Scale dependence of biotic homogenisation by urbanisation: a comparison of urban bird communities between central Argentina and northern Finland

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ABSTRACT

Recent studies showed contrasting results about the homogenising force of urbanisation on bird community composition at large and regional scales. We studied whether urbanisation promotes the homogenisation of wintering bird communities and if this varies when comparing towns located within a specific region and towns located in two different biomes of two countries. We used both similarity indices based on the presence/absence data and the abundance data in comparing communities. Processes governing bird community dissimilarity between urbanisation levels were examined with the partitioning of Sörensen index in species turnover and nestedness. We made bird surveys in town centres and suburban habitats of three cities located in the Pampean region of Argentina and in the boreal region of Finland using a single-visit study plot method. Rarefacted species richness did not differ amongst the town centres between the countries, but it was higher in the suburban areas of Argentina than in Finland. At the country-level comparison, we found a higher similarity amongst the town centres than amongst the suburban areas; whereas at the regional comparison, similarity between town centres was comparable to the similarity between suburban areas. The use of an abundance-based index produced a higher similarity between town centre communities of both countries than when using a presence-based index. The dissimilarity between habitats in Argentina was related to nestedness and to species turnover in Finland. Our results indicate that urban-based biotic homogenisation of bird communities is dependent on the scale used, being more evident when comparing cities of different biomes where the same and abundant bird species, such as sparrows and doves, dominate. At the regional scale, quite a high beta-diversity can still be found within urban habitats. Processes of community dissimilarity between urban habitats may differ according to the regional pool of species, being more related to nestedness toward the tropics.

KEYWORDS

Bird richness; bird abundance; latitude; nestedness; similarity; species turnover; winter

INTRODUCTION

The process of urbanisation can be defined as an increase in human habitation, related with increased per capita energy consumption and extensive modification of the landscape that can be irreversible (McDonnell & Pickett 1990; Morello et al. 2000). As urbanisation is increasing around the world, it is relevant to study its effects on urban wildlife (Marzluff et al. 2001). The most urbanised sites are occupied by a few species, most of them being cosmopolitan or having a generalist way of life (Huhtalo & Järvinen 1977; Blair 1996; Leveau & Leveau 2004; Juri & Chani 2005; Ortega-Álvarez & MacGregor-Fors 2009; Jokimäki et al. 2016; Sol et al. 2014). Therefore, urbanisation promotes the extinction of specialist and endemic species and reduces the evolutionary distinctiveness of bird communities (Devictor et al. 2008; González-Oreja 2011; Concepción et al. 2016; Morelli et al. 2016). Correspondingly, urbanisation may also lead to functional and genetic homogenisation (Sol et al. 2017; Godet et al. 2015; Ibáñez-Álamo et al. 2016).

The factors determining species richness vary with spatial scale (Wiens 1989 a,b; Böhning-Gaese 1997; Melles et al. 2003; Cueto 2006), and there is a need to study this variation also in urban environments (Hostetler 1999; Garden et al. 2006). Generally, bird species richness and community composition have been studied at several spatial scales by using the urban gradient paradigm (Jokimäki & Suhonen 1998; Jokimäki & Kaisanlahti-Jokimäki 2003; Clergeau et al. 2001, 2006). At the local and regional scales, species diversity may increase because of arrivals of new species may outnumber species departures, whereas at the global scale, species diversity may decrease as a result of extinctions of native species (Olden et al. 2016). By favouring the occurrence of non-native species and introducing new species, urbanisation may lead to biotic homogenisation on a global scale, where the urban centres are occupied by the same few species (Blair 2001; Clergeau et al. 2001; McKinney 2006; Olden 2006; Olden et al. 2016).

Results from different scales have reported partly contrasting results related to the homogenisation of communities (e.g. Cassey et al. 2008). Although the homogenising effect of urbanisation may be evident at large geographical scales (Clergeau et al. 2001; Ferenc et al. 2014; Filloy et al. 2015; Ibáñez-Álamo et al. 2016; Murthy et al. 2016), some studies have suggested that it may disappear at smaller regional scales (Jokimäki & Kaisanlahti-Jokimäki 2003; Kühn & Klotz 2006; Marchetti et al. 2006; Sorace & Gustin 2008; Luck & Smallbone 2011; Tryjanowski et al. 2015).
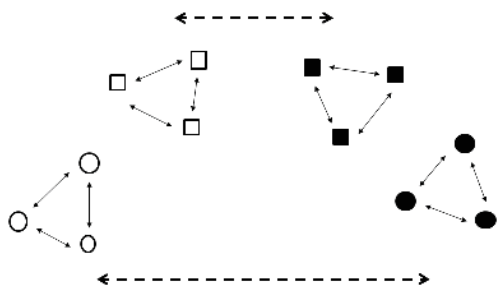
The scientific bird research is currently dominated by studies conducted in Europe and North America, causing an important bias in the urban ecological research (Marzluff et al. 2001; Hedblom & Murgui 2017). Global comparative studies are very few, and there is a lack of knowledge of urban bird communities of Southern Hemisphere (Lepczyk et al. 2017). Comparable data across the world are needed to assess the effects of urbanisation on birds and to evaluate what processes influence the observed patterns. Moreover, most of the biogeographical bird studies have considered the breeding season, whereas winter season studies have been less abundant. On the other hand, studies that analyse at the same time the similarity patterns of urban bird communities at different spatial scales are still rare (Olden 2006; Olden et al. 2016). Therefore, it is relevant to explore at what scale urbanisation induces the homogenisation of bird communities. Our hypothesis is that urbanisation promotes a homogenisation of bird communities only at the large biogeographical scale when sites in countries located at the two biomes are compared (Fig. 1). At this scale, homogenisation of communities may result from the introduction and establishment of cosmopolitan species that thrive in highly urbanised areas. However, at the more restricted regional scale (Fig. 1), beta-diversity could be still high in both centres and suburbs partly due to the extinction delay (Essl et al. 2015). This happens because towns are colonised by species typical of

Figure 1. Study design showing the expected results regarding the similarity of bird composition of town centres (squares) and suburban habitats (circles) in two biomes, the Argentine pampas (white) and the boreal Finland (black). When comparing urban habitats between biomes, a greater similarity among town centres is expected (discontinuous vectors), suggesting a process of biotic homogenisation. When comparing habitats within each biome, comparable similarity exist within habitat types (continuous vectors), suggesting an absence of biotic homogenisation.

forest edges and surrounding areas in a process called regional homogenisation (McKinney 2006).

On the other hand, results might be different if one uses similarity indices based on the species presence/absence or abundance-based indices (La Sorte & McKinney 2007; Cassey et al. 2008; Yang et al. 2015). Some authors have suggested that when using the abundance data, instead of the presence/absence data, impacts of homogenisation on urbanization may be more easily detected (La Sorte & McKinney 2007; Cassey et al. 2008). This might be due to the super-dominance of some few species across the world (e.g. Blair 2001). However, these two types of indices have seldom compared simultaneously and across different spatial scales (Olden 2006).

The dissimilarity between communities may be due to two different processes that usually occur simultaneously: species turnover and nestedness of assemblages; the former is related to species replacement, whereas the second is associated to species loss (Baselga 2010). This approach has been scarcely used to analyse the dissimilarity of biotic assemblages in urban areas (Knop 2016). Therefore, in this study, we also use partitioning of similarity index to explore how these processes act at different latitudes in differentiating the bird assemblages of urban and suburban areas. It has been predicted that in natural communities at least in Europe, nestedness is a main driving mechanism in the north, whereas turnover is the main force in the south (Baselga 2010). However, the situation might be different in urban environments. Given that urbanisation may nullify the classic decreasing pattern of species richness towards the poles (Clergeau et al. 2001; Filloy et al. 2015, Jokimäki et al. 2016; Leveau et al. 2017, but see Murthy et al. 2016), the species loss provoked by urbanisation could be stronger toward the tropics (Filloy et al. 2015; Leveau et al. 2017). Therefore, a predominance of nestedness is expected at lower latitudes because urban bird community dissimilarity between habitats would be more likely to be explained by species loss. On the other hand, given the lower effect of urbanisation on species richness toward the poles, species turnover will be dominant in determining the bird community dissimilarity between urbanisation levels.

The main aim of this study is to analyse the relationship between urbanisation (town centres vs. single-family house areas; suburban habitats; hereafter) and similarity of bird communities during winter on six towns of similar sizes located in the two countries: Argentina located in the Pampean bioregion and Finland located in the boreal bioregion. Given the large differences between urbanisation levels, where town centres are dominated by impervious surfaces and suburban habitats are composed of houses with gardens, significant differences of bird communities are expected between them. We predict that (1) at a regional scale, focusing on towns in each country, the similarity of bird composition between the more urbanised habitats (centres of towns) will be comparable to the similarity between suburban habitats, reflecting the absence of homogenisation effect of urbanisation at the regional scale; (2) at a country scale, comparing town habitats (centres vs. subur-

ban) between countries, the more urbanised habitats (centres) will show a greater similarity in bird composition than the suburban habitats, suggesting a process of biotic homogenisation in centres of towns; (3) the use of abundance data in comparison to the presence/absence data will result in a higher similarity of bird communities between countries; (4) bird species richness amongst urban centres of both countries will be similar, whereas bird richness between suburban habitats will differ, being higher in the southern study site, Argentina; and (5) given the higher difference of bird richness between habitats in Argentina than in Finland, we expect that the dissimilarity of bird composition between habitats in Argentina will be more driven by nestedness than in Finland.

1. MATERIAL AND METHODS

1.1. Study areas
Bird counts were made in town centres and suburban habitats of three towns in Argentina and Finland. We used only towns with more than 20,000 inhabitants to control the possible town size effect found in earlier studies (Jokimäki & Kaisanlahti-Jokimäki 2003; Garraffa et al. 2008). The study towns in Argentina were Mar del Plata (500,000 inhabitants at the moment of bird surveys), Balcarce (35,000 inhabitants) and Miramar (24,000 inhabitants; data from the Argentina National Census). The study towns in Finland were Oulu (105,000 inhabitants), Rovaniemi (35,000 inhabitants) and Kemi (25,000 inhabitants; data from the Statistics Finland). The maximum distance between the study towns in Argentina was 59 km (between Balcarce and Miramar) and correspondingly 166 km in Finland (between Oulu and Rovaniemi). Because the study towns in both countries are located near each other, there are no confounding effects of latitude and climate within the countries. The minimum distance between individual study plots (centre and suburban) in Argentina was 1.27 km in Mar del Plata, 0.83 km in Balcarce and 0.27 km in Miramar, whereas in Finland, it was 6.2 km in Oulu, 2.7 km in Rovaniemi and 2.0 km in Kemi. The distances between town centres and suburban areas did not show significant differences between countries (*t-test* = 2.14, *P* = 0.10).

Argentinian study towns are located in the Austral pampas, with a landscape composed of cultivated land, pastureland, grasslands and exotic tree plantations. The winter climate in Argentina is temperate and the long-term average mean temperature of July (mid-winter) is 7.7 ºC (Mar del Plata; data from the Meteorological National Service). Study towns in Finland are located in the boreal forest zone area, with a landscape composed mainly of the coniferous dominated forests. The winter climate in Finland is cold temperate and the long-term average mean temperature of December (mid-winter) is −11.1ºC, whereas the average snow depth is 29 cm during December and 46 cm during January (Rovaniemi; data from the Finnish Meteorological Institute).

1.2. Habitat description
Two habitat types were surveyed: town centres and suburban areas. Town centre transects were located in the administrative and commercial centre of each town, and suburban habitats were located close to the urban fringe. Habitat characteristics of study plots were described using town maps (scale 1:4000), field notes and Google earth images. Town centres were dominated by the block of flats and non-detached houses (75–96%), whereas suburban habitats were dominated by single-family houses with gardens (77–89%; Table 1). Therefore, the human impact and urbanization level was much higher in the town centres than in the suburban habitats. In Finland, winter feeding sites occurred in suburban habitats. Examples of street views, obtained from the Google Maps, from both town centres and suburban habitats of each town are given in the Appendix S1 in Supporting Information.

1.3. Bird surveys
Bird surveys were conducted by a single-visit study plot method, during which the whole study plot was surveyed throughout. In Finland, zig-zag walks through study plots of 30 ha were conducted (see Jokimäki & Kaisanlahti-Jokimäki 2003), whereas in Argentina, between five and nine transects of 100 m long and 50 m wide separated by at least 200 m (about 35 ha of extension) were surveyed in each study plot. Surveys using a single visit are an accepted method in urban areas (Jokimäki & Suhonen 1998; Garaffa et al. 2008). For example, according to Jokimäki and Kaisanlahti-Jokimäki (2003), the results based on the single-visit survey are highly comparable to the results obtained during the five-visit survey conducted during the winter in urban areas. All surveys were done during the daylight between 8:00 and 14:00, on weekend days without rain or strong winds. Bird surveys in Argentina were done during winter 2005 for Mar del Plata and Miramar and during winter 2009 for Balcarce. Bird surveys in Finland were done during winter 2001.

We surveyed all birds except the over-flying ones that did not land in the study plot. The surveys were conducted during one winter in each site. However, according to the results of Jokimäki and Kaisanlahti-Jokimäki (2003), the average species richness and the total number of wintering individuals do not differ significantly between the study winters in urban areas in Finland.

1.4. Data analysis
Bird community similarity was analysed using the presence data and abundance-based indices, which vary between 0 and 1. The presence-based index was the Sörensen index, which takes into account the presence and absence of species shared between two sites:

$$S = 2C/ A + B,$$

where A and B are the number of species in communities A and B and C is the number of species shared by the two communities (Magurran 2004).

Table 1. Habitat characteristics (percentage cover) of study plots in Argentinian (1a) and Finnish (1b) towns during winter.

Cities	Habitat features	Town centre	Suburban habitat
(a) Argentina			
Mar del Plata	Block of flats and non-detached houses	84	13
	Single family houses with gardens		87
	Green areas	16	
	Open areas		
Miramar	Block of flats and non-detached houses	95	19
	Single family houses with gardens	5	81
	Green areas		
	Open areas		
Balcarce	Block of flats and non-detached houses	75	3
	Single family houses with gardens		79
	Green areas	25	9
	Open areas		9
(b) Finland			
Oulu	Block of flats and non-detached houses	92	
	Single family houses with gardens		77
	Green areas	8	20
	Open areas		3
Rovaniemi	Block of flats and non-detached houses	96	
	Single family houses with gardens		89
	Green areas	3	9
	Open areas	1	2
Kemi	Block of flats and non-detached houses	90	
	Single family houses with gardens		86
	Green areas	7	13
	Open areas	3	1

The abundance-based index used was the Morisita-Horn index, which takes into account the percentage frequencies of species shared in both communities and it is unbiased by differences in sample size:

$$MH = \frac{2 \sum (a_i * b_i)}{(d_a + d_b) * (N_a * N_b)}$$

where N_a is the total number of individuals at community A, N_b is the total number of individuals at community B, a_i is the number of individuals in the ith species in A, b_i is the number of individuals in the ith species in B, and d_a and d_b are calculated as follows:

$$d_a = \frac{\sum a_i^2}{N_a^2}$$

The level of similarity of the study plots was visualised using the non-metric multidimensional scaling (NMDS) with package vegan (R development core team 2011). NMDS finds both non-parametric monotonic relationship between the dissimilarities in the site-site matrix and the Euclidean distances between sites and the location of each site in the low-dimensional space. NMDS attempts to represent, as closely as possible, the pairwise dissimilarity between objects in a low-dimensional space. Points represent objects, and objects that are more similar to one another are ordinated closer together. Reliability

of the ordination was evaluated by using the stress value. A stress value ≥0.2 is deemed suspect, a stress value approaching 0.3 indicates that the ordination is arbitrary, stress values ≤0.1 are considered good, whilst values ≤0.05 indicate excellent fit (Clarke 1993). Moreover, significant differences between habitats and countries were analysed with the Adonis test, with a nested design for which habitat types were nested in countries. Both analyses were made using the Sörensen index and the Morisita-Horn index.

To analyse what processes determined community dissimilarities between habitats in each country, we used the function beta.pair of package betapart (Baselga et al. 2017). This allows computing the dissimilarity of bird composition between sites using the Sörensen index, and the additive parts of this index belong to species turnover and species nestedness. For example, two bird communities have a dissimilarity of 0.80, for which 0.50 correspond to nestedness and the remaining 0.30 belongs to species turnover. Moreover, we calculated the proportion of each process relative to the total dissimilarity between communities. In the aforementioned example, nestedness contributed to a proportion of dissimilarity of 0.63, whereas species turnover contributed to a proportion of 0.37.

We compared bird community similarity indexes between same habitats within countries (regional level comparison) as well as the same habitats amongst countries (country-level comparison) by using the one-way ANOVA tests. We used habitat type as a fixed factor and similarity index type as a repeated measure. The analysis at the regional scale included country type (Argentina and Finland) as a random factor and was made only comparing the same habitat amongst different cities of the same country. The analysis at the country level included habitat as a fixed factor and the type of similarity index as a repeated measure and was made comparing the same habitat between Argentina and Finland. Assumptions of normality and homoscedasticity were verified with the Kolmogorov–Smirnov and the Levene test, respectively.

For each study site, we calculated species richness using the coverage-based rarefaction index Chao1 (Chao 1984), implemented in the online software iNEXT (https://chao.shinyapps.io/iNEXT/). The software extrapolates species richness until the double of individuals observed and then calculates a sampling coverage value with 95% confidence intervals. Therefore, estimated values of species richness were obtained at similar values of sampling completeness (between 0.96 and 1.00, with overlapping confidence intervals). Differences of the estimated species richness between habitats and countries were analysed by the nested analysis of variance (ANOVA), with habitats nested within countries. We made planned comparisons for each habitat type between countries, as we expected a significant difference in species richness only for suburban habitats. Species richness values were log-transformed to approach assumptions of the homoscedasticity and the normality.

2. RESULTS

A total of 20 species was observed in Argentina and all of them were observed in the suburban habitats, whereas a total of 12 species were observed in the town centres. A total of 14 species were observed in Finland, all species except *Corvus monedula* were observed in the suburban habitats and nine species were observed in the town centres (see Appendix S2 in Supporting Information). Expected bird species richness per plot based on the Chao1 index tended to be greater in the suburban than in the town centre habitats ($F_{2, 8}$ = 4.13, P = 0.06), but it did not vary between countries ($F_{1, 8}$ = 2.37, P = 0.16; Fig. 2). Bird species richness did not vary amongst the town centres between countries ($F_{1, 8}$ = 0.002, P = 0.97), but it showed a significant difference amongst suburban habitats (one-sided hypothesis, $F_{1, 8}$ = 4.56, P = 0.033), being higher in Argentina (Fig. 2). However, the total number of individuals was always higher in the suburban habitats than in the town centres in Argentina, whereas the opposite was the case in Finland (see Appendix S2 in Supporting Information).

Town centres were dominated (proportion at least 5% of a total number of individuals) by three species in Argentina and seven species in Finland (Table 2). Suburban habitats were dominated by nine species in Argentina and eight species in Finland (Table 2). The proportion of the most abundant bird species in each town centre varied between 50% and 52% (being *Passer domesticus, Zenaida auriculata* or *Columba livia*) in Argentina and 32% and 85% (being *C. livia*, *P. domesticus* or *Parus major*) in Finland. The corresponding proportions in the suburban habitat were 21–44% (either *Zonotrichia capensis* or *P. domesticus*) in Argentina and 23–30% (*Carduelis flammea, P. major* or *Pica pica*) in Finland.

According to the presence-based and the abundance-based similarity indices, bird community composition varied between countries and habitat types (Table 3). When using the presence-based similarity index, the country was clearly a more important factor (R^2 = 0.74) than habitat (R^2 = 0.07) in separating the study plots (Table 3). However, the importance of habitat (R^2 = 0.18) was more comparable to the importance of the
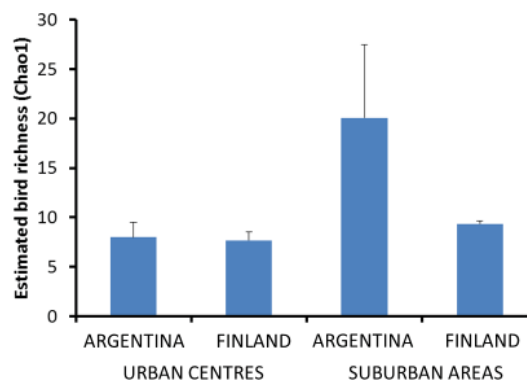

Figure 2. Mean bird richness estimation (Chao1 index) per plot in town centres and suburban habitats (single family house areas) of Argentina and Finland. Vertical bars are standard errors.

Table 2. List and percentage frequency of the dominant bird species with ≥5% of total abundance, registered in town centres and suburban habitats of three study towns in Argentina (2a) and Finland (2b).

	Town centre	Suburban habitat
a) Argentina		
Mar del Plata	Passer domesticus 52%	Passer domesticus 48%
	Zenaida auriculata 29%	Zenaida auriculata 9%
	Columba livia 18%	Columba livia 9%
		Turdus rufiventris 8%
		Patagioenas picazuro 6%
		Furnarius rufus 6%
		Pitangus sulphuratus 6%
Balcarce	Zenaida auriculata 50%	Zonotrichia capensis 21%
	Passer domesticus 31%	Passer domesticus 20%
	Columba livia 9%	Zenaida auriculata 12%
		Patagioenas picazuro 10%
		Furnarius rufus 8%
		Spinus magellanica 6%
Miramar	Columba livia 52%	Passer domesticus 44%
	Passer domesticus 32%	Zenaida auriculata 17%
	Zenaida auriculata 7%	Columba livia 6%
		Furnarius rufus 6%
		Patagioenas picazuro 5%
		Zonotrichia capensis 5%
b) Finland		
Oulu	Columba livia 85%	Carduelis flammea 30%
	Passer domesticus 9%	Passer domesticus 20%
		Parus major 17%
		Chloris chloris 15%
		Parus caeruleus 10%
		Pica pica 7%
Rovaniemi	Passer domesticus 45%	Parus major 23%
	Parus major 9%	Passer domesticus 21%
	Pica pica 12%	Pica pica 12%
	Carduelis flammea 11%	Carduelis flammea 12%
		Chloris chloris 9%
		Parus caeruleus 9%
		Emberiza citrinella 9%
Kemi	Parus major 32%	Pica pica 29%
	Columba livia 23%	Pinicola enucleator 27%
	Passer domesticus 16%	Parus major 18%
	Chloris chloris 14%	Chloris chloris 9%
	Corvus corone 10%	Parus caeruleus 6%

country ($R^2 = 0.39$) when the relative abundance of species was taken into account (Table 3).

Also, the NMDS analysis separated study plots located in different countries and different habitats, and that town centres of different countries had more similar bird communities than corresponding suburban areas (Fig. 3). The stress value (0.05) of the ordination indicated a good reliability of the result.

At the regional scale, when comparing different habitats within a country, similarity values did not differ between town centres and suburban habitats (the presence-based Sörensen index: *mean* = 0.71, *SE* = 0.05 (centres); *mean* = 0.74, *SE* = 0.06 (suburbs); the abundance-based Morisita-Horn index: *mean* = 0.54, *SE* = 0.11; *mean* = 0.68, *SE* = 0.09, respectively; $F_{1,1}$

Table 3. Bird community qualitative (Sörensen index, 3a) and quantitative (Morisita-Horn index, 3b) similarity variation between countries and habitat types in towns of Argentina and Finland (based on the Adonis –test).

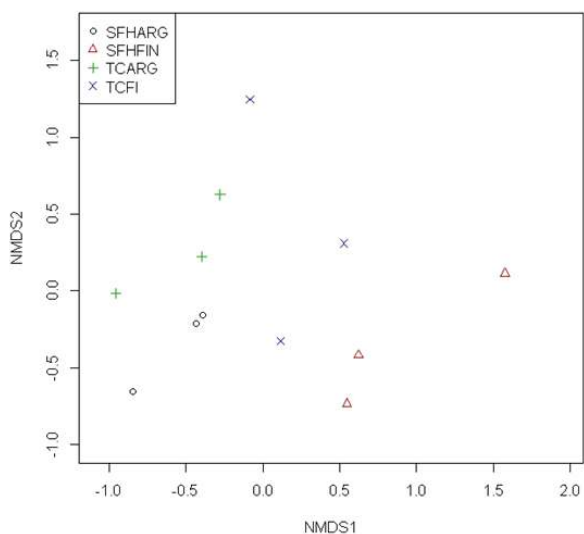| a) Sörensen index				
	df	*F*	*R^2*	*P*
Country	1	34.327	0.739	0.005
Habitat	1	3.119	0.067	0.005
Residuals	9		0.194	
Total	11		1	
b) Morisita-Horn index				
	df	*F*	*R^2*	*P*
Country	1	8.102	0.388	0.025
Habitat	1	3.768	0.181	0.025
Residuals	9		0.431	
Total	11		1	

Figure 3. Non metric multidimensional scaling (NMDS) of bird composition in town centres and suburban (single family house areas) habitats of towns in Argentina and Finland, based on the Morisita-Horn index (Stress value = 0.05). SFHARG: single family house areas of Argentina; SHFFIN: single family house areas of Finland; TCARG: town centres of Argentina; TCFI: town centres of Finland. NMDS based on the Sörensen index could not be performed due to insufficient data.

= 4.31, *P* = 0.29; Fig. 3), suggesting the absence of homogenisation process. Similarity values did not differ between indexes ($F_{1,1}$ = 0.45, *P* = 0.62).

At the continental scale, when comparing the same habitat between countries, we found a higher similarity amongst the urban centres than amongst the suburban habitats (the presence-based Sörensen index: *mean* = 0.32, *SE* = 0.02 (centres), *mean* = 0.15, *SE* = 0.02 (suburbs); the abundance-based Morisita-Horn*: mean* = 0.51, *SE* = 0.07; mean = 0.27, *SE* = 0.07, respectively; $F_{1,16}$ = 16.72, *P* < 0.001; Fig. 3), suggesting a process of biotic homogenisation. The similarity between bird communities of both countries was higher when using the abundance-based Morisita-Horn index than the presence-based Sörensen index ($F_{1,16}$ = 8.68, *P* = 0.010). However, this increase in similarity was higher between town centres (Planned comparison, $F_{1,16}$ = 6.82, *P* = 0.019) than between suburban habitats (Planned comparison, $F_{1,16}$ = 2.42, *P* = 0.140; Figure 3).

On the basis of both similarity indices, the dissimilarity between urban and suburban habitats was comparable amongst the cities of Argentina and Finland (the presence-based Sörensen index: *mean* = 0.37, *SE* = 0.05, *mean* = 0.29, *SE* = 0.05, respectively; *t-test* = 1.07, *P* = 0.345; the abundance-based Morisita-Horn index: *mean* = 0.31, *SE* = 0.10, *mean* = 0.57, *SE* = 0.21, respectively; *t-test* = 1.09, *P* = 0.335). Regarding the Sörensen index, different processes contributed to the dissimilarity between habitat types in each country. Given that nestedness and turnover components were negatively correlated (Pearson correlation, *r* = −0.75, *P* = 0.086), we only focused on nestedness. This process played a more important role in Argentina than in Finland (*mean* = 0.32, *SE* = 0.03; *mean* = 0.09, *SE* = 0.04, respectively; *t-test* = 4.57, *P* = 0.010). Moreover, nestedness contributed to a higher proportion of the dissimilarity in Argentina than in Finland (*mean* = 0.90, *SE* = 0.10; *mean* = 0.31, *SE* = 0.10, respectively; *t-test* = 4.22, *P* = 0.014). Bird communities of town centres were subsets of the suburban bird communities in Argentina; no corresponding results were observed in the Finnish data (see Appendix S2 in Supporting Information).

3. DISCUSSION

Our results indicated that the homogenising effect of urbanisation on bird community composition is scale dependent. At the regional scale, increased urbanisation does not homogenise wintering bird communities, at least when town centres and suburban areas are compared within a particular biome. On the other hand, when urbanisation is compared between two countries located in different biomes, the homogenising force of urbanisation becomes evident (Clergeau et al. 2001; Blair and Johnson 2008; Ferenc et al. 2014; Filloy et al. 2015; Murthy et al. 2016; Leveau et al. 2017; Vázquez-Reyes et al. 2017), with communities of the more urbanised town centres being more similar to each other than the less urbanised suburban bird communities.

There are several, not necessarily mutually exclusive, possible processes behind the observed similarity patterns. One factor might be related to the species extinction and colonisation dynamics (Olden et al. 2016). Humans construct physically similar environments all around the world, and consequently, highly urbanised areas filter similar species from the regional species pool (McKinney 2006). Alternatively, homogenisation of urban communities might increase due to the exotic species that are more abundant in towns than in their surrounding areas (Kühn & Klotz 2006). When comparing countries located in different biomes, the process of biological invasion of cosmopolitan non-native species adapted to highly urbanised areas seems to be the dominant factor promoting taxonomical homogenisation (McKinney 2008). Indeed, our comparison showed that species such as the *C. livia* and *P. domesticus* were dominant bird species in the town centres of both countries, as found worldwide (Aronson et al. 2014).

At the regional scale, suburban habitats are colonised by the urban adapter species from the regional pool of species (Blair 1996). Suburban habitats usually are composed of gardens with lawn, trees and shrubs that are occupied by 'edge' species adapted to forest edges and surrounding open areas (Adams 1994; Marzluff 2001; McKinney 2006). The expansion of the agriculture to grasslands and the forest fragmentation homogenise the landscape, promoting the expansion of forest edge species that, in turn, colonise suburban areas. Examples of such kind of bird species in our study are *Turdus rufiventris* and *Furnarius rufus* in Argentina and *P. pica* and *Carduelis flammea* in Finland.

According to the results found by other authors (La Sorte & McKinney 2007; Cassey et al. 2008), our analyses revealed that similarity values between communities were higher when using abundance data. However, this increase in compositional similarity varied across spatial scales, having relevance only when comparing urban centres between different biomes. This pattern suggests that biotic interchange and the posterior dominance of a few cosmopolitan species in the highly urbanised areas are the main drivers of biotic homogenisation (La Sorte & McKinney 2007). The decreased variability of the relative abundance of the Rock Dove and the House Sparrow amongst urban centres of Argentinian and Finnish cities may be achieved by resources subsidies, such as food wastes, and shelter provided by buildings (Murthy et al. 2016). Moreover, studies focusing only on the presence/absence data may be underestimating the homogenising effect of urbanisation (McKinney & La Sorte 2007).

Although bird composition varied consistently between habitats, bird richness varied differently between habitats in each country. This suggests different processes acting on bird communities in different biomes. Despite that the species composition of different habitats varied greatly in Finland, species richness in centres and suburban habitats was similar. Ferenc et al. (2014) suggested that bird species of northern latitudes in Europe are more able to colonise urban habitats because they have larger population sizes and wider ecologi-

cal niches. Moreover, the similar species richness and different composition between habitats suggest that species turnover might be an important process affecting the bird community structure and beta diversity in the north. In contrast, both the species composition and species richness varied a lot between habitats in Argentina. Our detailed analysis revealed that nestedness was the dominant process differentiating bird communities in Argentina. A recent study conducted in different cities of Brazil, surrounded by tropical forests, also showed that the dominant process-driven composition dissimilarity between urban and natural areas was nestedness (Villegas-Vallejos et al. 2016). Our results clearly demonstrated that the roles of nestedness and species turnover might differ between cities in different latitudes, and they must be disentangled in beta diversity studies (Baselga 2010).

Differences in species composition and species richness between town centres and suburban habitats may be related to the contrasting vegetation characteristics of habitats. Suburban habitats are generally composed by several vegetation strata, which may favour the presence of a very distinctive set of species in comparison to town centres. Many common suburban bird species feed on seeds during the winter season. In Finland, such kinds of bird species are *Emberiza citrinella* and *C. flammea*. In Argentina, *Molothrus bonariensis, Z. capensis* and *Z. auriculata* use suburban lawns to search food during winter. However, town centres have fewer vegetation layers and their ground layers are mainly covered by impervious surfaces, such as roads and the parking areas, and correspondingly their dominant bird species, such as *P. domesticus* and *C. livia*, forage gregariously on the pavement. In Finland, because of the intensive feeding of birds in suburban areas, winter bird assemblages composition between town centres and suburban areas differ greatly (Jokimäki & Suhonen 1998; Jokimäki & Kaisanlahti-Jokimäki 2003).

Suburban bird species richness was greater in Argentina than in Finland. This result agrees well with the global decreasing latitudinal trend in species richness from the Equator to the Poles and reflects the spatial variation in temperature and rainfall (Gaston 2000; Hawkins et al. 2003; Hillebrand 2004). A possible explanation for the greater species richness in suburban habitats in Argentina than in Finland might be the greater regional species pool in Argentina, allowing a greater colonisation rate of species into suburbs. Alternatively, possible differences in vegetation structure between suburban areas of both countries, unfortunately not measured in this study, may play a role determining the contrast values of species richness between countries.

On the other hand, bird richness of town centres was comparable between the study countries, supporting a view that species richness does not decrease toward the poles in heavily urbanised areas (Jokimäki & Suhonen 1993; Jokimäki et al. 1996, 2016; Clergeau et al. 2001; Filloy et al. 2015; but see Murthy et al. 2016). One reason for the lack of decreasing latitudinal trend in wintering species richness may be that only a few species are able to live in town centres, and these species

are the same all over the world (Jokimäki et al. 1996). The generally similar habitat and vegetation of the town centres allow the existence of the same kind of species. On the other hand, because of the urban heat island phenomenon, temperature differences between southern and northern areas are not so great in town centres than in their surrounding areas (Hall et al. 2016). Also, that town centres may offer food resources and energy inputs from humans, which are exploited by a few super-dominant bird species (Pautasso et al. 2011; Filloy et al. 2015; Galbraith et al. 2017).

It is necessary to note that the results of this study correspond to winter season (i.e. nonbreeding season), and certain bird species during this period can have a broader habitat use than during the breeding season (Wiens 1989a, b; Delgado & Moreira 2000; Caula et al. 2008). Thus, the degree of similarity in bird assemblages of town centres and suburban habitats can change between the breeding and nonbreeding seasons (see Clergeau et al. 1998), so the comparison of our study with the studies of breeding season assemblages (Blair 2001; Garaffa et al. 2008) would not be completely adequate. In addition, the spatial extent of the gradient may also affect the value of similarity indices. The inclusion of non-urban areas or the analysis of urban-natural gradients instead of the use of urban gradients (this study) could give different results. For example, Luck and Smallbone (2011) found, at the regional scale, that bird assemblages of cities were more similar between them than bird assemblages of non-urban areas surrounding each city.

4. CONCLUSIONS

Our study suggests that the process of biotic homogenisation is scale dependent. Urbanisation does not seem to homogenise bird communities at the regional scale. However, bird composition amongst town centres was more similar than communities amongst suburban areas when they were compared between countries. This clearly indicates that a high level of urbanisation homogenises bird communities when comparing different biomes. The environmental conditions of town centres may be more similar to each other than to suburban and more natural areas, likely supporting similar bird species. The observation that similarity values were higher whilst using the abundance data than the presence/absence data indicates that the same common and abundant bird species live in town centres across a large spatial scale. Our results suggest that one should consider the spatial scale and include abundance data in the analysis of the possible effects of urbanisation on homogenisation of bird communities.

Our results indicate that the urbanisation changes the general latitudinal decreasing trend of species richness towards the poles. However, this observation could be detected only in the most urbanised areas of the towns. Moreover, different process-driven community dissimilarities between urbanisation levels acted in both countries; species turnover was more important in the north, whereas nestedness dominated in the south. More studies focusing on the varying roles of species turnover and nestedness with latitude are needed.

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APPENDIX S1.
EXAMPLES OF STREET VIEWS, OBTAINED FROM THE GOOGLE MAPS, FROM BOTH TOWN CENTRES AND SUBURBAN HABITATS OF EACH TOWN.

Mar del Plata – Town centre

Mar del Plata – Suburban

Miramar – Town centre

Miramar – Suburban

Balcarce – Town centre

Balcarce – Suburban

Oulu – Town centre

Oulu – Suburban

Rovaniemi – Town centre

Rovaniemi – Suburban

Kemi – Town centre

Kemi - Suburban

APPENDIX S2 LIST AND NUMBER OF INDIVIDUALS OF SPECIES FOUND IN TOWN CENTRES (TC) AND SUB-URBAN HABITATS (SINGLE FAMILY HOUSE AREAS; SFH) OF THE ARGENTINIAN (A) AND FINNISH (B) STUDY TOWNS. EXOTIC SPECIES ARE IN BOLD.

a) Argentina	Mar del Plata		Balcarce		Miramar	
	TC	SFH	TC	SFH	TC	SFH
Chimango Caracara (*Milvago chimango*)	0	0	0	0	0	2
Rock Dove (*Columba livia*)	36	9	8	3	63	10
Picazuro Pigeon (*Patagioenas picazuro*)	0	6	2	9	0	8
Eared Dove (*Zenaida auriculata*)	22	9	44	11	9	26
White-throated Hummingbird (*Leucochloris albicollis*)	0	0	0	1	0	0
Golden-breasted Woodpecker (*Colaptes melanolaimus*)	0	0	0	1	0	1
Rufous Hornero (*Furnarius rufus*)	1	6	0	7	2	9
Tufted Tit-Spinetail (*Lepthastenura platensis*)	0	0	0	1	0	0
White-crested Tyrannulet (*Serpophaga subcristata*)	0	0	0	2	0	0
Great Kiskadee (*Pitangus sulphuratus*)	0	6	0	3	1	4
Rufous-bellied Thrush (*Turdus rufiventris*)	0	8	0	1	3	7
Chalk-browed Mockingbird (*Mimus saturninus*)	0	4	0	4	3	5
House Wren (*Troglodytes aedon*)	1	2	1	1	0	4
White-rumped Swallow (*Tachycineta leucorrhoa*)	0	0	0	0	0	2
House Sparrow (*Passer domesticus*)	63	49	27	19	39	68
Hooded Siskin (*Spinus magellanica*)	0	0	2	6	0	0
European Greenfinch (*Chloris chloris*)	0	1	1	0	0	2
Rufous-collared Sparrow (*Zonotrichia capensis*)	0	2	3	20	1	8
Saffron Yellow-Finch (*Sicalis flaveola*)	0	0	0	4	0	0
Shiny-Cowbird (*Molothrus bonariensis*)	0	0	0	1	0	0
b) Finland	Oulu		Rovaniemi		Kemi	
Sparrow hawk (*Accipiter nisus*)	0	0	0	0	0	1
Rock Dove (*Columba livia*)	234	0	1	0	21	3
Great Spotted Woodpecker (*Dendrocopos major*)	0	0	0	0	0	1
Willow Tit (*Parus montanus*)	0	0	0	2	0	0
Blue Tit (*Parus caeruleus*)	1	12	3	7	0	5
Great Tit (*Parus major*)	1	20	8	19	29	15
Magpie (*Pica pica*)	2	8	11	10	4	24
Jackdaw (*Corvus monedula*)	6	0	0	0	0	0
Hooded Crow (*Corvus corone cornix*)	6	1	4	2	9	4
House Sparrow (*Passer domesticus*)	26	23	40	17	14	0
Greenfinch (*Chloris chloris*)	0	17	12	7	13	7
Redpoll (*Carduelis flammea*)	0	35	10	10	0	0
Pine Grosbeak (*Pinicola enucleator*)	0	0	0	0	0	22
Yellowhammer (*Emberiza citrinella*)	0	1	0	7	0	0