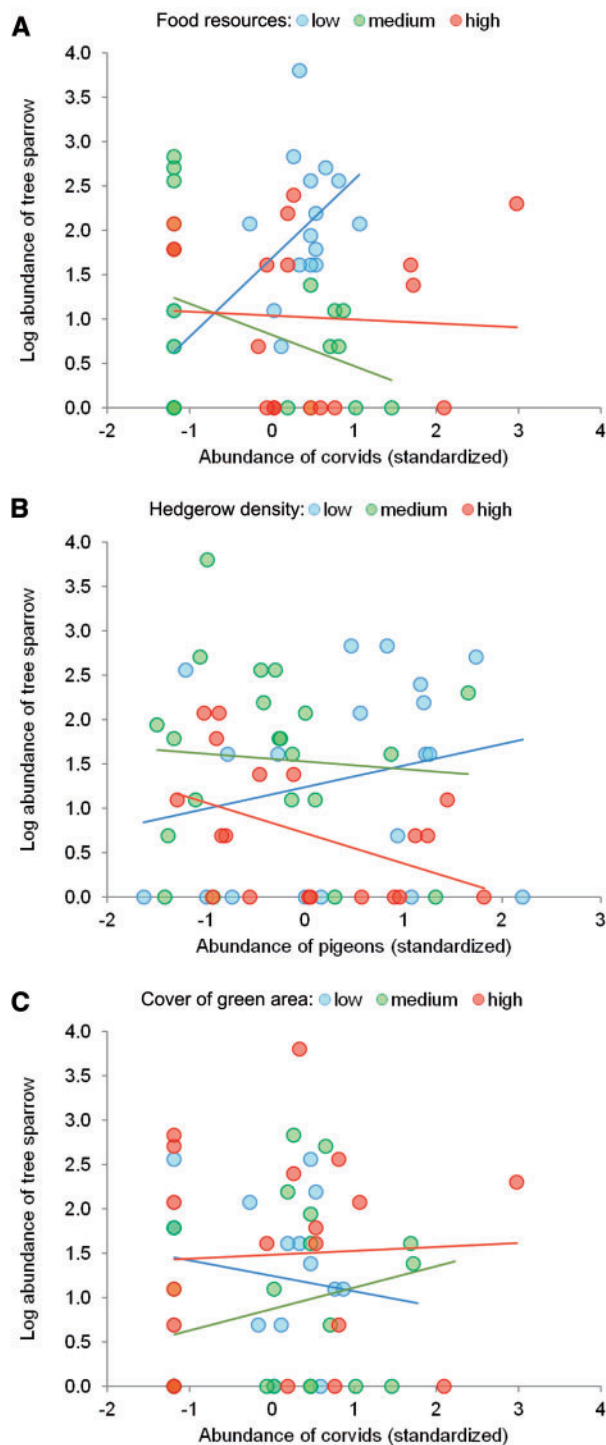
**Figure 4.** The effect of the abundance of other species on the abundance (number of individuals per 25 ha) of tree sparrows modified by environmental variables: (A) the interaction between the abundance of corvids and food resources, (B) the interaction between the abundance of pigeons and the density of hedgerows, (C) the interaction between the abundance of corvids and the cover of green areas. For further explanations: see Figure 3.

(Pinowski 1965, 1967). The spatial autocorrelation was also a statistically significant predictor of house sparrows after accounting for other effects. In models for tree sparrow abundance, however, the spatial autocorrelation was non-significant indicating that physical

attributes and biotic interactions play a more important role in the colonization of urban environments by this species.

In statistical models for the abundance of house sparrows, the abundance of tree sparrows was one of the predictors that interacted with the number of food resources as well as the cover of tall building. When human-related food resources were low, the abundance of tree sparrows was negatively associated with the abundance of house sparrows. This was not the case at a higher level of food supply. These results may be an indication of competition for food between the species; however it must be underlined that human-related food resources generally negatively affected the abundances of house sparrow. The abundance of tree sparrows also negatively correlated with the abundance of house sparrows when the cover of tall buildings was high. We speculate that, if competition for breeding sites plays a role then the negative association between tree sparrows and house sparrow should be the highest at a low cover of high buildings. It is also possible that a high cover of tall buildings attracts a large number of pigeons that may actually indirectly increase competition for breeding sites between the two sparrow species. Interestingly, no statistical model explaining the abundance of tree sparrows contained significant effects of house sparrow abundance. Assuming competitive interactions between these two sparrow species this indicates that the tree sparrow is possibly a stronger competitor than the house sparrow despite its generally smaller body size (Cordero 1993). Therefore, the colonization of an urban environment by tree sparrows might be another factor responsible for the population decrease of house sparrows in towns and cities of Europe (Pinowski and Kendeigh 1977).

## Study limitations

Our data on the abundance of house and tree sparrows have limitations which should be taken into account when interpreting the results and generalizing to other areas and species. First, our study is correlative. Abiotic and biotic interactions are very complex and our data might not allow for an explicit delineation of mechanisms of the interactions between species and environmental variables (Wisz et al. 2012). Thus, our finding should be treated as a starting point to better understand the underlying mechanisms shaping the observed patterns of sparrow abundance.

Several associations between the abundance of sparrows and environmental variables seem to be difficult to explain, for example, interaction terms between abundance of pigeons and hedgerow density, or interaction between the pigeons' abundance and the cover of tall buildings. Difficulties in explaining these statistically significant interactions suggest that our biological interpretation should be treated with caution. Given the complexity of biotic interactions we must also accept the possibility that some hypotheses stated by us to explain our results may be biologically irrelevant.

Results of our study might be also affected by the manner in which variables were defined (Gregory et al. 2004). However, our sample size, despite being large, could not allow us to accomplish complex species-specific analyses including models with many interaction terms. Analyses performed with only the most abundant pigeon (feral pigeon) produced similar results as in the case of analysis with pooled abundances of pigeons and doves. We believe this latter variable is good as it includes the total potential impact of large-bodied species with a diet highly overlapping that of both sparrow species. Such multiple competitors are common in bird assemblages (Triplet et al. 1999). Similar criticism applies to the definition of human-related food resources, which do not include natural food

sources (Hutto 1990). However, numbers of all types of human-related food resources were positively correlated among each other which supports joining them into one variable.

Despite all these limitations, our general conclusion remains unchanged. Our study showed that each individual species is entangled in complex biotic relations that are altered if habitat composition changes. Despite these relationships seeming to be complicated, our approach allowed us to more deeply understand the functioning of sparrow species populations in the urban environment. Our results indicate that there were interactions between the two sparrow species as well as among other species. The mechanisms of these relationships are complex and possibly include inter-specific competition between sparrows (and corvids) and the social facilitation of sparrows (e.g., by pigeons) that may switch from one to another as habitat composition or food resources change. Thus, relationships between biotic factors and habitat variables should be included in statistical models predicting species abundances and occurrences as the interaction term between these two types of factors.

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## Supplementary Material

Supplementary material can be found at http://www.cz.oxfordjournals.org/.

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