



Urbanization and species occupancy frequency distribution patterns in core zone areas of European towns

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ABSTRACT

More and more of the globe is becoming urbanized. Thus, characterizing the distribution and abundance of species occupying different towns is critically important. The primary aim of this study was to examine the effect of urbanization and latitude on the patterns of species occupancy frequency distribution (SOFD) in urban core zones of European towns (38 towns) along a 3850-km latitudinal gradient. We determined which of the three most common distributional models (unimodal-satellite dominant, bimodal symmetrical, and bimodal asymmetrical) provides the best fit for urban bird communities using the AICc-model selection procedure. Our pooled data exhibited a unimodal-satellite SOFD pattern. This result is inconsistent with the results from previous studies that have been conducted in more natural habitats, where data have mostly exhibited a bimodal SOFD pattern. Large-sized towns exhibited a bimodal symmetric pattern, whereas smaller-sized towns followed a unimodal-satellite dominated SOFD pattern. The difference in environmental diversity is the most plausible explanation for this observation because habitat diversity of the study plots decreased as urbanization increased. Southern towns exhibited unimodal satellite SOFD patterns, central European towns exhibited bimodal symmetric, and northern towns exhibited bimodal asymmetric SOFD patterns. One explanation for this observation is that urbanization is a more recent phenomenon in the north than in the south. Therefore, more satellite species are found in northern towns than in southern towns. We found that core species in European towns are widely distributed, and their regional population sizes are large. Our results indicated that earlier urbanized species are more common in towns than the species that have urbanized later. We concluded that both the traits of bird species and characteristics of towns modified the SOFD patterns of urban-breeding birds. In the future, it would be interesting to study how the urban history impacts SOFD patterns and if the SOFD patterns of wintering and breeding assemblages are the same.

KEYWORDS

urban, core-satellite species patterns, disturbance, birds

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INTRODUCTION

The shape of species occupancy frequency distributions (i.e., the distribution of the number of species occupying different numbers of sites independent of their abundance; SOFD, hereafter) has received interest from ecologists for a long time (Hanski 1982; Brown 1984; Collins & Glenn 1991; Gilpin & Hanski 1991; McGeoch & Gaston 2002; Jenkins 2011). SOFD patterns can be random, uni-, bi- or multimodal (McGeogh & Gaston 2002). SOFD patterns may vary between communities (Magurran 1988; Evans et al. 2009, 2010; Jenkins 2011). In natural communities, SOFD curves have generally been observed to be bimodal; in other words, most species are either common ('core species') or rare ('satellite species') with respect to the number of occupied sites (Hanski 1982, 1999; Hanski & Gyllenberg 1993; Hanski & Gilpin 1997; McGeoch & Gaston 2002; Jenkins 2011). For example, bimodal distributions have been

recently reported for breeding birds of Czech Republic and central Europe (Storch & Šizling 2002).

Several mechanisms have been proposed to explain different SOFD patterns (Brown 1984; McGeoch & Gaston 2002; Jenkins 2011). In many cases, SOFD patterns can be largely explained by the effects of sampling procedure. For example, the grain, extent and intensity of sampling can vary extensively (McGeoch & Gaston 2002). A decrease in sample area or sample sites may change the observed SOFD patterns from uni- to bimodal. However, SOFD patterns may also depend on abiotic and biotic factors, such as environmental or habitat heterogeneity, species specificity and adaptation to habitat, productivity of habitat, species distributions and levels of disturbance (Collins & Glenn 1997; McGeoch & Gaston 2002; Møller 2009; Conole & Kirkpatrick 2011; Conole 2014; Jokimäki et al. 2014).

Despite the fact that SOFD patterns have been studied across a broad range of taxa and habitats, large-scale studies conducted in urban environments are still lacking. Pautasso et al. (2011) showed in their macroecological study that species-abundance, species-area (see also Ferenc et al. 2014) and species-biomass relationships did not differ between urbanized and more natural environments. In a study conducted in Mexico, MacGregor-Fors et al. (2011) found that the species-area relationships are steeper in human settlements than in their surroundings. However, whether urbanized breeding bird communities exhibit general macroecological patterns observed in more natural environments is uncertain (McGeoch & Gaston 2002; Jenkins 2011; see also Jokimäki et al. 1996; Jokimäki & Suhonen 1998; Alberti 2005; Anderies et al. 2007; Fuller et al. 2009; Warren & Lepczyk 2012).

Currently, more people live in urban areas than in rural areas, and the urbanized areas are growing much faster than the urban population due to an urban sprawl (UN 2014). Urban environments with large spatial extents and many replicated towns with relatively homogeneous habitat structures provide superb opportunities to test several predictions of SOFD patterns (Clergeau et al. 2006ab; McDonald 2008; Pautasso et al. 2011; Aronson et al. 2014; Shanahan et al. 2014). Firstly, with respect to environmental heterogeneity, the number of satellite species is predicted to increase with the extent or the number of study sites due to increase in environmental diversity (McGeoch & Gaston 2002). Therefore, a satellite-dominated unimodal SOFD pattern is predicted to occur in heterogeneous areas. In contrast, samples from more restricted areas that are more similar in their habitat composition are predicted to exhibit bimodal SOFDs that have many core (common) and satellite (rare) species.

Second, the urban areas can be used to study the impacts of anthropogenic factors, such as human disturbance, on SOFD patterns (Fernández-Juricic & Jokimäki 2001; Jenkins 2011; Francis & Chadwick 2013). Heavy and frequent disturbances may inhibit the occurrence of some species and support the occurrence of resistant species, thereby leading to unimodal SOFD patterns that occur in either a satellite or a core mode (Jenkins 2011). In contrast, an intermediate level of disturbance may lead to bimodal SOFD patterns.

Third, urban areas are characterized by high levels of predictable anthropogenic food resources (e.g., Gilbert 1989; Rebele 1994; Shochat et al. 2006; Francis & Chadwick 2013; Adams 2016). High productivity areas may contain more individuals, and thus, more viable populations and greater species richness (Evans et al. 2005). Because a greater availability of resources may allow many species to co-occur, high productivity areas may also contain many satellite-species, leading to unimodal SOFD patterns. However, low productivity areas with high dominance of a few species should lead to bimodal SOFD patterns, with both core and satellite species co-occurring (McGeoch & Gaston 2002).

Fourth, most species that occur in urban environments have special traits (Conole & Kirkpatrick 2001; Leveau

2013; Jokimäki et al. 2016). This observation leads to the prediction that generalist species with broad niche requirements will occur in most sites ('core species'), whereas specialist species will only occur in a few sites ('satellite species'). Earlier studies have reported that urbanization causes functional homogenization (Devictor et al., 2007). According to species specificity explanations for SOFD patterns, if a species habitat use (i.e., if a species is a specialist or generalist) is an important determinant of the SOFD patterns, the species are predicted to be classified into core and satellite species across different areas (McGeoch & Gaston 2002).

Finally, species are most abundant in the centre of their geographical distributions (McGeoch & Gaston 2002). In addition, the occupancy and abundance of species are positively related in natural (Brown 1984) and urban areas (Jokimäki et al. 2014). Generally, the species pool is larger in the south than in the north; therefore, more species live near their geographical range edges in the north than in the south. Therefore, a high ratio of species is predicted to occur at their range edges at northerly latitudes, whereas a high ratio of species is predicted to occur at or near the centre of their ranges at southerly latitudes. Consequently, more satellite species are predicted to occur at northerly latitudes than at southerly latitudes (McGeoch & Gaston 2002). However, depending on the species pool, range centres of different groups of species may differ, for example, the forest dwelling bird species have, on an average, more northern range centres than steppic or shrubland species in Europe (Covas & Blondel, 1998). Therefore, it is important to also study the role of species population size, distribution range, marginality and northern distribution limit of species on species occupancy (e.g., Møller 2008, Cuervo & Møller 2013).

In this study, SOFD patterns of breeding birds were analysed within the urban core zone areas (see definition; Adams 2016) of European town centres (i.e., within the most urbanized areas) along a 3850-km latitudinal gradient. Previous studies have used more heterogeneous urban definitions that included data collected within the administrative boundary of the town, which includes inner core urban areas, as well as the suburban areas, peri-urban areas and sometimes rural areas (Aronson et al. 2014; Ferenc et al. 2014). We tested which of the three most common SOFD patterns (out of eight; McGeoch & Gaston 2002; Jenkins 2011), (i) unimodal-satellite dominant, (ii) bimodal symmetrical, or (iii) bimodal asymmetrical pattern, best fitted the breeding bird assemblages of the urban core zone areas in Europe, and if the urbanization level and geographical location influence these patterns. Because urbanization might lead to homogenization of the environment (Blair 2001; McKinney 2006), we predicted that SOFD patterns in the urban core zone areas will be bimodal and consist of both core and satellite species. Because urbanization phenomena are more recent in northern latitudes, we predicted that SOFD patterns might differ between towns located in different latitudinal areas. We predicted that there will be more species found in single towns in northerly latitudes than at more southerly

latitudes. In addition, we determined whether the number of core species and their composition differed across latitudinal and urban gradients (number of inhabitants). We predicted that the core species composition should be relatively similar because the environment of urban core zone areas is quite homogenous (Francis & Chadwick 2013; Adams 2016). In addition to the study of general SOFD patterns, we explored possible processes behind the observed patterns. We analysed if the occupancy of species in the European urban core areas were dependent on the species breeding population sizes or trends, migration distance, geographical range, northern distribution limit and time since the species has urbanized. In addition to species traits, we studied if the city traits (the age of town, extent of built-up area and human population size) influence the occupancy of individual bird species.

1. MATERIAL AND METHODS

1.1. Study areas

We used data collected from 38 core zone areas of European towns (Fig. 1, Appendix 1) to analyse the European-scale consequences of urbanization on breeding bird SOFD patterns along

a 3850-km latitudinal gradient. Data collection was finished during the early 2012. Only data collected by the multiple-visit method (see chapter 1.2. in more detailed) and from the urban core area of each town were accepted for the analyses. The human population of study towns varied from 20,605 to 4,661,219 (Appendix 1). The data of human population refers to the people living within the administrative municipality boundaries of each town; this data was collected from Wikipedia. To control for differences in the local habitat structure, we used bird data collected from the most urbanized area of each town (i.e., from the restricted urban core zone of each town; Adams 2016). Based on our Google map analyses using a 1 km x 1 km square located in the middle of each town, study sites are dominated (>50%) by large-sized buildings (primarily stores, businesses and work places), roads and parking areas, which corresponds to the 'urban' definition of Marzluff et al. 2001. These sites correspond well to the location of the historical centre of each town (e.g., Pellissier et al. 2012). As was done in previous studies (Aronson et al. 2014; Ferenc et al. 2014), the bird data from the suburban areas (30-50% built-up, building density 2.5-10/ha, and human density >10/ha; Marzluff et al. 2001) was not collected in this study. In addition, our data included several study towns located in northern Europe, dissimilar to



Figure 1. The location of the 38 urban town centres in Europe. The symbols indicate the different levels of urbanization (dot = Small towns, with less than 200 000 inhabitants; triangle = Medium-sized towns with 200,000 to 1,000,000 inhabitants, and square = Large towns, with more than 1,000,000 inhabitants).

Table 1. Description of study sites in relation to their size (a: based on the number of inhabitants) and location (b: latitude). Variables differing ($p < 0.01$) between town size and latitudinal categories are given in bold.

a) Study towns in relation to their size								
	Large-sized (n = 11)		Medium-sized (n = 12)		Small-sized (n = 15)		Test statistics	
	Mean	sd	Mean	sd	Mean	sd	H _{df=2}	p
Study plot size (km ²)	6.3	15.2	5.8	11.7	1.1	1.4	3.17	0.205
Human population (inhab.)	2665144	2612506	547689	375801	99071	45390	31.12	<0.001
Age of the town (years)	1474	856	1671	750	780	653	9.42	0.009
Built-up area (km²)	706	476	374	346	59	51	13.33	<0.001
Human density (people/km²)	3342	944	2350	1434	1544	1422	13.00	0.002
Wooded area %	3.1	1.9	5.0	4.0	12.6	11.5	12.6	0.002
Open area %	1.3	1.5	1.1	1.2	1.6	2.4	0.10	0.950
Water areas %	0.3	0.9	0.8	2.1	01.3	2.6	1.48	0.477
Buildings %	71.4	6.8	70.3	6.6	62.0	10.5	8.2	0.018
Streets %	22.1	4.5	21.8	6.5	20.0	4.7	1.3	0.599
Parking areas %	2.3	1.8	1.3	1.3	2.5	3.0	1.57	0.457
Impervious area total %	95.6	2.6	93.3	4.4	84.5	10.7	14.60	0.001
Habitat diversity	0.44	0.08	0.45	0.07	0.53	0.10	10.70	0.005
b) Study towns in relation to their latitudinal location								
	Southern (n = 13)		Central (n = 16)		Northern (n = 9)		Test statistics	
	Mean	sd	Mean	sd	Mean	sd	H _{df=2}	p
Study plot size (km ²)	5.0	11.4	5.0	12.6	1.1	0.3	1.97	0.374
Human population (inhab.)	643377	1515909	1318266	2392297	807097	789770	5.41	0.067
Age of the town (years)	1763	755	1407	638	281	180	21.54	<0.001
Built-up area (km ²)	431	420	314	404	280	445	1.11	0.574
Human density (people/km ²)	2501	1568	2698	1424	1383	1111	5.42	0.067
Wooded area %	7.1	7.3	4.7	4.7	12.9	13.2	6.36	0.042
Open area %	1.0	1.2	1.6	2.2	1.3	1.9	0.21	0.902
Water areas %	0.5	0.2	1.2	2.5	0.7	1.3	1.30	0.522
Buildings %	71.0	9.2	68.4	7.4	60.0	9.2	7.45	0.024
Streets %	19.2	5.1	22.5	5.9	22.0	3.2	3.16	0.206
Parking areas %	1.5	1.3	1.8	1.5	3.3	3.7	0.61	0.737
Impervious area total %	91.7	7.8	92.7	6.3	85.3	11.8	4.57	0.102
Habitat diversity	0.44	0.10	0.47	0.09	0.55	0.06	8.21	0.017

the datasets of Aronson et al. (2014) and Ferenc et al. (2014), whose northernmost study sites were located in southern Sweden and central Europe.

Because the surrounding matrix of the study plot may influence the results (e.g., Rodewald 2003; Pellissier et al.

2012), we extracted background data of the extent of built-up areas and data on the densities of inhabitants living within the built-up areas around the study sites from Demografia.com. According to Demografia.com, built-up area (i.e., the immediate matrix of the urban core area) is a continuously built up

land mass of urban development that is within a labour market (metropolitan area or region) and contains no rural land. All our study plots were embedded within the built-up areas. The built-up area of the study towns varied from 15 to 2845 km² (Appendix 1). The human population density per km² within the built-up areas varied from 173 to 5800 (Appendix 1).

We grouped our study towns into three categories based on their levels of urbanization: large-sized towns > 1 mill. inhabitants, *n* = 11; medium-sized towns > 200,000 inhabitants but < 1 mill. inhabitants, *n* = 12; and small-sized towns < 200,000 inhabitants, *n* = 15 (Fig. 1). Human population size, built-up area cover, human population density within the built-up area, and impervious area cover increased, whereas wooded area cover and habitat diversity decreased with the level of urbanization (Table 1a). These results indicated that groups based on the number of inhabitants were distinctive from each other with respect to other measures of the level of urbanization and that our grouping of the study sites according to the number of inhabitants was justified.

Urban centres were divided among three geographical groups depending on their location (northern Europe > 59°N latitude; *n* = 9; central Europe 47–53°N latitude, *n* = 16; and southern Europe, < 45°N latitude, *n* = 13; Fig. 1). Study sites located in southern, central and northern Europe did not differ from one another (Table 1b), indicating that the urbanization level of our study sites did not differ across latitude. The only exception was the age of the study town: northern towns were younger than the towns located in central and southern Europe (Table 1b). Basic information on the study plots is given in Appendix 1.

1.2. Bird data

We used the breeding presence/absence of species in each of the urban core areas to estimate the ‘frequency’ at which these species were present across all the urban core zone areas of the focal towns. In this study, we only used the data collected by the standard multiple-visit survey method (atlas, territory mapping, point counts; Bibby 2000) within an area covering the size normally used in urban bird atlas work (1 km x 1 km or 0.5 km x 0.5 km). Study plot size did not differ between urban or latitudinal classes (Table 1a, b); therefore, study plot size did not influence our comparisons between urban and latitudinal classes. Species occupancy in a specific site was based on multiple observations of singing males at the same site (territory mapping and point-counts) or detection of at least one probable breeding bird (e.g., permanent territory, nest found; atlas method). Bird species richness did not differ between datasets that were collected by mapping (mean = 21.5 species, *sd* = 14.4, *n* = 11), point (mean = 26.0, *sd* = 8.9, *n* = 8) and atlas (mean = 22.8, *sd* = 8.3, *n* = 19) methods (ANOVA: $F_{2,35} = 0.43$, *p* = 0.652). Thus, data collected with different survey methods could be directly compared.

The breeding range (=northern distribution limit degree-southern distribution limit degree), northern distribution limit and migration distance of each bird species was measured

using data provided in the maps of the book ‘Birds of the Western Palearctic’ (Cramp & Perrins 1977–1994) and following the method used by Møller 2008 and Cuervo and Møller 2013. The year of urbanization of species was taken mainly from Møller et al. 2012 by averaging the individual countries’ values. The bird species list and their main traits is shown in Appendix 2.

1.3. Statistical methods

We used the multi-model inference approach to regress empirically ranked species-occupancy curves (RSOCs) against core-satellite species patterns (Jenkins 2011). Each dataset (species listed in rows and sites listed in columns) was processed as described by Jenkins (2011). First, we counted the number of urban centres in which each species was observed (occupancy). Next, we calculated the relative occupancy per species by dividing the number of sites where the species occupied by the total number of urban centers in each of the three datasets. All the analyses described below are based on relative occupancy. Second, we sorted the species by their relative occupancy values in decreasing order. Species observed in the largest number of urban centres were ranked as being most abundant. In contrast, species observed in the least number of urban centres were ranked as least abundant. The plot of relative occupancy of a species as a function of its rank gave its RSOC. Third, we compared which of the three most common core-satellite species patterns (unimodal-satellite dominant, bimodal symmetrical, and bimodal asymmetrical) gave the best fit among urban breeding bird communities (McGeoch & Gaston 2002; Jenkins 2011). In this study, each of the three SOFD patterns was fitted to each of the datasets (three size classes of towns or three geographical locations) using regression analysis and the RSOC models approach. We compared each of the three SOFD patterns using the Akaike Information Criteria (AICc) (Andersson et al. 2000; Jenkins 2011). The best SOFD pattern was selected based on the results of regression analyses (Jenkins 2011) and by using the Akaike Information Modelling procedure. The best model explaining the SOFD pattern has a Δ AICc value of 0; models with a delta value under 2 explain substantial variation, models with a delta value within 4–7 explain considerable variation, and models with a delta value greater than 10 do not explain any of the variation (Burnham & Anderson 2002). The three models compared in this study were:

- 1) Core-satellite species pattern #1: Unimodal-satellite (exponential concave): $O_i = y_0 + a \cdot \exp(-bR_i)$, where the initial parameters were $y_0 = 0.01$, $a = 1.0$, $b = 0.01$.
- 2) Core-satellite species pattern #2: Bimodal symmetric (sigmoidal symmetric): $O_i = a / (1 + \exp(-bR_i + c))$, where the initial parameters were $a = 1.0$, $b = -0.1$, $c = -1.0$.
- 3) Core-satellite species pattern #3: Bimodal asymmetric (sigmoidal asymmetric): $O_i = a [1 - \exp(-bR_i^2)]$, where the initial parameters were $a = 1.0$, $b = -1.0$, $c = -1.0$.

The tails and shoulders of the data and models were evaluated visually.

We used nonlinear regression in the PASW statistical package version 18 to evaluate the fit of the three SOFD

models with data. Non-linear regressions were computed using ordinary least square (OLS) with the Levenberg-Marquardt algorithm (< 999 iterations). We graphically evaluated the assumptions of regressions, such as, the normality of residuals, homogeneity of variance, and independent error terms.

Kruskal-Wallis ANOVA tests were used to analyse the differences in background variables and bird species richness between size of the town and latitudinal categories. Spearman's rho correlation analyses were used to study the relationships between background and bird variables.

We measured habitat heterogeneity by the Simpson index ($1 - \sum p_i^2$), where p_i is the proportion of different habitat types (wooded, open, water, buildings, streets and parking areas) in the study plots using Google maps.

The occurrence (presence coded as 1 and absence coded as 0) of individual species occurring at least 10 sites was modelled using a logistic regression analysis (Trexler & Travis 1993). Analyses were conducted using the following variables: built-up area (ha), age of town (years) and human population size of the town (number of inhabitants). The adequacy of each model is tested by the goodness-of-fit test with $df = 3$. The significance of each variable is analysed by the Wald-test (* $P < 0.05$, ° $P < 0.10$).

2. RESULTS

2.1. Bird species richness

A total of 108 bird species (mean = 23.2, sd = 10.3, $n = 38$) were found to breed in the town centres (Appendix 2). The average number of species did not differ between the level of urbanization ($F_{2,29} = 0.65$, $p = 0.53$) or the geographical location of the site ($F_{2,29} = 2.11$, $p = 0.14$). The interaction term of the level of urbanization and geographical location was not correlated with species richness ($F_{4,29} = 0.51$, $p = 0.73$).

Bird species richness was not correlated with the number of inhabitants (Spearman's rho = -0.13, $p = 0.434$, $n = 38$), latitude (Spearman's rho = -0.16, $p = 0.339$, $n = 38$), age of the town (Spearman's rho = -0.30, $p = 0.065$, $n = 38$) and human population density (Spearman's rho = -0.13, $P = 0.451$, $n = 38$). Species richness tended to decrease with the extent of built-up areas (Spearman's rho = -0.33, $p = 0.046$, $n = 38$).

2.2. Species composition

Only three species (*Alopothen aegyptiaca*, *Phasianus colchicus*, and *Psittacula krameri*) out of 108 were non-native. Four species (*Columba livia domestica* [occupying 36 town centres out of 38], *Apus apus* [35], *Parus major* [34] and *Carduelis chloris* [32]) were found in almost all towns. Sixteen species occupied at least half of the urban core zones of European towns, and 27 species were observed in only a single town (Appendix 2, Fig. 2-3).

The number of core species increased with the level of urbanization. *Columba livia*, *Apus apus*, *Parus major*, *Passer domesticus* and *Chloris chloris* were the core species (occurring

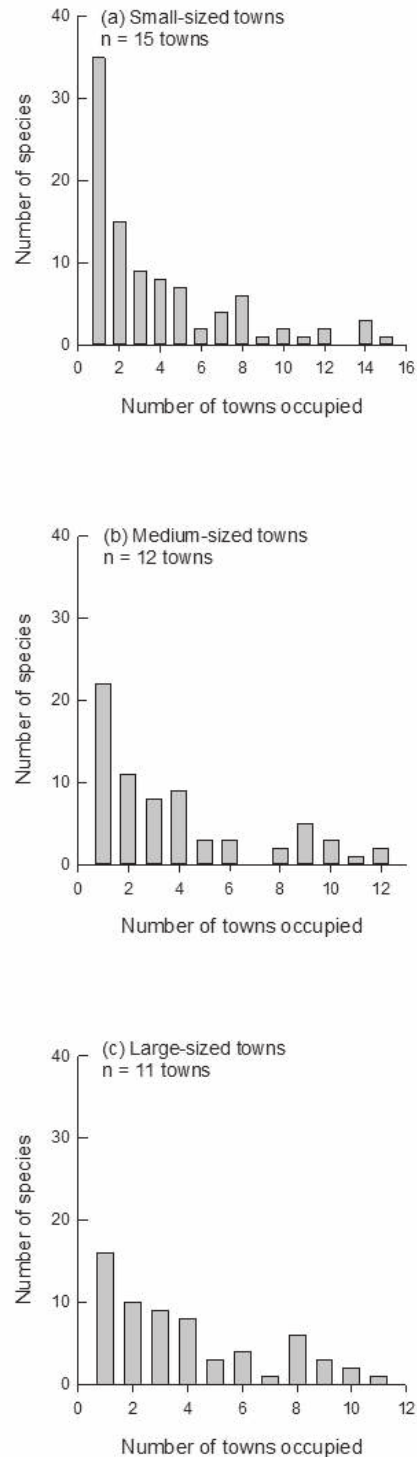


Figure 2. The number of breeding bird species in relation to the number of occupied urban town centres grouped according to (a) Small towns, with less than 200,000 inhabitants ($n = 15$), (b) Medium-sized towns, with 200,000 to 1,000,000 inhabitants ($n = 12$), and (c) Large towns, with more than 1,000,000 inhabitants ($n = 11$) in Europe.

at >80% of sites) in all three town-size categories (Appendix 2). Some species (*Streptopelia decaocto*, *Serinus serinus*, *Sylvia atricapilla* and *Columba palumbus*) were not included in the core species list in the north, whereas some species (*Pica pica*, *Motacilla alba* and *Turdus pilaris*) were only included in the core species list in the north (Appendix 2). The proportion of core species was approximately 19% in large towns, 9% in medium-sized towns, and 6% in small-sized towns (Appendix 2). The proportion of satellite species (occurring at <20% of sites) decreased with urbanization. The proportion of satellite species was 17% in large-sized towns, 47% in medium-sized towns and 52% in small-sized towns (Appendix 2).

The proportion of core species was approximately the same regardless of location: 11% in southern Europe, 12% in central Europe and 16% in northern Europe (Appendix 2). However, the proportion of satellite species was lower in southern Europe (24%) than in central Europe (51%) and northern Europe (48%) (Appendix 2). We did not detect any cases where a species classification changed from a core species to a satellite species between town-size groups or latitudinal categories (Appendix 2).

Species occupation frequency in the town centres increased with the range area of a species (Spearman's rho = 0.52, $p < 0.001$, $n = 108$), breeding population size in Europe (Spearman's rho = 0.56, $p < 0.001$, Fig 4b), and decreased with the year of urbanization of the species (Spearman's rho = -0.55, $p < 0.001$, $n = 59$, Fig. 4a), northern distribution limit of species (Spearman's rho = -0.41, $p < 0.001$, $n = 105$) and latitudinal range-size of species (Spearman's rho = -0.49, $p < 0.001$, $n = 105$).

The occurrence of *Anas platyrhynchos*, *Falco tinnunculus*, *Motacilla alba*, *Phoenicurus ochruros*, *Phylloscopus collybita* and *Turdus merula* increased with the extent of the built-up area, and the occurrence of *Carduelis carduelis* decreased and the occurrence of *Troglodytes troglodytes* increased with the age of the study town (Table 2).

2.3. SOFD patterns

Pooled data analysis of all towns indicated that the urban core area zones of European towns followed a unimodal-satellite SOFD pattern (Table 3). Most species only occurred in a single town, and this effect was independent of the level of urbanization of the town (Fig. 2). Subsamples of small-sized and medium-sized towns exhibited unimodal-satellite patterns (Fig. 2a, b; Table 3), whereas large-sized towns exhibited bimodal symmetric patterns (Fig. 2c; Table 3). Based on the Δ AICc values (<4.0), also the unimodal satellite patterns explained considerable variation in SOFD patterns in large-sized towns (Table 3).

With respect to geography, the proportion of bird species occurring only in one town was smaller in southern Europe than in central Europe and northern Europe (Fig. 3). In addition, northern towns exhibited bimodal asymmetric SOFD patterns (Fig. 3a, Table 3), central European towns exhibited bimodal symmetric patterns (Fig. 2b, Table 3), and southern towns exhibited unimodal satellite SOFD patterns (Fig. 3c, Table

Table 2. Logistic regression models for the core bird species occurring in at least 10 sites.

Species	Variables	G ²	P
<i>Aegithalos caudatus</i>		3.4	0.335
<i>Anas platyrhynchos</i>	log (built-up) ^o	4.4	0.224
<i>Apus apus</i>		2.6	0.457
<i>Carduelis carduelis</i>	-log (age of town)*	15.2	0.002
<i>Carduelis chloris</i>		4.0	0.262
<i>Certhia brachydactyla</i>		6.2	0.104
<i>Columba livia</i>		3.3	0.351
<i>Columba palumbus</i>		5.8	0.121
<i>Corvus corone</i>		2.1	0.554
<i>Corvus monedula</i>		1.1	0.788
<i>Delichon urbicum</i>		1.6	0.663
<i>Dendrocopos major</i>		4.2	0.237
<i>Erithacus rubecula</i>		5.5	0.141
<i>Falco tinnunculus</i>	log (built-up)*	9.3	0.026
<i>Fringilla coelebs</i>		4.4	0.218
<i>Garrulus glandarius</i>		7.4	0.060
<i>Hirundo rustica</i>		1.7	0.644
<i>Motacilla alba</i>	log (built-up)*	6.9	0.074
<i>Muscicapa striata</i>		1.7	0.645
<i>Passer domesticus</i>		2.5	0.469
<i>Parus caeruleus</i>		2.7	0.449
<i>Passer montanus</i>		2.8	0.422
<i>Parus major</i>		3.9	0.270
<i>Phoenicurus ochruros</i>	log (built-up) ^o	6.7	0.081
<i>Phoenicurus phoenicurus</i>		5.8	0.119
<i>Phylloscopus collybita</i>	log (built-up) ^o	3.2	0.358
<i>Pica pica</i>		6.5	0.089
<i>Serinus serinus</i>		3.4	0.333
<i>Sitta europaea</i>		3.7	0.297
<i>Sylvia atricapilla</i>		4.1	0.252
<i>Streptopelia decaocto</i>		2.3	0.512
<i>Sturnus vulgaris</i>		3.5	0.322
<i>Turdus merula</i>	log (built-up) ^o	4.5	0.215
<i>Troglodytes troglodytes</i>	log (age of town) ^o	5.0	0.173

3). Based on the Δ AICc values (<4.0.), also bimodal symmetric patterns explained considerable variation in SOFD patterns in southern European towns (Table 3).

Table 3. The results of breeding bird species occupancy frequency distribution pattern analyses. The three most likely core-satellite patterns (unimodal-satellite, bimodal symmetric, and bimodal asymmetric) were analysed in regard to seven data sets. AIC_c is the corrected AIC coefficient. The lowest AIC_c is the best model of those tested.

Source	# species	Model	AIC_c	ΔAIC_c
Pooled data	109			
		Unimodal-satellite	-876.8	0
		Bimodal symmetric	-872.5	4.4
		Bimodal asymmetric	-268.4	608.4
Size of town	63			
		Bimodal symmetric	-440.2	0
		Unimodal-satellite	-437.0	3.2
		Bimodal asymmetric	-411.9	28.3
Medium	69			
		Unimodal-satellite	-494.7	0
		Bimodal symmetric	-484.6	10.1
		Bimodal asymmetric	-479.7	14.9
Small	97			
		Unimodal-satellite	-671.9	0
		Bimodal symmetric	-638.6	33.4
		Bimodal asymmetric	-619.5	52.4
Location of town	54			
		Unimodal-satellite	-392.9	0
		Bimodal symmetric	-388.7	4.2
		Bimodal asymmetric	-343.7	49.2
Central	77			
		Bimodal symmetric	-554.8	0
		Unimodal-satellite	-525.8	28.9
		Bimodal asymmetric	-470.1	84.7
Northern	58			
		Bimodal asymmetric	-346.4	0
		Unimodal-satellite	-328.4	18.0
		Bimodal symmetric	-320.0	26.5

3. DISCUSSION

3.1. Species richness

In general, urbanization can have tremendous impact on species richness. Indeed, urbanization is considered to be one of the most important factors responsible for much of the ongoing biodiversity loss and homogenization of environments (McKinney 2002, 2006; Sol et al. 2014). We found a relatively high breeding bird species richness (108 species) in core zone areas of European towns. This is approximately 20% of the total

number of European breeding bird species. Schlesinger et al. (2008) have suggested that disturbance due to human activity is one of the most important factors explaining species richness in urban environments. Despite the high levels of disturbance within urban environments, there is evidence that many species are able to colonize urban environments. According to the results of Aronson et al. (2014), of the 10,052 recognized bird species worldwide, 20% of them occur in cities. In contrast to the breeding bird species richness of natural habitats, Jokimäki and Suhonen (1993) have suggested that the breeding bird

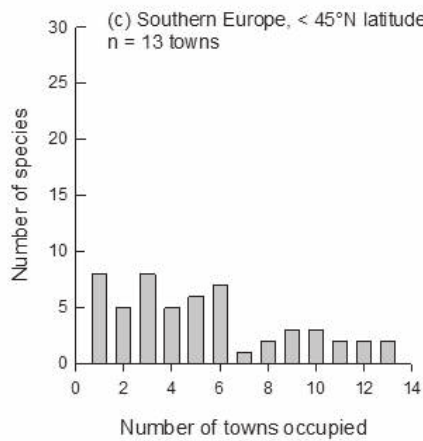
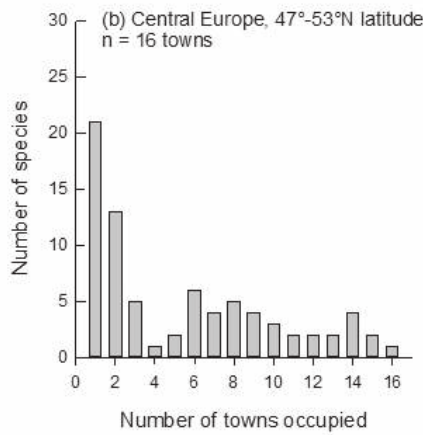
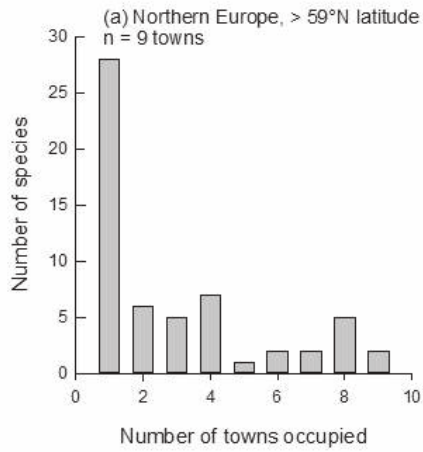


Figure 3. The number of breeding bird species in relation to the number of occupied urban centres grouped according to their geographical location: (a) Northern towns (Latitude > 59° N, n = 9), (b) Central towns (Latitude 47 – 53° N, n = 16) and (c) Southern towns (Latitude < 45° N, n = 13) in Europe.

species richness of urban communities does not decrease as latitude increases. In fact, Ferenc et al. (2014) proposed that species richness of European cities may even increase with the latitude. Our results are consistent with the hypothesis that species richness does not decrease as latitude increases in the heavily urbanized areas in Europe. However, more detailed analyses is needed, for example, to study the possible role of regional species pool on the species richness in urban habitats.

Based on our results, the size of the town (i.e., the number of inhabitants), the age of town and geographical location (i.e., latitude) did not impact breeding bird species richness. An increasing degree of urbanization has been shown to have a negative impact on bird species richness (Blair 1996; Marzluff 2001; Chace & Walsh 2006; Ortega-Álvarez 2009). In some cases, species richness has been shown to peak at intermediate levels of urbanization (Jokimäki & Suhonen 1993; Blair

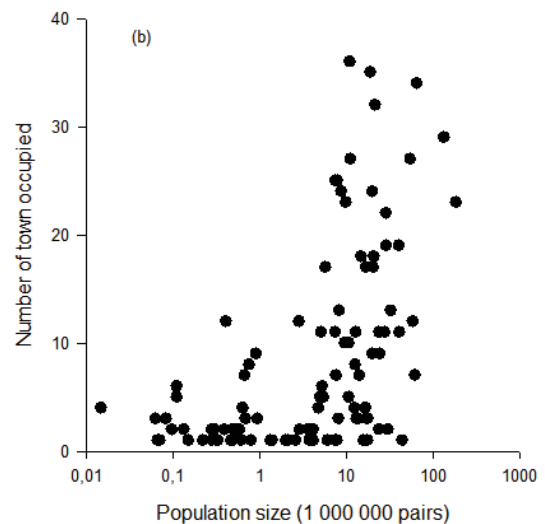
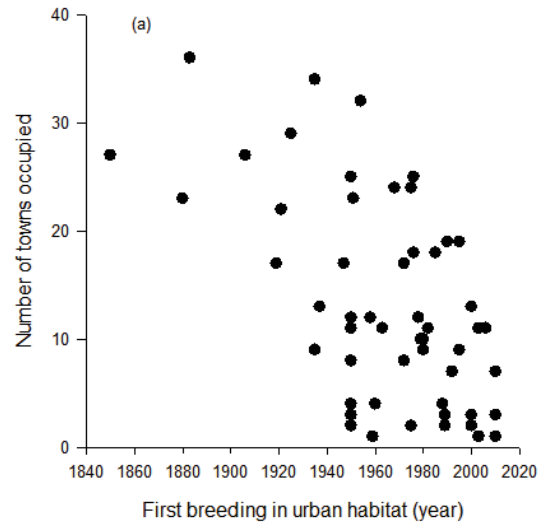


Figure 4. Relationships between the number of site occupied and a) year of urbanization of species and b) species European breeding population size (in million pairs).

1996; Conole 2014). In general, the lowest diversities along urban gradients are observed in intensively built-up environments (i.e., in urban core areas; McKinney 2002). Our study was conducted in urban core zone areas with a relatively homogeneous habitat structure among study sites; therefore, the fact that there was no effect of urbanization on species richness was not a surprise.

3.2. Species composition

Urbanization acts as a filter on species that can tolerate urban constraints such as disturbance (e.g., Shanahan et al. 2014; Sol et al. 2014). Some species may benefit from urbanization (urban exploiters) and occur in most towns worldwide. In contrast, some species may suffer ('urban avoiders') from urbanization. Other species may neither benefit nor suffer from urbanization (suburban adaptable species) (Blair 1996). The species richness of urban avoiders is often greater than the number of urban exploiters (Palomino & Carrascal 2006). Our data suggest that bird species adapted to the most heavily urbanized habitats are generalists and/or they are early-adapted to nesting in/on buildings, such as *Columba livia* and *Delichon urbica* (see also Blair 1996, Jokimäki et al. 2016).

Several studies have also indicated that bird community structures are quite similar between towns (Jokimäki & Kisanlahti-Jokimäki 2003; Chace & Walsh 2006; Clergeau et al. 2006a, Ferenc et al. 2014). In support of this homogenization effect of urbanization, only five core species, *Columba livia*, *Apus apus*, *Parus major*, *Passer domesticus* and *Chloris chloris*, were observed in all three town-size categories in our study (see also Clergeau et al. 2006a). However, the response of species to urbanization can vary among different biogeographical areas (González-Oreja 2011; Ferenc et al. 2014). Our results indicate that southern urban environments are more similar than northern urban environments, and probably therefore southern urban bird communities contain fewer satellite species than northern communities. In addition, some bird species (*Streptopelia decaocto*, *Sylvia atricapilla* and *Columba palumbus*) were only included in the core species list in southern Europe, whereas some species (*Pica pica* and *Motacilla alba*) were only included in the core species list in northern Europe. Therefore, the hypothesis that bird communities have been homogenized worldwide in urbanized areas is tenuous based on an analysis of urbanized areas in Europe.

We found that core species in European town centres are widely distributed and their regional population sizes are large, whereas opposite is true for the satellite species. In addition, supporting to the results of Møller et al. (2012), we found that earlier urbanized species were more common in town than species that have urbanized later. Our results also indicated that in addition to species traits, many core species, like *Falco tinnunculus* and *Motacilla alba*, in European towns have a positive relationship with the built-up structures, whereas some core species, like *Carduelis carduelis* and *Troglodytes troglodytes* were more affected by the age of town. Therefore, future studies should consider both species- and town-related

factors simultaneously, when analysing the effects of urbanization on birds.

3.3. Species occupancy frequency distribution in urban core zone areas

3.3.1 Sampling artefacts

Our results indicated that give the best fit of the pooled data. This finding indicates that most species occurred either in a single or few urban core zone areas of European towns and that the beta-diversity is relatively high even in these highly urbanized areas (see also Aronson et al. 2014). However, the results varied across urban and latitudinal gradients. In small-sized towns, most breeding species only occurred in a single town. In contrast, more bird species were shared between large towns than between small towns (see also Blair 2001; Clergeau et al. 2006a). Our results suggest that as the urbanization level increases, SOFD patterns change from unimodal satellite dominant mode to bimodal symmetric mode.

There are several possible explanations for why SOFD patterns in urban core zone areas may differ across town-size and latitudinal categories. First, SOFD patterns may differ due to sampling methods, such as the number of samples and the extent of sampling (McGeoch & Gaston 2002). Our data was collected using standard bird survey methods from 38 sample sites within a latitudinal extent of 3850 km, constituting a total of 108 species. In general, samples from large areas are more heterogeneous than samples from smaller areas; therefore, these samples will contain many satellite (rare) species and exhibit unimodal species distributions. Our data partially supported this hypothesis because our pooled data exhibited a unimodal satellite dominant pattern, whereas bimodal SOFDs were often observed in subsamples of the data.

Study plot size may also influence SOFD patterns (McGeoch & Gaston 2002). However, in our study, the study plot sizes were similar between urbanization and latitudinal subgroups. Thus, the possible artefact of study plot size was controlled for in this study.

Data collected by different survey methods may produce different estimates of species richness and thus different SOFD patterns. In the current study, estimates of bird species richness did not differ between data collected by the different survey methods. In addition, species richness did not change across latitudinal or urbanization gradients. Therefore, observed differences in SOFD patterns are not likely related to the use of different bird survey methods.

3.3.2 Biological factors

In addition to the artefactual sampling effects on SOFD patterns, several biological mechanisms, such as environmental heterogeneity, species specificity, landscape productivity and position in the geographical range of species and assemblage, have been suggested to explain observed SOFD patterns (McGeoch & Gaston 2002). Because environmental diversity tends to increase as the sampling area increases, the number of satellite species

is predicted to increase as the extent or number of study sites increases. Therefore, a unimodal satellite dominated pattern is expected in heterogeneous areas, while bimodal SOFD patterns are expected in more homogeneous areas. Our results provide support for this expectation because large-sized towns that have also lower habitat diversity exhibit bimodal SOFD patterns. In contrast, small-sized towns with higher habitat diversity exhibit unimodal satellite dominated SOFD pattern.

The species specificity explanation for SOFD patterns suggest that, if species habitat use (e.g., if the species is a specialist or generalist) determines patterns, species classification as core- and satellite species should vary across different areas (McGeoch & Gaston 2002). In addition, urban birds have been reported to have a broader environmental tolerance (Bonier et al., 2007). We did not observe any cases when a core species in one area was a satellite species in another area, and *vice versa*. Thus, species specificity does not appear to be an important factor that determines SOFD patterns. Satellite species are primarily specialists, especially with respect to their feeding habits (urban avoider; Blair 1996). Indeed, most of the satellite species occurred in only one or two European town centres. However, in the north, some species may still be descendants of the original bird species living in the region; therefore, only a few species are shared by the towns there.

Urban core areas have a low natural productivity compared to their surrounding areas (e.g., Gilbert 1989; Rebele 1994), but they are characterized by a high amount of predictable anthropogenic food resources, such as wastes and feeding tables (Shochat et al. 2006; Francis & Chadwick 2013; Adams 2016). In low-productive sites (small-sized towns in our case), a high dominance of few species is possible; thus, a bimodal SOFD pattern is expected (McGeoch & Gaston 2002). In contrast, in high-productive sites (large-sized areas in our case), a greater availability of resources increases living possibilities of several species; thus, a unimodal SOFD pattern is expected. However, we found the opposite result. Productivity may decrease towards the north. We did not directly measure productivity, but our results from a latitudinal SOFD pattern are highly consistent with this prediction because southern assemblages exhibited a unimodal pattern, whereas northern assemblages exhibited bimodal SOFD patterns.

According to the range area frequency distribution hypothesis, bird communities at more southerly latitudes have fewer core species and more satellite species than communities at more northern latitudes (McGeoch & Gaston 2002). This hypothesis is based on the concept that species at low latitudes tend to have smaller latitudinal ranges than species occurring at higher latitudes. Moreover, species are known to be most abundant near the centre of their geographical distribution (Brown 1984). In addition, the occupancy and abundance of species are positively related to each other in urban areas (Jokimäki et al. 2014). Data from Møller et al. (2012) indicate that

species with high abundance in surrounding rural areas are more capable of colonizing urban habitats than species with low abundance in the surrounding urban areas. However, the results from our previous studies in European towns suggest that urban bird communities are quite independent of the bird diversity of adjacent landscapes (Clergeau, et al. 2001; Jokimäki et al. 2014).

Generally, the breeding bird species pool is larger in the south than in the north; thus, more species live near their geographical range borders in the north than in the south. Therefore, a high ratio of species in the assemblage at or near their range edges is predicted to occur in the north, whereas a high ratio of species in the assemblage at or near the centre of their ranges is predicted to occur in the south. As a consequence, more satellite species are predicted to occur in the north than in the south. Our study provides strong support for this prediction because the proportion of satellite species in assemblages was lower in the south than in the more northern assemblages. In addition, we observed that species occupation frequency in the town centre increased as the range area of species increased.

In conclusion, the observed SOFD patterns varied with latitude and with the level of urbanization. The ongoing process of urbanization and its impact on urban bird communities can still be observed in the European towns because SOFD patterns in northern and southern towns differ from each other. One reason for this difference may be related to the history of the towns. Northern towns are approximately 2,000 years younger than the southern towns. Thus, only a few species living in the north are currently adapted to surviving and reproducing in urbanized environments. In addition, the proportion of bird species that occur in only one town was smaller in southern Europe than in central or northern Europe. We suggest that many bird species in the north are still only in their incipient phase of adapting to urbanized environments (Evans et al. 2010). In contrast, in southern Europe, more species are already well adapted to urbanized environments (see also Møller 2014). Our results also provide support for the observation that species can still survive in single towns for some time due to extinction delay (Essl et al. 2015). More studies are needed to determine whether the observed SOFD patterns in urban environments are related to individuals tolerating or adapting to disturbance and urban lifestyles. For example, a high dominance of a few species and low species richness may cause homogenization of bird communities across urban environments (Blair 2001; Clergeau et al. 2006a; McKinney 2006).

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