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Research Paper

Occupancy-frequency distribution of birds in land-sharing and -sparing urban landscapes in Europe

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HIGHLIGHTS

- Species presence/absence patterns can estimate wide-scale metacommunity diversity.
- Land-sparing urban areas had more rare species than land-sharing areas across Europe.
- A land-sharing development type can increase the number of common bird species.
- City geographical locations explained core and satellite species number variations.

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ABSTRACT

Species richness is a widely used proxy for patterns of biodiversity variation in metacommunities. However, deeper analyses require additional metrics, such as the occupancy-frequency distributions (SOFD) of different local communities. The SOFD patterns indicate the number of shared species between study sites; therefore, they can provide new insights into the current debate on how to create more biodiversity-friendly cities. Breeding birds were counted from 593 point-count stations located in five 500 m × 500 m squares in land-sharing (LSH; low-density built areas interspersed with green spaces) and five similar nearby squares in land-sparing (LSP; densely built-up with set-aside, large-sized, continuous green spaces) landscapes in nine cities across Europe. High beta-diversity (with over 42% of the 103 species detected being restricted to a single city and only 7% found in all studied cities) showed the uniqueness of cities at the continental scale. Urban bird metacommunities followed the unimodal-satellite SOFD pattern at the European continental scale but a bimodal symmetric or asymmetric distribution at the city-level scale, suggesting that many common species occur in cities on a smaller scale. The LSP urban areas followed a unimodal satellite SOFD pattern with numerous rare species. In contrast, the LSH areas fit several types of bimodal SOFD patterns equally well, where communities share several common species. The findings also highlight the need to use multi-scale approaches to analyze the effects of LSH-LSP urban designs on urban bird diversity.

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1. Introduction

Monitoring the occupancy and distribution of populations is an integral part of ecological knowledge gathering and effective conservation management. Such studies are of interest in determining whether specific species occupy specific sites. For this purpose, data are collected from multiple sites, and species occupancies are recorded. In metacommunities, two types of species are most typical: satellite species are uncommon species found from only a few sites, whereas core species are common species found in most sites. In macro- and community ecology, species occupancy-frequency distribution (SOFD) and ranked species-occupancy curves (RSOCs) are often used to describe species distributions across multiple sites (Hui, 2012; Jenkins, 2011; McGeoch & Gaston, 2002). The SOFD indicates the distribution of the number of species occupying different numbers of study sites, producing a data matrix (where rows indicate species, columns indicate different sites), and the element indicates the presence/absence of a species in a specific site. On the other hand, RSOCs rank the species rather than assigning them to histogram bins (a pattern describing the row sums; Hui, 2012; Jenkins, 2011).

An RSOC can be constructed by sorting the occupancies of species from high to low and then plotting species occupancy as a function of its ranking (Hui, 2012; Jenkins, 2011). Both methods are suitable for characterizing metacommunities at regional scales (Jenkins, 2011; McGeoch & Gaston, 2002; Fig. 1). The SOFD/RSOC approach offers information on the number or proportion of locations at which each species occurs. Therefore, SOFD pattern analyses yield more detailed information than species richness alone, particularly regarding the spatial distribution of species and the metacommunity structure. The shape of the SOFD indicates the number of shared species between study sites; therefore, it can provide new insights into the current debate on how to create more biodiversity-friendly cities. Ultimately, SOFD patterns provide valuable information for evaluating the ecological processes and conservation values of metacommunities (Hui, 2012; Jenkins, 2011; McGeoch & Gaston, 2002). On the other hand, RSOCs improve OFDs by retaining more details while providing more definitive analyses of species occupancy patterns (Jenkins, 2011).

While several biological models have been proposed to explain SOFD and RSOC patterns (Fig. 1), two have received the most scientific attention thus far (Jenkins, 2011; McGeoch & Gaston, 2002; Tokeshi, 1992). First, the unimodal-satellite SOFD pattern relies on the idea that metacommunities have many rare narrow-niche specialist species and a few common broad-niche generalist species (Brown, 1984) (Fig. 1a, b) (hereafter niche-based model). Second, the bimodal core-satellite SOFD pattern relies on the idea that metacommunities share several (core) species and simultaneously have several species occupying only one or a few locations (satellites). This model results from a dynamic metapopulation model based on local extinction and colonization dynamics (Hanski, 1982, 1999) (hereafter dynamic metapopulation model). When bimodality occurs, it can follow symmetric (Fig. 1c, d) or asymmetric (Fig. 1e, f) patterns depending on the relative proportion of common and rare species. An additional pattern arises when communities have fewer shared common and more unshared species, conforming to a bimodal truncated pattern (Fig. 1g, h). The fifth possible SOFD pattern is random (Hui, 2012; Jenkins, 2011; McGeoch & Gaston, 2002; Tokeshi, 1992). To date, most studies have been carried out in natural environments, and they have found either unimodal satellite or bimodal truncated patterns (Brown, 1984; Hui, 2012; Jenkins, 2011; McGeoch & Gaston, 2002; Tokeshi, 1992).

Notably, SOFD/RSOC patterns have seldom been analyzed in human-modified urban habitats (Hui, 2012; Jenkins, 2011; Lepczyk et al., 2017; McGeoch & Gaston, 2002; Tokeshi, 1992). Urban habitats are particularly relevant, given their overall negative effects on biodiversity (Aronson et al., 2014; Ibanez-Alamo, Rubio, Benedetti, & Morelli, 2017; Morelli et al., 2016) and their exponential increase worldwide (Department of Economic and Social Affairs, Population Division, 2019). Urban areas challenge wildlife because of their heterogeneous and mosaic landscape structure, with grey (e.g., buildings and roads), brown (e.g., open fields), blue (e.g., small ponds), and green (e.g., parks, cemeteries) areas (Francis & Chadwick, 2013). Moreover, urban areas differ from natural areas in their warmer microclimate, frequent human disturbance, and anthropogenic food resources (Adams, 2016; Díaz et al., 2013, 2022; Ibañez-Alamo et al., 2017; Morelli et al., 2016). Correspondingly, urbanization may change the SOFD patterns observed in natural areas (Adams, 2016; Francis & Chadwick, 2013). Urbanization causes taxonomic, functional, and evolutionary homogenization of urban animals and plant communities across the globe (Devictor et al., 2007; Ibanez-Alamo, Rubio, Benedetti, & Morelli, 2017; McKinney, 2006; Morelli et al., 2016). However, this homogenization might differ between taxa (see Dar & Reshi 2014; Knop, 2016; Kühn & Klotz, 2006; Olden, 2006), implying changes in SOFD patterns, most likely from unimodal-satellite dominant patterns to bimodal patterns.

The few studies that have explored SOFD patterns in urban landscapes have given quite heterogeneous results (Ferenc et al., 2016; Jokimäki, Suhonen, & Kaisanlahti-Jokimäki, 2016; Storch & Sizling, 2002; Suhonen & Jokimäki, 2019b). However, these studies were affected by a wide variation in grain size (the size of the local community), the number of study sites, and the extent (the area where local community data were collected). Since these methodological issues are known to influence SOFD (McGeoch & Gaston, 2002), additional studies with replicated and homogeneous study designs are needed to understand the effects of urbanization SOFD patterns and their changes.

The landscape structure of urban areas could also explain the observed variations in the SOFD patterns. The two long-discussed extremes of urban development strategies are compact and sprawling city designs (Francis & Chadwick, 2013). On this basis, recent studies have classified urban landscapes into two main urban development types: (*i*) land-sharing (LSH) and (*ii*) land-sparing (LSP) (Finch et al., 2019; Ibanez-Alamo et al., 2020; Kremen, 2015; Lin & Fuller, 2013; Rodewald, 2003; Soga, Yamaura, Koike, & Gaston, 2014). Land-sharing areas contain low-density built areas (e.g., private house settlements) scattered in green spaces. In contrast, LSP areas are densely covered with multistory buildings, setting aside large-sized, continuous green areas (Lin & Fuller, 2013). Several factors such as habitat heterogeneity, productivity, disturbance, and study location have been found to modify SOFD patterns (McGeoch & Gaston, 2002). Based on these assumptions, we can predict potential differences in the SOFD patterns between the LSH and LSP urban areas. For example, satellite species are positively associated with environmental diversity (McGeoch & Gaston, 2002). Therefore, given that LSH urban landscapes have a higher diversity of habitats than an LSP urban landscape organization (Lin & Fuller, 2013), we could expect more satellite species in LSH than in LSP habitats, and we could expect that both core (common) and satellite (rare) species could be found in LSP habitats. The SOFD patterns can be used to analyze how different urban development types affect biodiversity and species composition across space and time. This knowledge is essential for city planning and biodiversity conservation (Ibanez-Alamo, Morelli, Benedetti, & Rubio et al., 2020; Jokimäki & Suhonen et al., 2020; Lin & Fuller, 2013).

In this study, we investigated how the scale (Uchida et al., 2021), urban development type (LSH and LSP; Ibanez-Alamo, Morelli, Benedetti, & Rubio et al., 2020; Jokimäki & Suhonen et al., 2020), and geographical location (Korkeamäki et al., 2018; McGeoch & Gaston, 2002) affect the shape of SOFD patterns and the potential factors that could modulate this response. We explored four main research questions. First, are there scale-dependent effects of urbanization on SOFD patterns? We predicted a decrease in the number of core species and an increase in the number of satellite species from a smaller (city) scale to a larger (continental) scale because many species are geographically restricted. Larger scales (e.g., continent-wide) would follow a unimodal satellite dominant pattern, whereas data collected from smaller (e.g., city-level) scales follow bimodal distributions (Collins & Glenn, 1997;

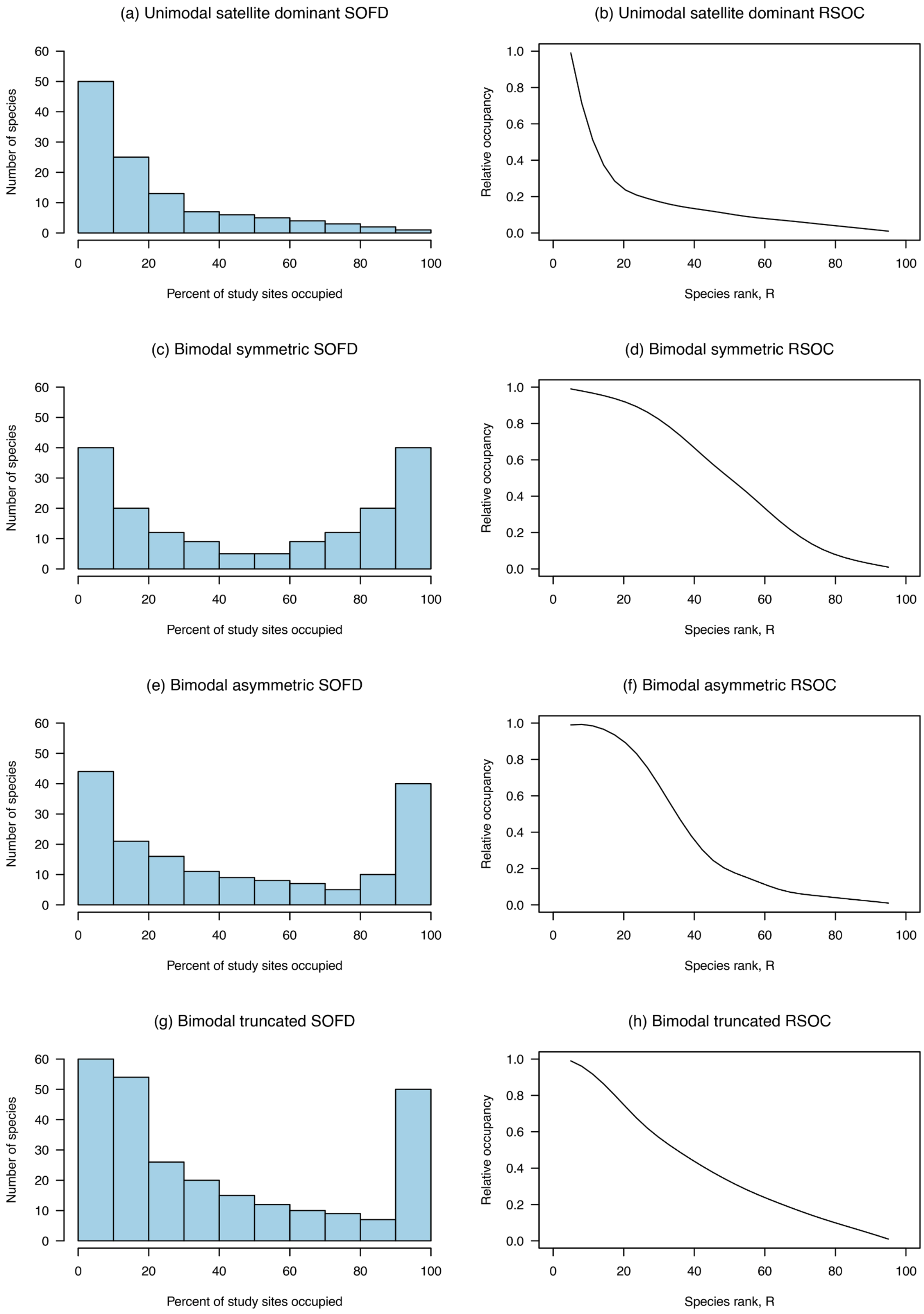


Fig. 1. Illustration of the four models for species occupancy frequency distribution (SOFD) patterns and corresponding ranked species occupancy curves (RSOC). The RSOC curves were calculated by dividing each bird species' occupancy frequency by the total number of study sites. Then, these relative occupancy values (O_i) were sorted in decreasing order. Each breeding bird species had its rank value, R_i, inversely correlated with the relative occupancy value. (a) Unimodal satellite dominant SOFD, (b) unimodal satellite dominant RSOC, (c) bimodal symmetric (SOFD, (d) bimodal symmetric RSOC, (e) bimodal asymmetric SOFD, (f) bimodal asymmetric RSOC, (g) bimodal truncated SOFD, and (h) bimodal truncated RSOC).

McGeoch & Gaston, 2002). Second, is there geographical variation in the SOFD patterns among European cities? We predicted differences in SOFD patterns among cities, given that our large-scale spatial approach potentially implies different local species pools. Third, does urban development type (LSH vs. LSP) affect SOFD patterns? A satellite-dominant unimodal SOFD pattern was predicted to occur in the LSH urban areas. In contrast, LSP areas are predicted to exhibit bimodal SOFDs with many core (common) and satellite (rare) species. Finally, are there differences in the compositions of core and satellite species between urban development types and cities? This last question attempts to establish whether species can change their status from core to satellite or *vice versa*, depending on the urban development type or city. Thus, we predict that a core species in some cities will become a satellite species in other cities.

2. Material and methods

2.1. Study areas

Data were collected from nine cities (Fig. 2) (64,000 – 3 170,000 inhabitants) located in three different vegetation zones along a 3700 km latitudinal gradient that expanded from the Mediterranean area up to the Arctic Circle in Europe (Table 1, see more details in Ibáñez-Alamo et al., 2020; Jokimäki & Suhonen et al., 2020). We selected several cities from each major climatic zone to capture a good representation of the variation in urban areas in Europe and quantified breeding bird communities in the LSH and LSP urban areas of nine European cities. Data on bird species occupancy was collected using a carefully planned and replicated study design, where we employed precisely the same grain size (500 m × 500 m), sample size, sampling cover, survey intensity, and bird survey methods in each studied city, thereby decreasing the possibility of methodological biases affecting the shape of SOFD patterns (McGeoch & Gaston, 2002). In each city, we selected ten 500 m × 500 m squares, half of which had the LSH urban landscape development type, while the other half corresponded with the LSP urban development type.

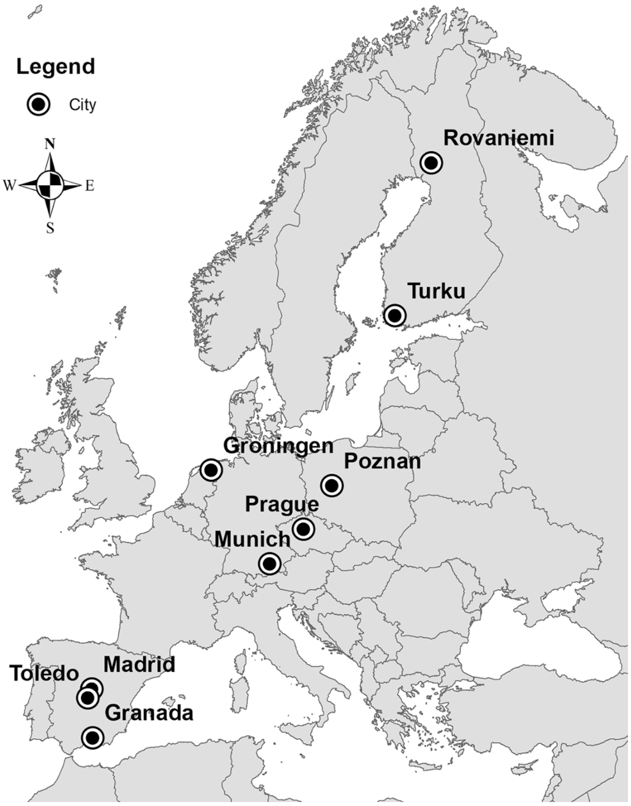


Fig. 2. Nine European cities investigated for breeding bird metacommunities in LSH and LSP landscapes.

The squares within each city were initially assigned to one or more types by visual inspection of the satellite images available on Google Earth. This classification was later confirmed based on a recent landscape urban index that used five landscape characteristics to identify a square as LSH or LSP (details in Ibanez-Alamo, Morelli, Benedetti, & Rubio et al., 2020; Jokimäki & Suhonen et al., 2020). The LSH squares consisted of areas with low-density housing and fragmented green areas, whereas the LSP squares corresponded to high-density housing areas. The majority (>50%) of the green surfaces aggregated into a single patch. Each LSH square in a given city was matched with the LSP square of the same city with a similar overall green area (Ibanez-Alamo, Morelli, Benedetti, & Rubio et al., 2020). The purpose of the matching was to control for the effect of the green area, the most important factor determining biodiversity within urban areas (Beninde et al., 2015). Hence, we were able to test for the effect of urban landscape organization without this potential bias (Ibanez-Alamo, Morelli, Benedetti, & Rubio et al., 2020).

2.2. Bird surveys

In this study, we used standard bird survey techniques (5 min point counts with a fixed 50 m radius; a total of 593 point-count stations; Bibby et al., 1992) to collect data on whether each species was observed within a 500 m × 500 m square. The locations of point-count stations within the 500 m × 500 m squares were selected so that counting points were located at least 100 m apart from each other and from the border of the study square. Point counts provide reasonable estimates of species richness, constituting a standardized method in ecology (Bibby et al., 1992). Therefore, they are extensively used across Europe to monitor bird populations (Voříšek et al., 2008).

We aimed to detect all breeding bird species; however, detectability might vary between bird species and habitats (e.g., van Heezik & Seddon, 2012; Johnston et al., 2014). We used only a 50-m radius in this study to avoid the problem of decreasing species detectability with increasing distance. Moreover, a previous study indicated that different bird counters had very similar estimates of species richness and abundance from the same counting points (Møller & Mousseau, 2007). All these factors reduced the probability that we missed some bird species that occurred in a particular location. It should also be noted that detectability cannot be calculated for rare bird species with only one or a few observations (van Heezik & Seddon, 2012). Our analyses were based only on the presence/absence of bird species within each 500 m × 500 m study square. This occupancy variable is not very sensitive to differences in detectability, such as abundance or density variables (Johnston et al., 2014). Nevertheless, to reduce the possibility of missing some bird species from each 500 m × 500 m square, we used spatial (6–7 point counts per square) and temporal replicates (two surveys during the breeding season, a month apart).

Therefore, our methodology considers potential differences between early-and late-breeding bird species. The distance between points within a study square was at least 100 m; therefore, the 50 m radius point-count areas did not overlap; thus, we avoided counting the same individual twice. Moreover, all surveys were conducted only under good weather conditions (no rain or heavy wind). Surveys started during sunrise and lasted a maximum of three hours after daybreak to minimize problems with species detectability due to weather and time of day issues. At northern latitudes, such as the Arctic Circle (Rovaniemi, Finland), where the sun does not set in mid-summer, surveys started between 02.00 and 03.00 (local time), and finished within three hours of starting time. A professional ornithologist with 10 years of bird-survey experience carried out all the surveys in each city. Surveys were carried out during the 2016 breeding season (April–June), taking into account seasonal differences due to the large latitudinal extent. We assume that our survey method provides reliable species occupancy lists that are comparable

Table 1
Study sites and vegetation zones in Europe, number of inhabitants, and elevation above sea-level (m).

City	Latitude	Longitude	Vegetation zone	Inhabitants	Elevation
	N	E			
Granada	37°10′	−3°36′	Mediterranean forests	235,000	700
Toledo	39°52′	−4°20′	Mediterranean forests	83,000	529
Madrid	40°26′	−3°41′	Mediterranean forests	3,170,000	650
Groningen	53°13′	6°34′	Temperate deciduous forests	205,000	7
Munich	48°08′	11°31′	Temperate deciduous forests	1,535,000	500
Prague	50°50′	14°25′	Temperate deciduous forests	1,325,000	200
Poznan	52°25′	16°56′’	Temperate deciduous forests	535,000	100
Turku	60°28′	22°17′	Boreal coniferous forests	195,000	20
Rovaniemi	66°29′	25°43′	Boreal coniferous forests	64,000	80

between sites.

2.3. *Statistical methods*

Because bird species detectability may vary between species and habitats, detection error might influence the results (McGeoch & Gaston, 2002). Therefore, we evaluated the species detectability by using the two most relevant models with parameters of “occupancy” (ψ) and “detection probability” (P) with the “unmarked” package in R (Fiske & Chandler, 2011, Mazerolle, 2015). First, in the null model, the species detection probability and occupancy were set to be constant P(.)ψ (.). In the second model, we compared differences in species detection probability between two types of habitats (LSH and LSP) and kept the occupancy constant P(habitat)ψ (.). Model parameters were estimated using the maximum likelihood with the “occu ()” function in the “unmarked” R package.

Species richness may vary between LSH and LSP landscapes. We estimated species accumulation curves with the “vegan” package version 2.5–7 in R (Oksanen et al., 2020). In species accumulation calculation we used option “random”.

We followed standard statistical procedures performed in previous analyses of SOFD patterns (Hui, 2012; Jenkins, 2011), namely a multimodel inference approach based on ranked species-occupancy curves (RSOCs) (Hui, 2012; Jenkins, 2011). First, we created binary (presence/absence) species-by-site matrices for each dataset. We then calculated the occupancy frequency of each species as the sum of all the study sites in which it was found. The occupancy frequency of each bird species was divided by the number of study sites, and the relative occupancy values (O_i) were sorted in decreasing order. Each breeding bird species had a rank value, Ri, inversely correlated with the relative occupancy value. We then performed five regression analyses (one for each of the currently described SOFD patterns, those depicted in Fig. 1, and the random pattern) in which the relative occupancy of a species (O_i) was the dependent variable and R_i was the independent variable. Finally, we determined which of the five core-satellite SOFD patterns provided the best fit for breeding bird species communities in urban habitats (Hui, 2012; Jenkins, 2011).

In the multi-model inference approach, we followed the statistical-ranked species-occupancy curve (RSOCs) method described by Jenkins (2011) and Hui (2012). First, we processed the 12 binary (presence/absence) species-by-site matrices for each of the datasets: (*i*) combined data for large-scale effects; (*ii*) one set of each urban landscape development type data (LSH vs. LSP), and (*iii*) nine different cities for studying city-level geographic variation. The following formula was used for each of the five SOFD patterns:

- Unimodal-satellite SOFD pattern (exponential concave): $O_i = y_0 + a{*}\exp(-bR_i)$, where the initial parameters were $y_0 = 0.01$, $a = 1.0$, $b = 0.01$ (Fig. 1a, b).
- Bimodal symmetrical SOFD pattern mode (sigmoidal symmetric): $O_i = a/(1 + \exp(-bR_i + c)$, where the initial parameters were $a = 1.0$, $b = -0.1$, $c = -1.0$ (Fig. 1c, d).
- Bimodal asymmetric SOFD pattern (sigmoidal asymmetric): $O_i = a[1 - \exp(-bR_i^c)]$, where the initial parameters were $a = 1.0$, $b = -1.0$, $c = -1.0$ (Fig. 1e, f).
- Bimodal truncated (power exponential) pattern: $O_i = aR_i^b\exp(-cR_i)$ with initial parameters $a = 100$, $b = 0.05$, $c = -0.04$ (Fig. 1g, h).
- Uniform (random) SOFD pattern: $Oi = aR_i + b$, where the initial parameters were $a = 0.01$, $b = 0.01$.

Where y_0, a, b and c are estimated parameters.

Finally, we used nonlinear regressions in the Levenberg–Marquardt algorithm (999 iterations)(Levenberg, 1944; Marquardt, 1963), and all parameters were estimated using ordinary least squares (OLS). We evaluated the assumptions of the regressions for normality of residuals, homogeneity of variance, independent error terms, and tails and shoulders of the data and models from the plotted graphs.

We compared the fit of our data to the five SOFD models described above by Akaike information criterion for small sample sizes (AICc) values. The AIC criterion selects the most parsimonious model; that is, it balances the model fit with model complexity by penalizing models with more parameters. It is assumed that higher parsimony implies a higher likelihood of reality. The most parsimonious fitted model has the smallest AICc (Burnham & Anderson, 2000). This approach is powerful for detecting differences between models if ΔAICc (=$AICc_{i\text{ - }AICc_{min}}$ values are greater than four; otherwise, the alternative models will fit the data almost equally well (Anderson et al., 2000; Burnham & Anderson, 2000; Jenkins, 2011). Following the recommendations of McGeoch and Gaston (2002), we used 10% occupancy classes (i.e., 10%, 20%, 30%) and the number of bird species in each class in the figures. The satellite species occupied less than 20% of study sites, and core species at least 90% of study sites.

We used a paired *t*-test to compare the unique species richness and total occupancy frequency in LSH and LSP squares within each of the nine study cities in Europe. These unique species occupied only the LSH or LSP squares within the city.

All data analyses were performed using the IBM SPSS statistical package, version 26.

3. Results

3.1. *Detectability*

We found that the detectability of bird species was very similar between the LSH and LSP habitats (Supplementary Table S1). The detectability probability differed statistically between LSH and LSP landscapes for only six out of 103 breeding bird species (see Appendix 1). The six species were: European robin *Erithacus rubecula*, European pied flycatcher *Ficedula hypoleuca*, common chaffinch *Fringilla coelebs*, spotted flycatcher *Muscicapa striata*, Eurasian magpie *Pica pica*, and European serin *Serinus serinus*. The detectability of the European robin, common chaffinch, spotted flycatcher, and European serin were greater in LSP habitats than in LSH habitats, whereas the opposite was true for the European pied flycatcher and Eurasian magpie.

3.2. Occupancy-frequency distributions (SOFD) patterns

A total of 103 breeding bird species were recorded in the nine study cities in their 90 study squares (500 m × 500 m; Table 2). We found an average of 36.0 (±4.2 SD) species per city, ranging from 29 to 42. Pooled data (n = 90 squares) indicated that urban breeding bird communities in Europe followed the unimodal satellite SOFD pattern (Table 2, Fig. 3). Other SOFD pattern models were a poor fit for the data (ΔAICc > 8; Table 2).

The species richness increased rapidly both LSH (Fig. 4a) and LSP (Fig. 4b) landscapes, and the maximum species richness was observed in approximately seven study cities. According to species accumulation curves, species richness was higher in LSP than in LSH landscape (Fig. 4). The LSP urban breeding bird communities were better explained by the unimodal satellite SOFD pattern (Table 2; Fig. 5). In contrast, LSH urban breeding bird communities were equally associated with bimodal truncated, unimodal satellite (ΔAICc = 0.0), and bimodal symmetric SOFD patterns (ΔAICc = 1.6; Table 2; Fig. 5a). All the alternative models fitted less well with the LSH and LSP landscape data (ΔAICc > 21.4; Table 2).

Bimodal SOFD patterns were consistently observed at the city level (Table 3). The results indicate two main groups of cities, those whose breeding bird communities better fitted a bimodal symmetric pattern (Poznan [Fig. 6a], Groningen [Fig. 6d], Munich [Fig. 6e], Prague [Fig. 6f], and Madrid [Fig. 6i]; Table 3). Other cities followed a bimodal asymmetric pattern (Turku [Fig. 6b], Rovaniemi [Fig. 6c], Granada [Fig. 6g], and Toledo [Fig. 6h]). Rovaniemi also fitted equally well (ΔAICc less than 4) to the bimodal symmetric SOFD patterns (Table 3, Fig. 6c).

3.3. Core and satellite species

Most species (43 species; 41.7% of observed breeding species) were detected only in a single city, whereas only seven species (6.8%) were detected in all cities: blue tit (*Cyanistes caeruleus*), Eurasian blackbird (*Turdus merula*), European greenfinch (*Chloris chloris*), Eurasian magpie, feral pigeon (*Columba livia domestica*), great tit (*Parus major*), and house sparrow (*Passer domesticus*).

The number of core and satellite species varied among cities

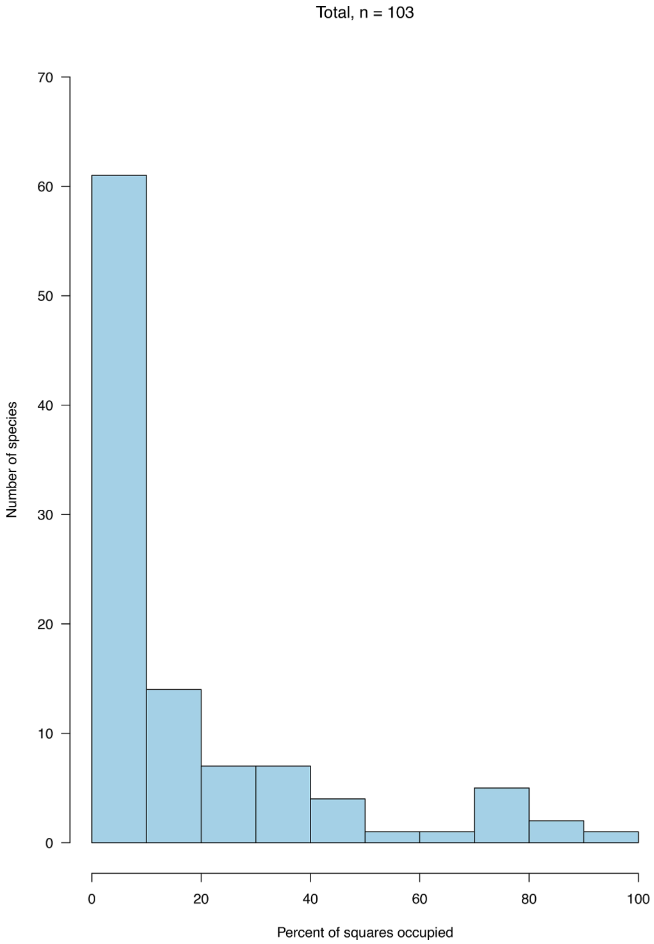


Fig. 3. Number of urban breeding bird species (n = 103 species) in relative to the proportion of the 500 m × 500 m squares occupied (%) (n = 90 squares) in Europe.

Table 2
Results of urban breeding bird species occupancy frequency distributions (SOFD) in Europe. We analyzed five SOFD patterns (unimodal-satellite dominant, bimodal symmetrical, bimodal asymmetrical, bimodal truncated, and random) using combined and separate data for the LSH and LSP urban development types. Figure column joins statistical models with data figures. Species denote the number of species in each study region. AICc (Akaike Information Criterion for small sample sizes) as well as ΔAICc (=AICc$_i$ -AICc$_{min}$) values are presented. The lowest AICc is considered the best of the tested models, and alternative models are equally valid for those with ΔAIC smaller than four (Burnham & Anderson, 2000). The best-fitted model is in italic.

Type of landscape	Figure	Species	AICc	ΔAICc
Combined	2	103		
Unimodal-satellite			*−817.0*	*0.0*
Bimodal truncated			−808.7	8.3
Bimodal symmetric			−808.6	8.5
Bimodal asymmetric			−745.2	71.9
Random			−405.6	411.4
LSH	3a	72		
Unimodal-satellite			*−537.2*	*0.0*
Bimodal truncated			*−537.2*	*0.0*
Bimodal symmetric			−535.6	1.6
Bimodal asymmetric			−505.5	31.7
Random			−293.9	243.3
LSP	3b	96		
Unimodal-satellite			*−751.2*	*0.0*
Bimodal truncated			−731.9	19.3
Bimodal symmetric			−729.8	21.4
Bimodal asymmetric			−688.9	62.3
Random			−387.6	363.6

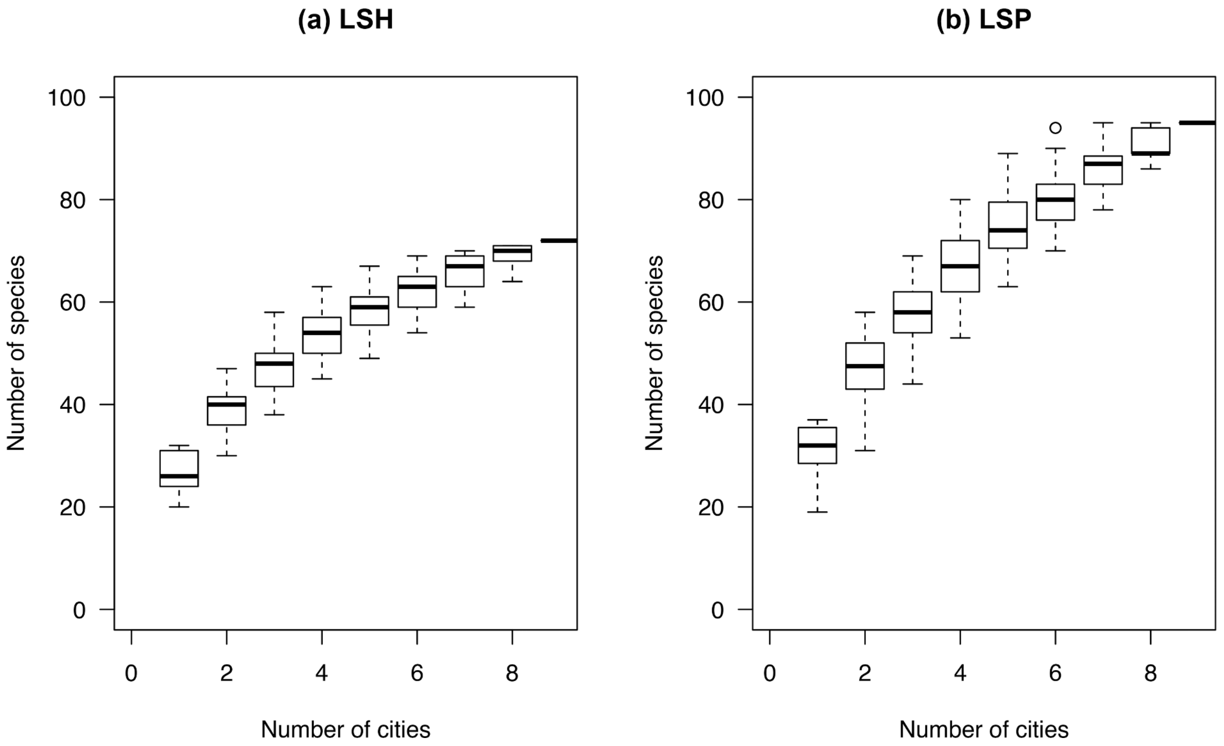


Fig. 4. Breeding bird species accumulation curves in LSH (a) and LSP (b) urban landscapes in relation to number of studied cities. In each city five 500 m × 500 m LSH and LSP squares data was pooled together.

(Table 4). The proportion of core species in the total number of species in individual cities varied between 15.2 and 45.2% (6–14 species), satellite species ranged between 29.0 and 50.0% (9–19 species), and intermediate species (present in three to eight study squares within each city) varied between 25.0 and 50.0% (8–21 species; Table 4). Six core species were detected in Groningen (Table 4) and Rovaniemi, and 14 in Granada and Toledo. Nine satellite species were detected in Granada and 18–19 species in Turku and Rovaniemi (Table 4).

Twenty-three different breeding bird species were considered core species in at least one city (Supplementary Table S2). However, only the great tit was classified as a core species in all nine cities. The Eurasian blackbird was a core species in eight cities, and the wood pigeon (*Columba palumbus*) in seven. We detected 13 cases when an individual bird species “changed” its status from the core to satellite species and *vice versa* among the study cities (Supplementary Table S1). For example, the feral pigeon was a core species in five cities but a satellite species in another two. The common swift (*Apus apus*) was the core species in two cities and a satellite species in the other two cities. In contrast, barn swallow (*Hirundo rustica*) was a satellite species in three cities but a core species in only one city. Nine bird species were classified as the core species in one city and as the satellite species in another city (Supplementary Table S2).

More species were classified as core species in the LSH squares than in the LSP squares. No species were detected in all the 45 LSH or 45 LSP squares, but some were present in>80% of the squares (at least 37 out of 45 squares). In both urban landscape development types (LSH and LSP), the main core species were the great tit (44 out of 45 LSH and LSP squares), Eurasian blackbird (40/45), and blue tit (37/45). In addition, the LSH areas also included the following core species: Eurasian magpie (39/45) and house sparrow (37/45).

In seven out of the nine cities, the LSP squares had more breeding species that had not been observed in the LSH squares (Fig. 7). Only Munich and Prague showed an opposite pattern (Fig. 7e, f). Within the city, there were a higher number of unique species, which occupied only LSH squares (mean = 8.9, SD = 4.1, n = 9) than unique species in LSP squares (mean = 4.8, SD = 3.1, n = 9), but this difference was not statistically significant (paired *t*-test, t = 1.87, df = 8, P = 0.098; Fig. 7). In total, unique species occupied a higher frequency in LSH squares (mean 13.4, SD = 7.1, n = 9) than in LSP squares (mean = 7.0, SD = 4.7, n = 9) within the city, but this difference was not statistically significant (paired *t*-test, t = 1.83, df = 8, p = 0.105; Fig. 7).

4. Discussion

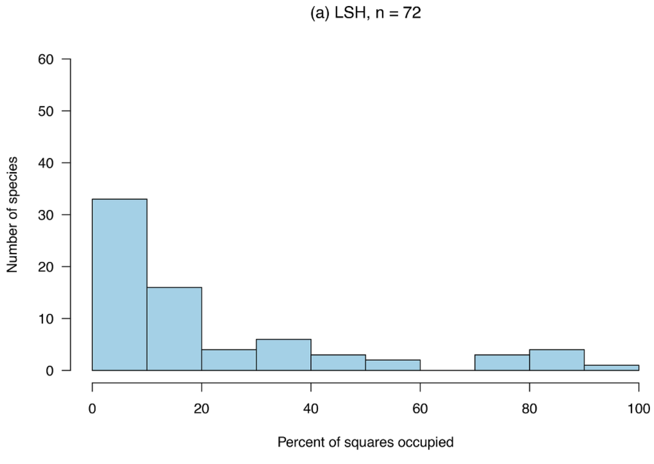
We found that the detectability of bird species was very similar between different habitat types (see also van Heezik & Seddon, 2012; Johnston et al., 2014); therefore, our results are not biased by factors related to detectability. All six species for which detectability differed between habitats were common species in the urban landscape.

As expected, the SOFD pattern followed unimodal satellite-dominant patterns at the continental-scale level but bimodal (symmetric or asymmetric) SOFD patterns at the city-scale level. Furthermore, we found evidence that the urban development type can influence SOFD patterns. For example, the LSP urban areas followed a unimodal, satellite-dominant SOFD pattern. However, LSH urban areas matched three SOFD patterns: bimodal truncated, unimodal satellite-dominant, and bimodal symmetric (ΔAICc smaller than 1.6). Additionally, we found that species frequently switched from core status to satellite status and *vice versa* between cities.

4.1. *Species occupancy frequency distribution patterns*

4.1.1. *Continental-level scale*

We showed that a unimodal satellite-dominant SOFD pattern prevailed in urban breeding bird assemblages in our pooled European data. Our results match another pan-European study on the same topic (but focused on highly-urbanized core areas and heterogeneous data sets; Jokimäki, Suhonen, & Kaisanlahti-Jokimäki, 2016). Moreover, our continental-scale results agree with most previously published studies indicating that the geographical extent modifies the SOFD pattern to a



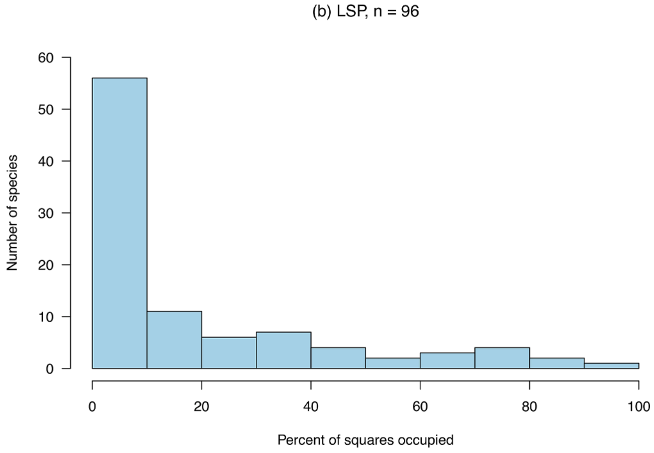


Fig. 5. Number of urban breeding bird species relative to the proportion of 500 m × 500 m squares (%) occupied in LSH (n = 45 squares) (a) and LSP (n = 45 squares) (b) landscapes in Europe.

unimodal satellite-dominant pattern (Collins & Glenn, 1997; Korkeamäki et al., 2018; McGeoch & Gaston, 2002). In contrast, Storch and Šizling (2002) used continental European and national Czech datasets and found that the bird SOFD pattern was bimodal at both scales. The grain size (50 × 50 km squares) in their study was much larger than in our study (500 m × 500 m squares), which might explain the observed difference. It has been predicted that an increase in grain size increases the number of core species and reduces the number of satellite species (McGeoch & Gaston, 2002). Suhonen and Jokimäki (2019) used multi-year wintering bird data collected using the single-visit study plot method (all birds seen or heard were counted within a restricted area of approximately 30 ha). They found that the bimodal symmetric SOFD pattern best fitted the species distribution. This finding was consistent among winters (years), the size of urban areas, and latitude (i.e., southern vs. northern Finland).

One potential explanation for the contrasting findings between this study and ours might be the differences in the pool size of the wintering and breeding species. In northern European countries, such as Finland, most wintering birds are residents. However, during the breeding season, a high proportion of migratory birds considerably increase the local species pool and correspondingly increase the number of satellite species in the breeding season assemblage. In addition, previous studies have indicated that regional species pools influence the richness of urban breeding bird species (Ferenc et al., 2014, 2018). Urban bird assemblages tend to be more similar across Europe than in the regional communities of adjacent landscapes, indicating urbanization-caused homogenization of bird assemblages (Ferenc et al., 2014). In addition, many urban gradient studies have indicated that this homogenization occurs via decreased species richness and super-dominance of some highly abundant species, such as sparrows and doves, in cities (Clergeau et al., 2006; Devictor et al., 2007; McKinney, 2006).

We showed that a unimodal satellite-dominant SOFD pattern prevailed in our pooled European data on urban breeding bird assemblages. Our results match another pan-European study, which tackled the same topic but focused on highly urbanized core areas and heterogeneous datasets (Jokimäki, Suhonen, & Kaisanlahti-Jokimäki, 2016). Moreover, our results agree with those of most previously published studies (Collins & Glenn, 1997; Ferenc et al., 2014; Korkeamäki et al., 2018; McGeoch & Gaston, 2002; Storch & Sizling, 2002). However, an urban wintering birds survey showed symmetric SOFD pattern which differs from our current study (Suhonen & Jokimäki, 2019b). For examble, Ferenc et al. (2014) indicated that the regional species pool influences the urban breeding bird species richness.

4.1.2. *Urban development type*

We found that the LSP urban areas had slightly more bird species than the LSH areas (Fig. 4) and, in particularly, rare, and unique species bird species (Figs. 5 and 7). Both urban development types (LSH and LSP) fitted well with the unimodal satellite-dominant SOFD pattern. This finding indicates that both urban development types had few common species and numerous rare species. However, the LSH development type also fit the bimodal truncated (ΔAICc = 0.0) pattern equally well, and the bimodal symmetric SOFD pattern was well supported (ΔAICc = 1.6). This result indicates that LSH urban areas have more common species than LSP urban areas do. If we assume a link between rarity and specialization, this matches the findings of Jokimäki and Suhonen et al. (2020).

In this study, we found that specialist (e.g., ground breeding) species were mainly restricted to the LSP urban squares. In contrast, more generalist species (at least regarding breeding substrates) occupied the LSH squares more often. According to this scenario, urban planners would select the LSH development type if they aimed to increase the number of common bird species and the LSP development type if they preferred to promote rare species in urban areas. However, we recommend caution in this respect, given that our results are inconclusive, and both urban development types could also follow the same unimodal-satellite-dominant SOFD pattern.

4.1.3. *Geographic variation and city-level scale*

Breeding bird assemblages in European cities followed three different bimodal SOFD patterns (symmetric, asymmetric, and truncated) that varied geographically. Jokimäki, Suhonen, and Kaisanlahti-Jokimäki (2016) indicated that a city's size and geographic location could modify its SOFD patterns. These authors observed that large cities exhibited a bimodal symmetric pattern more often than smaller cities. In addition, large cities (i.e., Madrid, Munich, Prague, and Poznan) followed the bimodal symmetric SOFD pattern. Jokimäki, Suhonen, and Kaisanlahti-Jokimäki (2016) also suggested a potential role for the age of cities, with older cities located in central Europe exhibiting bimodal symmetric patterns, while younger northern European cities exhibit bimodal asymmetric SOFD patterns. However, this did not match our data, as we found that ancient southern cities also follow bimodal asymmetric SOFD patterns (e.g., Toledo or Granada).

Alternatively, these results may be related to the species' geographical range (Ferenc et al., 2014; McGeoch & Gaston, 2002). The main geographical range of many of these species is central Europe, possibly leading to a bimodal symmetric pattern in central European cities. At the same time, northern and southern cities will hold more species located at the northern or southern edge of their distribution ranges, which may explain the bimodal asymmetric pattern in northern and southern cities. This finding also agrees with earlier observations that most species occur either at a few sites (satellite/rare species) or at many sites (core/common species), forming a bimodal symmetric or

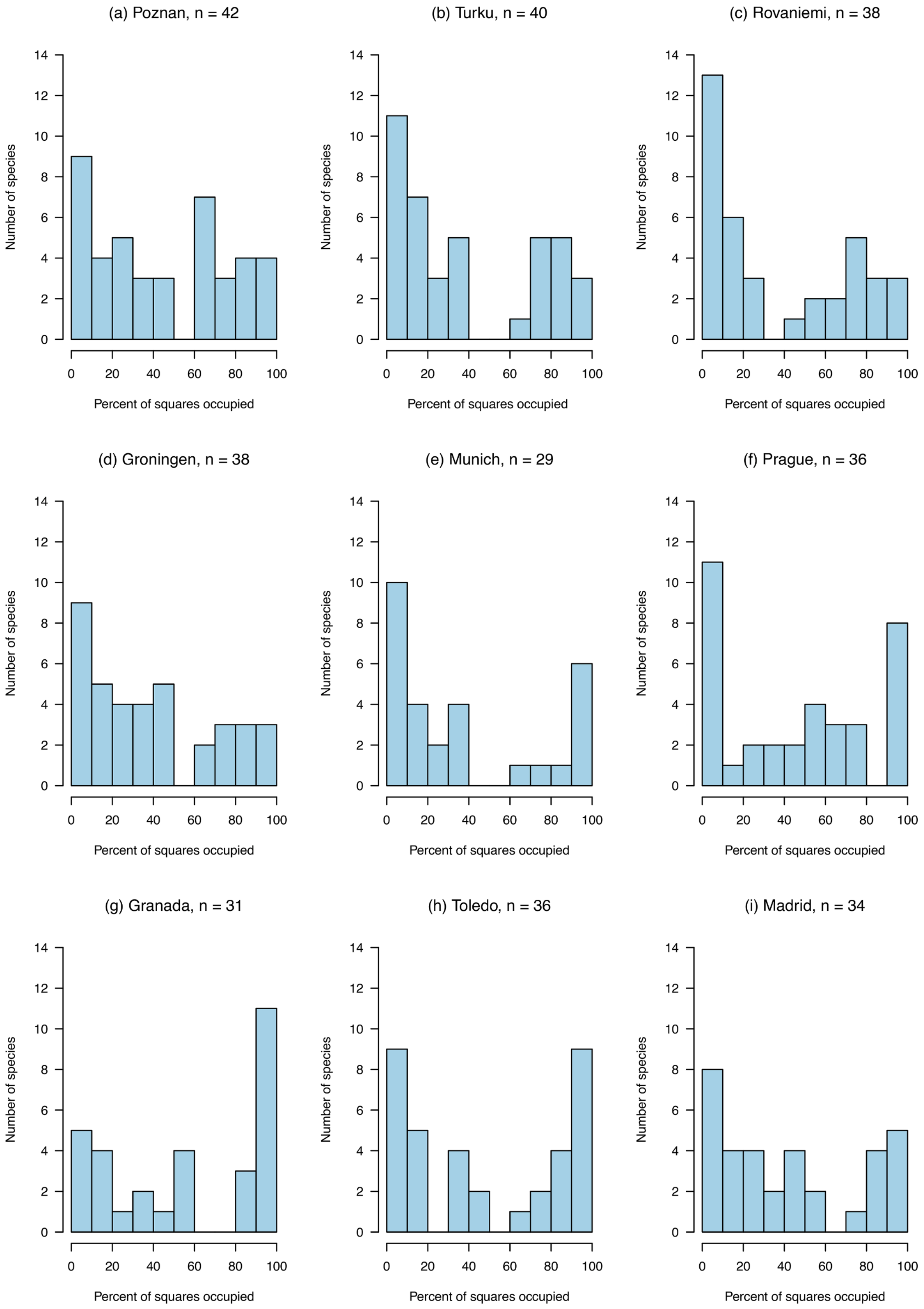


Fig. 6. Number of urban breeding bird species relative to the proportion of 500 m × 500 m squares (%) (n = 10 squares in each city) occupied in nine European cities.

Table 3
Results of urban breeding bird species occupancy frequency distributions (SOFD) for European cities. We show the fit of five SOFD patterns (unimodal-satellite dominant, bimodal symmetrical, bimodal asymmetrical, bimodal truncated, and random) for each studied city. The best-fitted model is in bold. Figure column joins statistical models with data figures. Species denote the number of species in each study town. AICc (Akaike Information Criterion for small sample sizes) and ΔAICc (=$AICc_i$ -$AICc_{min}$) values are presented. The lowest AICc-value is considered the best of the tested models, and alternative models are equally valid for those with ΔAIC smaller than four (Burnham & Anderson, 2000). The best-fitted model is shown in italics.

City	Figure	Species	AICc	ΔAICc
Poznan	6a	42		
Bimodal symmetric			*267.5*	*0.0*
Unimodal-satellite			−244.1	23.3
Random			−237.9	29.6
Bimodal truncated			−233.2	34.2
Bimodal asymmetric			−230.9	36.5
Turku	6b	40		
Bimodal asymmetric			−230.2	0.0
Bimodal symmetric			−216.5	13.7
Bimodal truncated			−211.2	19.1
Unimodal-satellite			−195.3	35.0
Random			−175.7	54.6
Rovaniemi	6c	38		
Bimodal asymmetric			*217.3*	*0.0*
Bimodal symmetric			−213.4	3.9
Bimodal truncated			−198.5	18.7
Unimodal-satellite			−184.1	33.2
Random			−163.6	53.7
Groningen	6d	38		
Bimodal truncated			*−245.0*	*0.0*
Bimodal symmetric			−243.5	1.5
Unimodal-satellite			−234.6	10.4
Bimodal asymmetric			−228.8	16.1
Random			−192.1	52.9
Munich	6e	29		
Bimodal symmetric			*−145.7*	*0.0*
Bimodal truncated			−154.7	9.0
Unimodal-satellite			−129.5	16.2
Random			−111.6	34.1
Bimodal asymmetric			−83.1	62.6
Prague	6f	36		
Bimodal symmetric			*−210.5*	*0.0*
Bimodal asymmetric			−186.6	23.9
Bimodal truncated			−186.4	24.1
Random			−183.0	27.5
Unimodal-satellite			−180.8	29.8
Granada	6 g	31		
Bimodal asymmetric			*−188.2*	*0.0*
Bimodal symmetric			−178.7	9.5
Bimodal truncated			−137.1	51.0
Random			−137.1	51.0
Unimodal-satellite			−134.9	53.3
Toledo	6 h	36		
Bimodal asymmetric			*−226.4*	*0.0*
Bimodal symmetric			−207.2	19.2
Bimodal truncated			−171.7	54.7
Random			−161.2	65.2
Unimodal-satellite			−159.4	67.0
Madrid	6i	34		
Bimodal asymmetric			*−210.5*	*0.0*
Bimodal truncated			−206.1	4.5
Bimodal symmetric			−201.1	9.4
Unimodal-satellite			−181.9	28.6
Random			−150.1	60.4

Table 4
Number of core (occupying 9 or 10 out of 10 study squares in each city), satellite (1 or 2 squares), and intermediate (3 to 8 squares) breeding bird species in the nine studied cities in Europe.

Study city (total number of species)	Number of core species (%)	Number of satellite species (%)	Number of intermediate species (%)
Granada (31)	14 (45.2)	9 (29.0)	8 (25.8)
Groningen (38)	6 (15.8)	14 (36.8)	18 (47.4)
Madrid (34)	9 (26.5)	13 (35.3)	13 (38.2)
Munich (29)	7 (24.1)	14 (27.6)	8 (27.6)
Poznan (42)	8 (19.0)	13 (31.0)	21 (50.0)
Prague (36)	7 (19.4)	12 (33.3)	17 (47.2)
Rovaniemi (38)	6 (15.8)	19 (50.0)	13 (34.2)
Toledo (36)	14 (38.9)	14 (38.9)	8 (22.2)
Turku (40)	8 (20)	18 (45.0)	14 (35.0)

asymmetric core-satellite species pattern (Brown, 1984; Hanski, 1982, 1999). Accordingly, bimodality results from species' stochastic colonization and extinction dynamics in local communities (Hanski, 1999). These dynamics mean that most species are either vulnerable to extinction (rare/satellite species) or relatively stable (abundant/core species), as was found in a long-term study of urban wintering bird species (Suhonen & Jokimäki, 2019a).

4.2. *Changes between core and satellite species between cities*

Most species occurred only in one or a few cities and only in one or a few study squares within a given city (Figs. 3 and 6). At a large spatial scale in Europe, only seven species (6.8% of all species) were detected in all nine study towns. These species, the blue tit, Eurasian blackbird, European greenfinch, Eurasian magpie, feral pigeon, great tit, and house sparrow, are residents and can use human-provided food resources in cities (Suhonen & Jokimäki, 2019b). These findings agree well with previous studies indicating that urbanization favors species that can use anthropogenic food resources and have a resident life pattern (Aronson et al., 2014; Jokimäki & Kaisanlahti-Jokimäki, 2012; Jokimäki et al., 2018; Møller et al., 2014).

We also found that the number of core and satellite species varied between cities. The lowest number of core species was observed in Groningen and Rovaniemi, whereas Granada and Toledo had the highest number of core species. These differences could be explained by variations in the length of the urbanization history (Jokimäki, Suhonen, & Kaisanlahti-Jokimäki, 2016). However, we could not test this prediction because of the small sample size. A large number of satellite species were detected, especially in northern study sites (i.e., Turku and Rovaniemi in Finland). The relatively young age of these northern cities could imply that many species have not yet fully colonized the urban environment at northern latitudes. In addition, there may be an extinction delay in some urban-sensitive species (Jokimäki, Suhonen, & Kaisanlahti-Jokimäki, 2016). These differences could also be due to differences in habitat heterogeneity or regional pools among cities (Ferenc et al., 2014, 2018). Whatever the reason for these differences in core and satellite species, the results suggest overall variation in the resilience of breeding bird communities (i.e., the capacity of the community to resist invasions, climate, and land-use changes) among cities (Morelli et al., 2020). Our results agree with those of Morelli et al. (2020), who suggested that breeding bird communities in Granada and Toledo could be more resilient than other cities, such as Groningen and Rovaniemi.

There are two explanations for the observation that one species can be a core species in one city but a satellite species in another city, and *vice versa.* This type of change can be explained by the dynamic metapopulation model (Hanski, 1982) based on local extinction and colonization dynamics, as shown in urban environments during winter (Suhonen & Jokimäki, 2019a). Alternatively, the observed results could be explained by a niche-based model (Brown, 1984). Core species in some cities could be satellite species elsewhere because of the different resources and niches available. According to the dynamic metapopulation hypothesis proposed by Hanski (1982), species can switch from core to satellite status and *vice versa*. Our results support this idea, as 16 of the 103 observed species changed from core to satellite in different urban areas.

It has been suggested that city traits, such as the structure and age of

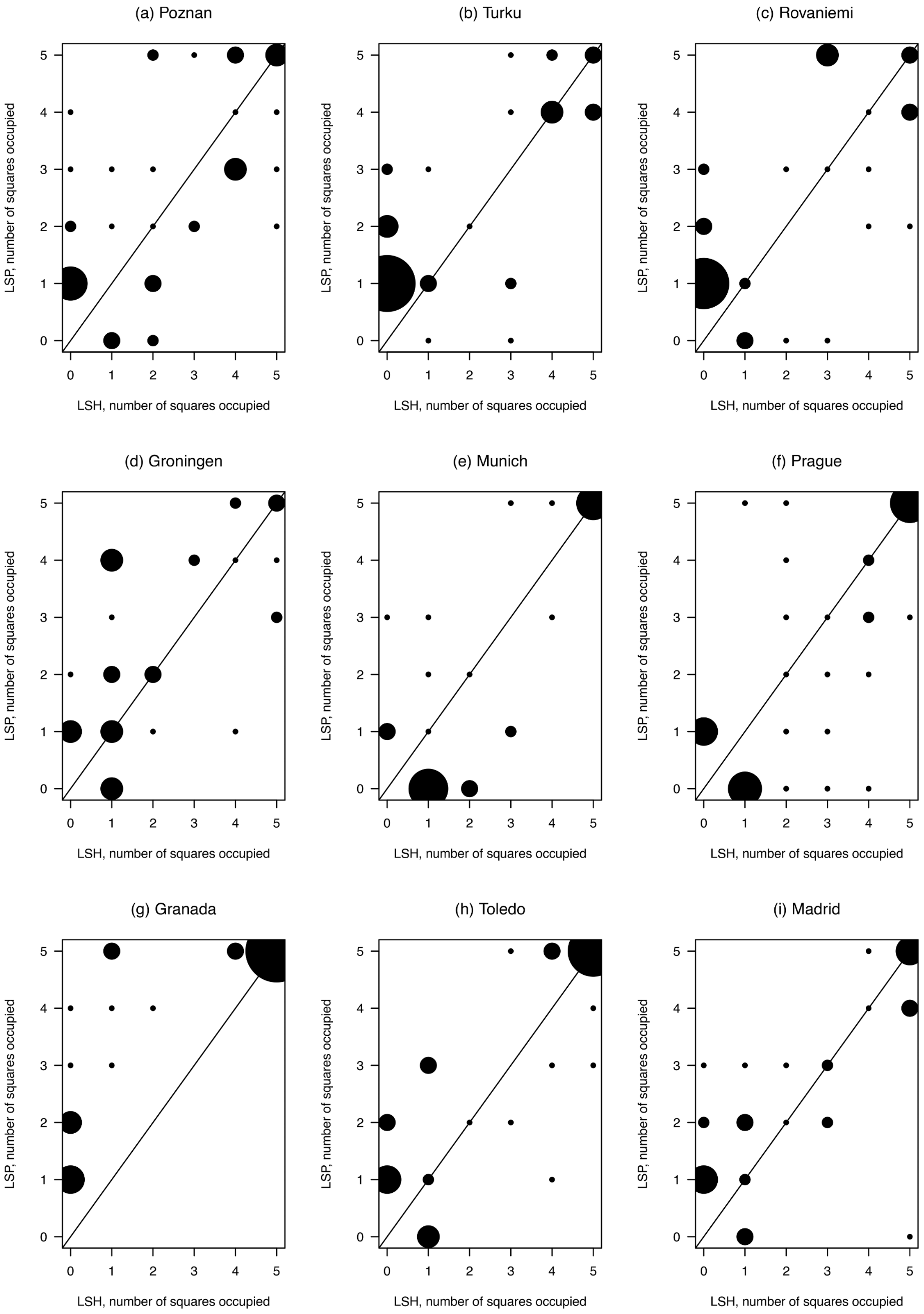


Fig. 7. Number of breeding bird species in LSP squares relative to LSH squares in nine European cities. In each city breeding birds were counted from five 500 m × 500 m LSP and LSH squares. The size of the black dot indicates the number of overlapping species.

buildings, could be an important factor explaining the change in species that use buildings as nesting sites, such as the common swift, feral pigeon, barn swallow, white wagtail (*Motacilla alba*), and house sparrow (Jokimäki, Suhonen, & Kaisanlahti-Jokimäki, 2016). These are core species in several European cities, but not in Rovaniemi, which was almost totally (90%) destroyed during the Second World War (Ahvenainen, 1970). Therefore, only a limited number of suitable nesting sites are available for cavity-nesting species in Rovaniemi, which has mainly modern buildings.

4.3. Conclusions

Overall, our study provides new information for city planners, managers, and conservation biologists regarding the effects of urbanization on breeding bird SOFD patterns in European cities. Although urban bird communities followed a unimodal satellite SOFD pattern at the European level, the SOFD patterns among European cities were bimodal. This indicates that the results from one city are not necessarily applicable to other cities. Bimodality also indicates that bird communities in European cities contain both common core and rare satellite species.

Therefore, to preserve biodiversity in cities, management actions should be directed toward both core and satellite species. We found evidence that the urban development type can influence SOFD patterns. We also found that LSP urban areas followed a unimodal satellite-dominant SOFD pattern regarding the landscape development type. In contrast, the results from LSH areas were more diverse and matched the three SOFD patterns. Therefore, care should be taken when extrapolating our results to other landscape development types. Land-sparing urban areas have many rare satellite species that increase the breeding bird diversity at the city level. However, many satellite species occur only at a few restricted sites; city inhabitants seldom encounter them.

Thus, we assume that easily observed core species, such as sparrows, blue and great tits, and European blackbirds, are important for people connected with nature in city areas. Our data suggest that urban planners should select an LSH development type to increase the number of common bird species but an LSP development type if the aim is to promote a higher number of rare species. Our results provide additional insights for the current challenge of creating more biodiversity-friendly cities and managing cities concerning human-nature interactions/ conflicts.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.landurbplan.2022.104463.

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