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Research Paper

Urban core areas are important for species conservation: A European-level analysis of breeding bird species

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ABSTRACT

Natural habitats and species richness have decreased due to the urbanization. The main aim of this study was to determine whether heavily urbanized town centers can also harbor threatened bird species. Twenty-six threatened species nested in the most urbanized areas of European towns. Species-rich areas had a high number of threatened species, indicating that overall species richness could be used as a surrogate for the large number of threatened bird species. Threatened species were more likely to be found in town centers as their distribution range increased. Neither landscape nor plot-level variables explained the species richness of threatened species, which was likely due to the homogeneous habitat structure of urban core zone areas in Europe. The occurrence of *Falco tinnunculus* increased with increases in human density within a built-up area. The occurrence of *Hirundo rustica* and *Muscicapa striata* decreased with increases in the proportion of built-up areas in the surrounding landscape. The occurrence of *Delichon urbica* and *Muscicapa striata* decreased with increases in habitat diversity and the proportion of buildings in the study plot. The most common threatened bird species nested in cavities or buildings. The availability of suitable nesting sites or protection from predators can support the occurrence of cavity nesters in towns. We suggest that modern architecture should account for the breeding habitat needs of cavity-nesting species in building design and that urban green management must consider the occurrence of old trees with cavities or alternatively use nest boxes to support the occurrence of threatened, cavity-nesting bird species.

1. Introduction

Globally, more people currently live in urban areas than in rural areas, and simultaneously, urbanized areas are increasing at a higher rate than urban populations due to urban sprawl (UN, 2014). Therefore, urban nature is important to an increasing number of people, and correspondingly, their views related to conservation are formed in urban environments (Savard, Clergeau, & Mennechez, 2000; Warren & Lepczyk, 2012; Shanahan, Strohbach, Warren, & Fuller, 2014). Therefore, wildlife conservation in urban environments is increasingly important (e.g., Miller & Hobbs, 2002; Dunn, Gavin, Sanchez, & Solomon, 2006; Lepczyk & Warren, 2012; Gil & Brum, 2014). In general, urbanization has been considered to be one of the most important factors responsible for ongoing biodiversity loss and the homogenization of environments (Blair, 1996, 2001; Marzluff, 2001; McKinney, 2002, 2006; Jokimäki & Kaisanlahti-Jokimäki, 2003; Chace & Walsh, 2006; Clergeau, Croci, Jokimäki, Kaisanlahti-Jokimäki, & Dinetti, 2006; Francis & Chadwick, 2013; Ferenc et al., 2014). A recent review indicated that towns have lost substantial amount of biodiversity compared to peri-urban areas (Lepczyk et al., 2017). It is important to know which species can tolerate human-induced disturbance and how to minimize the possible negative effects of urban management on species living in towns to support, or even increase, biodiversity in towns (Blair, 2001; Alvey, 2006; Devictor, Julliard, Couvet, Lee, & Jiguet, 2007; Kark, Iwaniuk, & Banker, 2007; Croci, Butet, & Clergeau, 2008; Rutz, 2008; Jokimäki, Suhonen, Jokimäki-Kaisanlahti, & Carbó-Ramirez, 2016).

Species do not respond to urbanization equally, and the results in different biogeographical areas might differ (Ortega-Álvarez & MacGregor-Fors, 2009; González-Oreja, 2011; Ferenc et al., 2014; Leveau, Jokimäki, & Kaisanlahti-Jokimäki, 2017). McDonald, Kareiva, and Forman (2008) indicated that urbanization is implicated in the listing of approximately 8% of the terrestrial vertebrate species on the IUCN Red List. Aronson et al. (2014) found quite a few threatened and endangered birds in towns around the world. However, an Australian study indicated that cities might be hotspot areas for threatened species, and approximately thirty percent of Australian threatened species were found to occur in towns (Ives et al., 2016). One reason for the

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Table 1
Basic information about the towns included in the study. Study methods: A = Atlas, M = Mapping, and P = Point surveys. Full references are given in ESM 1.

Town	Numb. of inhab.	Location N°	Species	Threatened	Study method	References
Alkmaar	94,216	52	20	1	M	Smit et al., 1995, 2005; Baeyens, unpub.
Angers	151,279	47	35	5	P	Clergeau, 2000
Arheim	142,636	51	55	8	M	Schoppers, 1999, 2001; Baeyens, unpub.
Berlin	3,405,469	52	12	1	A	Witt, 2005
Bologna	374,425	44	20	5	A	Bernini et al., 1998
Bonn	314,299	50	14	3	M	Rheinwald, 2005
Bratislava	425,459	48	30	11	M	Weiserbs, unpublished
Brussels	1,067,162	50	36	3	M	Weiserbs & Jacob, 2005; Weiserbs, unpub.
Florence	366,488	43	36	9	A	Dinetti & Romani, 2002
Groningen	181,819	53	9	0	M	Modderman et al., 2001; Baeyens, unpub.
Grosseto	77,057	42	16	3	A	Giovacchini, 2001
Hamburg	1,769,117	53	10	3	M	Mulsow, 2005
Heinola	20,605	61	18	5	M	Vauhkonen, 1999
Helsinki	569,611	60	14	4	A	Pakkala et al., 1998
Jyväskylä	130,735	62	18	3	A	Keski-Suomen lintutieteellinen yhdistys, 2011
Kemi	22,680	65	30	8	A	Rauhala & Suopajärvi, 2002
Lahti	99,419	60	26	5	A	Saikko & Loikkanen, 1999
Leiden	117,530	52	32	4	P	Epe et al., 2005; Baeyens, unpub.
Lisboa	564,447	38	9	1	M	Geraldes & Costa, 2005
Liverno	1,555,986	43	20	6	A	Dinetti, 1994
Lyon	470,000	45	21	6	P	Tatibouet, 1981
Marseille	820,900	43	12	3	P	Marchetti, 1976
Montpellier	251,634	43	25	6	P	Caula, 2007
Nantes	280,600	47	33	7	P	Clergeau, 2000
Napoli	1,046,987	40	22	5	A	Fraissinet, 1995
Oulu	131,786	65	19	4	A	Tynjälä et al., 2004
Paris	9,644,502	48	40	9	A	Pellissier et al., 2012
Pavia	71,486	45	27	6	A	Bernini et al., 1998
Pisa	90,482	43	26	6	A	Dinetti, 1988
Prague	1,212,097	50	12	2	A	Šťástný et al., 2005
Rennes	206,229	48	34	5	P	Clergeau et al.,1998; Le Lannic & Collias, 1997
Roma	2,705,603	41	37	7	A	Cignini & Zapparoli, 1996
Rovaniemi	58,943	66	21	5	A	Jokimäki & Kaisanlahti-Jokimäki, 2012
St. Petersburg	4,661,219	59	10	2	M	Khrabryi, 2005
Valéncia	797,654	39	15	6	A	Murgui, 2005
Vienna	1,678,435	48	26	5	M	Holzer & Sziemer, 2005
Warsaw	1,700,536	52	22	5	A	Luniak, 2005
Örebro	95,400	59	16	6	P	Sandström et al., 2006

large number of threatened species found in towns could be that cities are often established in areas of high natural biodiversity (Araújo, 2003; Francis & Chadwick, 2013). Urbanization in Australia is a relatively new phenomenon in a global context; therefore, the results from Europe might be different from those in Australia. In Australia, threatened species can still live in towns for some time due to extinction delay, whereas in Europe, which has a much longer history of urbanization, many threatened species have already disappeared from towns. Due to global urbanization, large-scale analyses are needed to obtain a more general understanding of the role of urbanization in bird species conservation (Marzluff, Bowman, & Donnelly, 2001; Møller, 2009; Evans, Hatchwell, Parnell, & Gaston, 2010; Pautasso et al., 2011; Warren & Lepczyk, 2012; Aronson et al., 2014; Leveau et al., 2017). A small-scale study performed in a restricted area or at few sample sites might contain an inadequate sample of species for analyses and may therefore provide a misleading picture of species occurrence at a global level (Wiens, 1989; Clergeau, Jokimäki, & Snep, 2006; Pellissier, Cohen, Boulay, & Clergeau, 2012).

The role of urban areas in the conservation of threatened species is inadequately understood, and even basic data are lacking from most towns (Niemelä, 1999). We need greater knowledge of threatened breeding bird species richness and occupancy across an entire range of urban environments (Blair, 1996; Fernandéz-Juricic & Jokimäki, 2001; Chace & Walsh, 2006; Kowarik, 2011; Shanahan et al., 2014). Earlier urban ecological studies on threatened birds were mainly conducted in urban green areas, such as parks and woodlots (e.g., Mörtberg & Wallentinus, 2000; Fernandéz-Juricic & Jokimäki, 2001; Donelly & Marzluff, 2004; Fuller, Tratalo, & Gaston, 2009; Aronson et al., 2014; Jokimäki, Kaisanlahti-Jokimäki, & Carbó-Ramirez, 2014; Beninde, Veith, & Hochkirch, 2015; Sorace & Gustin, 2016). However, some studies have also highlighted the important role of the urban matrix (e.g., the whole urban landscape or developed area surrounding the urban parks) for birds (e.g., Tilghman, 1987; Jokimäki, 1999) and mammals (Dickman, 1987).

Given recent findings that urban areas in some regions of the world harbor endangered species, our goal was to examine the occurrence of threatened bird species in the most urbanized parts of European towns. In addressing our goal, we had two prior hypotheses. First, can heavily urbanized town centers also harbor threatened bird species and do species-rich areas harbor also many threatened species? Second, do species richness and the occurrence of individual threatened species depend on landscape and plot-level factors?

2. Materials and methods

2.1. Study selection and data extraction

We used the following criteria in the search for the data: (1) the data had to be collected during the breeding season, (2) the data had to be collected from the urban core area of the town (i.e., central part of the town that is > 50% covered by impervious surface area, containing large buildings, primarily stores, businesses and work places and usually includes the historical center of the town; see definitions in Adams, 2016; and demographia.com), (3) the data had to be collected 1990–2012, (4) the data had to be collected by the standard multiple-visit method (atlas, territory mapping, point counts; Bibby, Burgess, &

Hill, 1992), and (5) the study had to contain a complete list of breeding species in the urban core zone area.

One of the main data sources (data from 10 towns) in this study was the book of Kelcey and Rheinwald (2005) about the birds of European cities. We also searched for data using Google Scholar with the following search words: urban*, birds and Europe occurring in the title of the article (data from 5 towns). In addition, we also sent an inquiry to the European Network for Urban Landscape Ecology's (ENULE@yahoogroups.com) email list to contact to urban ecological bird researchers working in Europe at the beginning of our data search (early 2007). This inquiry was very effective because we got new data from 16 towns located in Italy, France and the Netherlands. In addition, we collected all urban bird atlas data published in Finnish from Finland (data from 7 towns). Finally, we used data from 38 European town centers (41–66 N°, Table 1; see references in the Electronic Suppl. 1) to analyze European-scale impacts of urbanization on species richness and occurrence patterns of threatened birds during the breeding season. Data on fourteen towns were published in English, whereas the rest (24 towns) of the data were either published in languages other than English. Therefore, our data are not biased towards only articles published in English. Also, our data represent a good balance between southern (13 towns), central (16 towns) and northern (9 towns) Europe. Bird species richness did not differ between datasets that were collected with different survey methods (Jokimäki, Suhonen, & Kaisanlahti-Jokimäki, 2016).

One of the major challenge in urban ecology is clearly defining and delineating the urban study area. Instead of using data collected from the whole city within its administrative borders (e.g., Ferenc et al., 2014), we used data collected from only the most urbanized area of each town, i.e., the urban core zone (Adams, 2016). In doing so, we at least partly avoided problems related to the definition of urban based on administrative borders, which might have led to scaling problems. Some heavily urbanized towns cover large areas and therefore, for example, have very low human density (< 1/ha) in their peripheral areas, which can also lead to low human population density within the administrative municipality boundaries of each town. No bird data from e.g., suburban areas were included in our data set. We checked the description and location of each study area in the corresponding publications and used Google maps of each area to ensure that the study site locations corresponded to the urban core area of each town. In addition, we confirmed that the urban core area was embedded within a continuously built-up area. This step was performed because the results can be influenced by a heterogeneous matrix surrounding the study plot (e.g., Pellissier et al., 2012).

2.2. Urbanization metrics

In each urban core area, we measured the areas covered by woods, open areas, buildings, streets, parking areas and water using a 1 km × 1 km grid in aerial Google maps. All of our study sites were dominated by multi-story commercial buildings and asphalt surfaces, such as roads and car parks; in some cases, rivers crossed the center. Approximately 90% of the core zone study plot area of the towns was covered by an impervious surface, i.e., buildings, roads or car parks (Jokimäki, Suhonen, & Kaisanlahti-Jokimäki, 2016).

Basic build-up area data surrounding the urban core study plots were extracted from Demographia.com. We used data on the built-up area (km^2) and density of inhabitants (inhabitants/km^2) living within the built-up area in our analyses. According to the detailed definition by Demographia.com, a built-up area is a continuously built-up land mass of urban development that is within a labor market (metropolitan area or region) containing no rural land. Jokimäki, Suhonen, and Kaisanlahti-Jokimäki (2016) indicated that different measurements of urbanization (e.g., number of inhabitants, human population density, and built-up area cover) are strongly positively correlated, suggesting that different measurements of urbanization provide similar, reliable information.

2.3. Bird survey data

We used breeding bird species presence/absence data to count the number of towns each species occurred in (Table 1). In this study, we used only data collected by the standard multiple-visit survey method (atlas, territory mapping, and point counts; Bibby et al., 1992). Bird species richness did not differ between data sets collected by different survey methods (Jokimäki, Suhonen, & Kaisanlahti-Jokimäki, 2016), indicating that data collected with different survey methods are comparable.

Species conservation status is taken from BirdLife International (2004). This classification is widely used, and it refers to species that have an unfavorable conservation status in Europe. Thus, these species are threatened in Europe. SPEC2 status refers to species concentrated in Europe with an unfavorable conservation status in Europe, and SPEC3 status refers to species not concentrated in Europe with an unfavorable conservation status in Europe (BirdLife International, 2004; see species classification in the Electronic Suppl. 2). Hereafter, we use the term "threatened" in reference to SPEC2 and SPEC3 species in Europe.

Because species are patchily distributed across their distribution range, we measured the distribution range of each bird species included in this study using a frame of 63 squares (7 × 9; 35–70°N and 10°W–35°E; with a 5° assurance level) given in the maps of the book "Birds of the Western Palearctic" (Cramp & Perrins, 1977–1994). From these maps, we counted the number of occupied squares for each breeding species. The range area, occupancy and threatened status of the breeding bird species are provided in Electronic Supplement 2.

2.4. Statistical methods

Spearman's rho correlation test was used in association tests of urbanization metrics and latitude and also for analyzing the relationship between the total bird species richness and threatened species richness. The cumulative distribution between threatened and non-threatened species was compared by the independent sample Kolmogorov-Smirnov test. Pearson correlation was used to analyze the association between the occurrence of threatened bird species and their distribution range. Distribution ranges of threatened and non-threatened species were compared by the Mann-Whitney U test.

Because species richness and number of threatened species from cities close to each other are expected to be more similar than those from cities spaced further apart, we measured the geographical distance (km) between each city. We then performed two Mantel tests, one for total species richness and the other for number of threatened species. Correlation coefficients between the matrices of distances and the differences in species richness and number of threatened species were then calculated. Probability estimates were based on 9999 perturbations. Spatial autocorrelations were calculated using the R package 'Vegan' (Oksanen, Kindt, Legendre, & O'Hara, 2006).

Two species from the same genus are not statistically independent because their evolutionary past is shared. To incorporate possible phylogenetic relatedness between bird species, we used phylogenetic analysis in R Studio in this study (version 0.99.903; R Core Team, 2015) and built a phylogenetic tree with the ape package (Paradis, Claude, & Strimmer, 2004) and caper package (Orme et al., 2015). First, we constructed a phylogenetic tree with branch lengths of the 107 bird species using the webpage application at Birdtree.org in Nexus format. Because *Passer italiae* did not exist in the Birdtree.org database, we added it to phylogenetic tree as related to *Passer domesticus* with a branch length of 0.100000. The phylogenetic tree can be seen in Fig. 1. Pagel's λ (Pagel, 1999; Freckleton, Harvey, & Pagel, 2002) was used to measure the phylogenetic signal in a continuous trait (the frequency of species occurrence for bird species in an urban core area of the town). Pagel's λ varies between 0 and 1; a λ of 0 indicates a trait is random with respect to phylogeny (i.e. there is no phylogenetic signal), whereas a λ of 1 indicates phylogenetic trait conservatism (i.e. phylogenetic

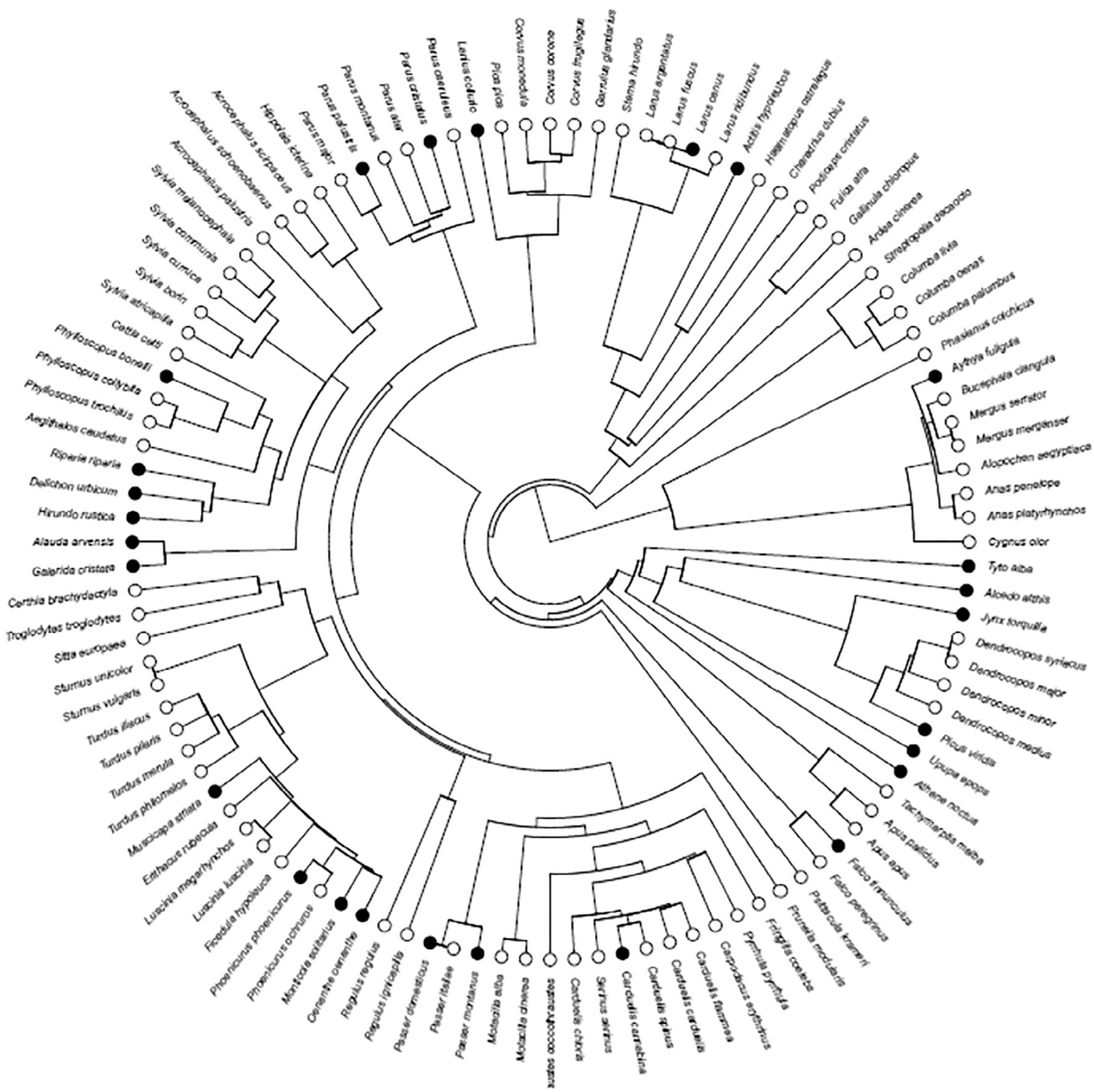

Fig. 1. Phylogenic "fan" tree of bird species observed in this study. Species marked with a black dot are threatened bird species.

dependence; Freckleton, Harvey, & Pagel, 2002). Pagel's λ was calculated with the R function phylosig in the phytools package (Revell, 2012). We also used a *D*-statistic (Fritz & Purvis, 2010) to measure the phylogenetic signal in the binary trait (if the bird species is threatened or non-threatened). A *D* statistic near zero means a phylogenetically clustered pattern (i.e. a trait is clumped), and a value near 1 means a phylogenetically random pattern (i.e. a trait has a phylogenetically random distribution; Fritz & Purvis, 2010). D values were calculated with the R function phylo.d in the caper package (Orme et al., 2015). These two phylogenetic signal metrics perform well in statistical tests for patterns of phylogenetic trait conservatism. All phylogenetic statistical analyses were performed with RStudio version 1.1.383 (R Core Team, 2015).

We tested the variation in species richness using Generalized Linear Models with type III errors and using a Poisson distribution with a log link function. In this model, latitude, longitude, study area, size of the human population, density of the human population and age of the town were used as continuous covariates. The variables study area, size of the human population, density of the human population and age of the town were $\log_{10}$ transformed before performing statistical tests. Due to over-dispersion of the data of the total bird species richness (Deviance value/df –ration of 4.48), we re-analyzed the data with a negative binomial distribution with a log link function, and the over-dispersion problem disappeared (Deviance value/df –ration 0.20). The over-dispersion problem was minimal in cases of threatened species richness (Deviance/df –ratio of 1.43).

Multiple regression analysis (entry method; i.e., all independent variables were entered into the equation at the same time) was used to test the relationship between the number of threatened species and matrix-level and plot-level variables. Prior to these analyses, we checked for possible collinearity of the predictive variables. For landscape matrix-level variables (latitude, longitude, study plot area, total number of inhabitants and human population density), the tolerance values were larger than 0.43 in all cases, indicating that there were no collinearity problems in this regression analysis. For plot-level variables (cover of woods, open areas, buildings, streets, parking areas or water and habitat diversity [the Simpson index ($1-\Sigma p_i^2$), where p_i is the proportion of different habitat types in the study plot]), the tolerance values were very low (0.005–0.112), indicating significant collinearity problems. Therefore, we excluded variables that primarily measured the same topic and used only woods, open areas and water areas in the subsequent analysis. In this analysis, the tolerance values were large (0.966–0.985), indicating that the collinearity problems were successfully removed.

The occurrence (presence coded as 1 and absence coded as 0) of individual threatened species was modeled using binary logistic regression analysis (Trexler & Travis, 1993). In analyzing species occurrence and habitat variable relationships, species occurring in fewer than 10 sites (n = 7 sp.) were not used in the analyses because of their small sample size. Separate analyses were conducted using the main plot-level variables (wooded area [%]; building area [%] and habitat diversity) and using the main landscape matrix-level variables surrounding the study plot (built-up area [ha] and human density living within the built-up area). All of the abovementioned statistical tests were computed using IBM SPSS Statistics version 22.0 (Corp, 2013).

We used phylogenetic logistic regression analyses (Ives & Garland, 2010) to model the probability that the nesting locations of urban threatened birds are influenced by the frequency of species occurrence in European town centers. The nesting location of each threatened bird species was used as the dependent variable in phylogenetic logistic regressions. Regarding nesting location, we divided the threatened birds into two groups: species that breed in cavities, nest boxes or buildings (coded as 1; see Electronic Suppl. 2) and those that breed in other places (coded as 0). The number of towns that each bird species occupied (i.e., number of town centers in which the species was observed to breed) was used as an independent covariate. Phylogenetic logistic regression was calculated with the R function phyloglm in the phylolm package (Ho et al., 2016).

3. Results

3.1. Study areas and their urban metrics

The built-up area around our urban core area study plots varied from 17 to 2845 km^2, and their corresponding human population density per km^2 varied from 173 to 5524. Thus, our urban core zone study plots were clearly embedded within highly urbanized areas. The total number of inhabitants correlated positively with the built-up area (Spearman's rho = 0.62, $p < 0.001$, n = 38) and the human density in the built-up area of the town (Spearman's rho = 0.68, $p < 0.001$, n = 38). The latitude did not correlate with the built-up area of the town (Spearman's rho = −0.10, p = 0.565, n = 38), human density (Spearman's rho = −0.22, $p = 0.191$, n = 38) or human population size (Spearman's rho = −0.30, $p = 0.072$, n = 38).

3.2. Bird species richness and occurrence of threatened species

A total of 26 (mean = 4.8, *s.d.* = 2.4, n = 38; approximately 20% of the 108 species observed in this study) threatened species were observed in the core zone areas of European towns (Electronic Suppl. 2). The distances between cities did not significantly affect either the total species richness (Mantel test r = −0.07, $p = 0.838$) or threatened species richness (Mantel test r = −0.06, $p = 0.757$). Species-rich areas also had a high number of threatened breeding birds (Spearman's rho = 0.71; $p < 0.001$, $n = 38$).

We did not find any phylogenetic signals in our data. The occupancy frequency of urban breeding bird species did not show any phylogenetic signals because Pagel's λ did not differ from zero ($p = 0.256$). Also, threatened urban bird species were not phylogenetically closely related ($D = 0.620$ differed from 0 ($p = 0.01$) and from 1 ($p = 0.009$); Fig. 1). Therefore, phylogeny cannot explain differences between bird species in occupancy frequency of urban habitats.

Six out of 26 threatened bird species were observed in only a single town, and there were no species that occurred in all town centers (Fig. 2). *Passer domesticus* (observed in 29 out of 38 town centers), *Delichon urbica* (27), *Hirundo rustica* (19), *Muscicapa striata* (18), *Falco tinnunculus* (12), *Passer montanus* (11) and *Phoenicurus phoenicurus* (10) were the species that were found in the most town centers (Electronic Suppl. 2). The cumulative distribution of the number of towns occupied by a species was the same between threatened and non-threatened species (independent sample Kolmogorov-Smirnov test, $z = 1.30$, $p = 0.069$; Fig. 2).

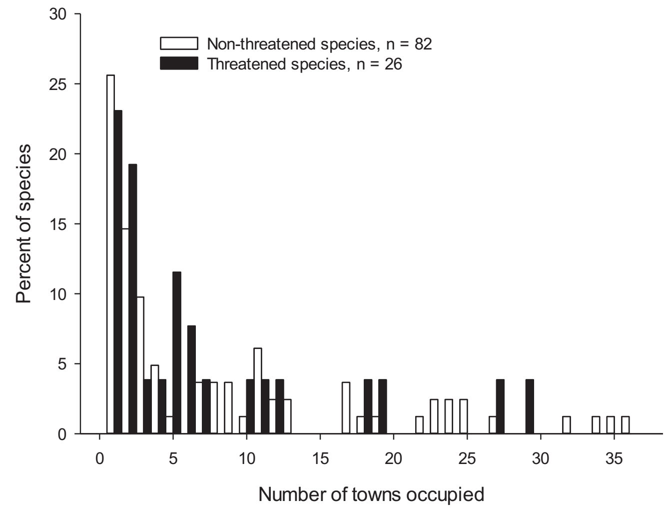

Fig. 2. Percent of species (%) of breeding species in relation to the number of occupied town centers in 38 European towns. Open bars indicate species with a non-threatened status and filled bars indicate species with a threatened status.

As the distribution range of threatened species increased, bird species were more likely to be found in town centers (Pearson r = 0.47, $p = 0.015$, $n = 26$; Fig. 3). The distribution ranges of threatened species and other species did not differ significantly (Threatened species: mean = 44.8, s.d. = 9.7, n = 29; Other species: mean = 40.4, s.d. = 13.5, n = 82; Mann-Whitney U test, $z = 1.29$, $p = 0.20$).

The richness of threatened species did not depend on matrix-level variables (latitude, longitude, study plot area, total number of inhabitants and human population density; Regression analysis: $F_{5,32} = 0.65$, $p = 0.661$; Table 2). The richness of threatened species did not depend on the study plot-level cover (%) variables (woods, open areas, or water; Regression analysis: $F_{3,34} = 0.82$, $p = 0.492$; Table 2).

The occurrence of *Falco tinnunculus* increased with increases in the human density within a built-up area (Table 3). The occurrence of *Hirundo rustica* and *Muscicapa striata* decreased with increases in the proportion of the built-up area in the surrounding matrix (Table 3). The

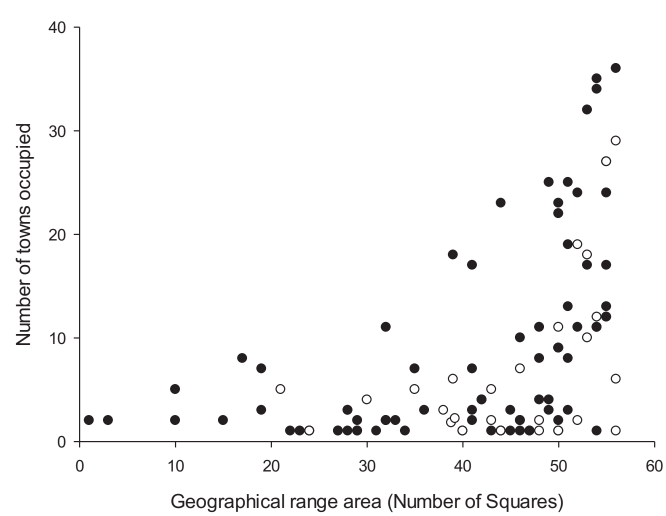

Fig. 3. Breeding bird species occupancy in urban centers in relation to their general breeding distribution ranges in Europe based on the maps in the book "Birds of the Western Palearctic" (Cramp & Perrins 1977–1994) in 63 squares (35–70°N and 10°W–35°E; with a 5° assurance level). Filled dots indicate species with a non-threatened status and open dots indicate species with a threatened status.

Table 2
Results of the regression analyses (see methods) of the relationships between threatened bird species richness (Poison distribution) and matrix- and plot-level variables. β ± SE of each variables, *t*-test values and significance of each variables as well as their collinearity statistics (Tolerance value) are presented.

Model	*β ± SE*	*t*	*p*	Tolerance
Matrix variables:				
Constant	14.40 ± 6.35	2.27	0.03	
Latitude	−0.07 ± 0.08	−0.95	0.35	0.46
Longitude	0.02 ± 0.07	0.20	0.85	0.48
Log_Area	0.56 ± 0.78	0.72	0.48	0.76
Log_Human	0.14 ± 0.83	0.15	0.88	0.48
Log_Human_Density	−2.12 ± 1.63	−1.30	0.20	0.43
Plot variables:				
Constant	4.92 ± 0.65	7.63	< 0.001	
Wooded (%)	0.57 ± 4.75	0.12	0.91	0.97
Open (%)	7.54 ± 22.42	0.34	0.74	0.99
Water (%)	29.05 ± 2.10	−1.45	0.15	0.97

Table 3
Logistic regression models for the threatened bird species occurring at least in 10 sites (7 species). The adequate of each model is tested by the goodness-of-fit test. The significance of each variable is analyzed by the Wald-test (*P < 0.05, °P < 0.10). Beta-values and their SE values as well as significance of all variables are presented after each variable in parentheses.

Species	Variables (Beta-value ± SE)	G^2	P
Matrix variables:			
Falco tinnunculus	Log human density (4.2 ± 1.8)*	8.6	0.014
Delichon urbica	No model	0.1	0.797
Hirundo rustica	-Log built-up area (−1.2 ± 0.5)*	7.2	0.007
Muscicapa striata	-Log built-up area (−1.0 ± 0.5)*	4.9	0.026
Passer domesticus	No model	0.2	0.680
Passer montanus	No model	2.6	0.104
Phoenicurus phoenicurus	No model	1.4	0.230
Plot variables:			
Falco tinnunculus	Wooded (−44.5 ± 25.6)°	15.7	0.001
Delichon urbica	-Buildings (−115.9 ± 48.5)* -Habitat diversity (103.7 ± 41.8)*	11.6	0.003
Hirundo rustica	No model	0.4	0.523
Muscicapa striata	-Buildings (−61.5 ± 27.8)*; -Habitat diversity (−57.2 ± 5.2)*	8.3	0.015
Passer domesticus	No model	2.1	0.144
Passer montanus	No model	0.3	0.587
Phoenicurus phoenicurus	No model	0.1	0.836

occurrence of *Delichon urbica* and *Muscicapa striata* decreased with increases in habitat diversity and the proportion of buildings within the study plot (Table 3).

The threatened species in most towns had a higher probability of being a cavity or building nester than a species with other nesting traits (logistic regression model: Beta-value = 1.22 (SE = 0.57); Wald = 4.57, $df = 1$, $p < 0.033$; Fig. 4). Phylogeny did not affect this relationship (Phylogenetic logistic regression, beta 0.87 (SE = 0.40), z = 2.20, $p = 0.028$).

4. Discussion

We found a total of 26 threatened bird species in the core zone areas of European towns. Therefore, our results indicated that heavily urbanized areas are important sites to conserve biodiversity (see also Ives et al., 2016). Threatened urban breeding birds were not phylogenetically clumped, i.e., their occupancy in the core zone areas of European towns was spread randomly across phylogeny. However, Friz and Purvis (2010) indicated that threatened British breeding birds and world mammals exhibited phylogenetic clumping. These conflicting results indicated that urban-based changes of bird communities are scale-dependent, and therefore researchers should consider the spatial

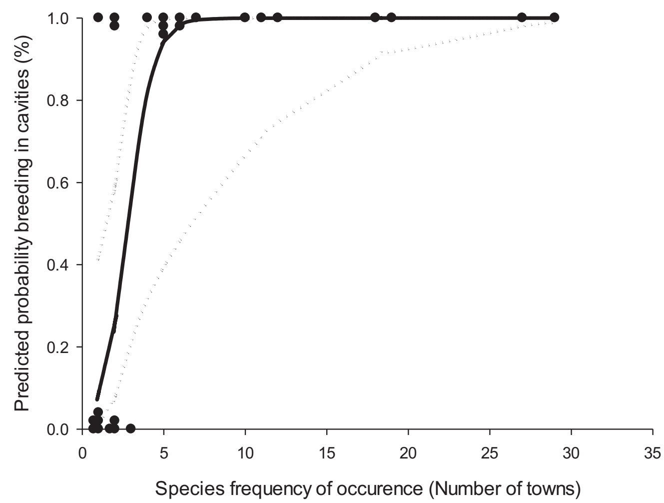

Fig. 4. Observed (filled dot) frequency of occurrence of threatened breeding bird species in European town centers. Regarding nesting location, we divided the threatened birds into two groups: species that breed in cavities, nest boxes or buildings (1) and those that breed in other places (0). Note that the original values were slightly changed to reduce overlapping data points. The predicted probability (0-1) (the continuous line) that the bird species nests in buildings and/or tree cavities is shown. The dotted lines indicate 95% confidence intervals. Estimated logistic regression coefficient for the constant (1.28 ± 0.56 (SE), Wald = 5.24, df = 1, $p = 0.022$) and the species frequency of occurrence (−3.62 ± 1.49 (SE), Wald = 5.90, df = 1, $p = 0.015$) are noted.

scale e.g. in the analysis of the possible effects of urbanization on homogenization of bird communities (Leveau et al., 2017).

According to our results, many threatened bird species were found in only one or a few towns (see also Sorace & Gustin, 2010); none were breeding in all towns. In general, bird species occurrence in European town centers had a unimodal distribution (Jokimäki, Suhonen, & Kaisanlahti-Jokimäki, 2016). It is possible that some towns were not occupied simply because the geographical range of the bird did not overlap the town. Our results at least partly supported this scenario because as the distribution ranges of the threatened species increased, bird species were more likely to be found in the town.

Our results showed that even urban cores had very diverse breeding bird communities, and the large number of species found in only one urban center indicated that there is considerably high beta-level diversity of birds in the towns of Europe (see also Aronson et al., 2014; Ives et al., 2016; Jokimäki, Suhonen, & Kaisanlahti-Jokimäki, 2016). This result is interesting considering that urban homogenization predicts that beta-diversity should be low (McKinney, 2006; Groffman et al., 2014). However, certain threatened species can occur in specific towns for some time due to extinction delay, but it is possible that this effect will disappear in the future (Essl et al., 2015; Jokimäki, Suhonen, & Kaisanlahti-Jokimäki, 2016). These results highlight the need for a wider environmental view in bird conservation in urban habitats.

However, we observed a positive correlation between overall species richness and the richness of threatened species. Thus, overall species richness could also be used as a surrogate for species richness of threatened bird species. The relatively high breeding bird species richness in European town centers might be related to the old history of European towns (Francis & Chadwick, 2013). Many towns were established along good transportation routes (at the sea coast or along rivers or their delta areas) and are therefore in places that already have great biodiversity. It should be noted that most earlier urban ecological bird studies were conducted in Europe or in the USA, and more studies in biodiversity rich areas, such as in the tropics, are urgently needed (Marzluff et al., 2001; Marzluff, 2017).

We were unable to explain the richness of threatened species with our landscape and plot-level cover variables, such as the amount of green areas. This result indicates that reasons other than the amount of green patches, such as species-specific nest site behavior, impact the occurrence of threatened species in urban core areas. Many threatened species occurring in urban core zone areas of European towns are aerial insectivores, such as swallows, and obviously their occurrence would not be impacted as much by changes in vegetation cover.

It is clear that urban habitats are more suitable environments for some species than others. Our results indicated that many threatened species could be found in urban core areas of European towns; many of these species, such as *Delichon urbica,* have adapted to cities and have been nesting in buildings/cavities for a long time (Blair, 1996; Jokimäki, Suhonen, & Kaisanlahti-Jokimäki, 2016). However, we also showed that several other threatened bird species frequently breed in buildings or cavities in town centers, including *Passer domesticus*, *Hirundo rustica*, *Muscicapa striata*, *Falco tinnunculus*, *Passer montanus*, *Phoenicurus phoenicurus, Jynx torquilla*, *Lophophanes cristatus*, and *Tyto alba*. Also earlier studies have indicated that the number of species nesting in buildings in Europe is positively related to the number of inhabitants, population density and distance from the town center (Jokimäki, Suhonen, & Kaisanlahti-Jokimäki, 2016; Sorace & Gustin, 2016).

Some cavity-nesting species, such as *Passer domesticus, Delichon urbica* and *Falco tinnunculus,* have been reported to respond positively to architectural features that provide resting and nesting places (Sorace & Gustin, 2016). It is important to note that only one of the threatened cavity-nesting species, *Lophophanes cristatus*, is a primary cavity-nesting species that excavates cavities of other species, so called secondary-cavity nesters. This result suggests that standing dead trees (snags) used by primary-cavity nesters for breeding are rare within urban core zone areas as indicated by Blewett and Marzluff (2005) in Washington (but see opposite results from Australia; LaMontagne, Kilgour, Anderson, & Magle, 2015). According to Tomasevic and Marzluff (2017), primary-cavity nesters mostly nest in snags, whereas secondary-cavity nesters use both snags and anthropogenic cavities. Urban parks have the potential to attract species of conservation interests, e.g., *Picus viridis, Jynx torquilla,* if they are managed for wildlife (Sorace & Gustin, 2016). Retaining old trees in town parks is a good management option to support the occupancy of primary-cavity nesters (e.g., *Lophophanes cristatus*, woodpeckers) and afterwards, secondary-cavity nesters. However, at the same time, urban planners should consider safety topics when saving dead trees in human-dominated landscapes (Sorace & Gustin, 2016). Urban core areas are important, especially for conserving bird species that nest in cavities or buildings, whereas ground-nesting birds particularly suffer from a lack of suitable and safe nesting sites (e.g., Jokimäki & Huhta, 2000; Jokimäki et al., 2005, 2014). Good availability of suitable nesting sites (e.g. buildings, nest-boxes) or protection of nests from urban predators can support the occurrence of cavity nesters. The main urban nest predators in Europe are birds, like corvids, that are unable to predate effectively nests located in cavities (Jokimäki & Huhta, 2000; Jokimäki et al., 2005).

According to Kowarik (2011), urban environments can harbor self-sustaining populations of endangered native species. Cavity-nesting birds have been reported to successfully breed in urban areas in Seattle, Washington, USA (> 50% of nesting attempts produced fledglings; Blewett & Marzluff, 2005; 72–89% of nests were successful; Tomasevic & Marzluff, 2017). However, some studies have suggested that fledgling production of nest-box breeding tits (like *Parus major*) is lower in urban habitats than in rural habitats, which is probably due to poor food quality in urban environments (Solonen, 2001). Therefore, these cavity-nesting populations are not necessarily self-sustainable. Thus, city planners and private sectors should also consider other options (e.g., reducing pesticides, providing supplemental food, enacting regulations related to house cats and landscaping food resources) in addition to offering suitable nesting sites to support the occurrence of wildlife and threatened species in core zone areas of towns (Adams, 2016; Lepczyk et al., 2017).

Some threatened species were detected in only one of our urban sites (e.g., *Alauda arvensis, Galerida cristata, Carduelis cannabina* and *Lanius collurio*). These species are more typical in agricultural environments, and their conservation actions should be more focused on their main habitat instead of on urban ones (Sorace & Gustin, 2016). Our results indicated that ground nesters, such as *Alauda arvensis*, and many waders (e.g., *Actitis hypoleucos*), waterfowl (e.g., *Aythya fuligula*) and coniferous forest species (e.g., *Lophophanes cristatus* and *Phoenicurus phoenicurus*) especially suffer from a lack of suitable habitats (e.g., open fields, lakes, large-sized coniferous patches) in towns (see also, Jokimäki et al., 2014; Jokimäki, Suhonen, & Kaisanlahti-Jokimäki, 2016; Sorace & Gustin, 2016). Due to the inadequate sheltering shrub vegetation, the visibility of ground nests in urban areas is high, and therefore, ground-nesting birds suffer from heavy nest predation in urban areas (Jokimäki & Huhta, 2000; Jokimäki et al., 2005). Increasing shrub cover in urban woodlots and parks might obviously be a good management option for ground-nesting birds. Assisting the persistence of threatened coniferous bird species by using more coniferous trees instead of deciduous trees in park management might help these species. Furthermore, many disturbance-sensitive bird species, such as eagles and game birds, are missing from highly urbanized areas (Jokimäki & Kaisanlahti-Jokimäki, 2012). The conservation of disturbance-sensitive species with large territories in urban environments may be a more difficult task than the conservation of species with smaller territories and less sensitivity to disturbances.

Clergeau, Jokimäki, and Savard (2001) suggested that urban bird communities are independent of the diversity of the adjacent landscape; therefore, local features are more important than the surrounding landscapes in determining bird species diversity. However, Pellissier et al. (2012) and Jokimäki (1999) have indicated that birds are also sensitive to landscape structure within the city center. We found that the occurrence of many species (*Delichon urbica*, *Muscicapa striata* and *Hirundo rustica*) decreased with increases in the proportion and extent of built-up areas. One explanation for this result may be that the architecture of modern buildings in urban centers is not suitable for nesting (Murgui, 2002). Alternatively, reduced insect populations in urban areas due to poor air quality, traffic, loss and fragmentation of natural green areas and grass mowing within urban core areas may lead to a lack of food resources for these insectivore species (Newman, Novakova, & McClave, 1985; Jones & Leather, 2012). Insect populations can also be reduced if their host plants are not available due to urban landscaping with nonnative species (Burghardt, Tallamy, Philips, & Shropshire, 2010). In a study conducted in the USA, it was observed that bird species of regional conservation concern were 8 times more abundant and significantly more diverse on native properties (Burghardt, Tallamy, & Gregory Shriver, 2009).

On the other hand, the frequency of occupancy of *Falco tinnunculus* increased with increasing human density within the built-up area. In recent years, urban areas have also become more important for *Falco tinnunculus* (e.g., Sorace & Gustin, 2016), the populations of which have decreased in its main rural habitats but have increased in urban habitats. The ruins of older towns and abundant prey items, especially birds, may at least partially explain the large numbers of many falcon species in town centers (Salvati, Manganaro, Fattorini, & Piattella, 1999; Sorace & Gustin, 2016). Unfortunately, we were unable to explain the occurrence of the two *Passer* species and *Phoenicurus. phoenicurus* in urban centers with our variables. In regard to *Passer domesticus*, important resources (e.g., high-quality breeding season food) needed by sparrows may differ between towns as House Sparrows have been observed to decline in some towns but not in others (Summers-Smith, 2003; De Laet & Summers-Smith, 2007).

5. Conclusions

Most threatened species were detected in only one or a few towns. Our results indicated that even heavily urbanized areas have many species with specific conservation values. Town centers are important areas for conservation, particularly for those threatened bird species, which main populations are breeding in towns, e.g., *Passer domesticus, Apus apus* and *Delichon urbica*. According to our results, towns are also important sites for many threatened species that are nesting in cavities in trees and/or buildings. Therefore, saving large-sized trees with cavities in urban green areas (Treby & Castley, 2015) or erecting nest boxes in urban green areas (Jokimäki, 1999; Fernandéz-Juricic & Jokimäki, 2001) may benefit their occurrence. Furthermore, architects must systematically consider the status of a species, presenting suitable nesting sites in building designs. It would be interesting to know why some widely distributed and abundant species (e.g., *Passer domesticus, Delichon urbica* and *Hirundo rustica*) occur in some sites but are lacking from other places. It should be noted that occurrence does not indicate that these species populations are sustainable. Therefore, additional studies should be directed towards the breeding success of threatened species living within urban environments and mechanistic urban ecology with studies on behavioral ecology, species interactions, genetics and evolution (Shochat, Warren, Faeth, McIntyre, & Hope, 2006). The potential of urban areas to preserve the occurrence of threatened species and biodiversity in general (Madre, Clergeau, Machon, & Vergnes, 2015) is an important consideration for city planners. Urban areas with a large number of inhabitants offer the possibility of educating people to recognize biodiversity and many threatened species near their living surroundings (Savard et al., 2000; Lepczyk & Warren, 2012; Warren & Lepczyk, 2012; Shanahan et al., 2014). City-level, top-down government policies have an especially important role related the amount and extent of suitable habitat for species living in urban core areas, whereas household-level, bottom-up factors have a greater role in e.g., vegetation structure and composition, especially in areas surrounding urban cores (Lepczyk et al., 2017).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.landurbplan.2018.05.020.

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