Residential areas support overwintering possibilities of most bird species

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Spatial variation in wintering bird communities in different types of urban residential areas is poorly understood. The objective of this study was to find out which bird species from the regional species pool are able to inhabit residential areas, whether bird communities in different types of residential area differ from one another, and what are the factors affecting birds. We conducted our study in five apartment-building areas, five family-house areas, and five villages in northern Finland by using the single-visit study plot method during five winters, i.e. 1998/1999-2003/2004. Oldgrowth-forest-specialist species, in particular, avoided residential areas, whereas the other species appeared to benefit from residential development. The species richness, the total number of individuals, and the abundance of most of the species were higher in the family-house areas and in villages than in apartment-building areas. The proportion of individuals belonging to resident species was higher in the apartment-building areas than in the other habitats, whereas the proportion of individuals belonging to feeding-table species was higher in the villages than in the other habitats. The species richness and the total number of individuals increased with the increasing number of feeding tables and decreased with increasingly larger proportions of apartment buildings within the study plot. Parus montanus, P. major, P. caeruleus, Passer domesticus, and Carduelis flammea benefitted from feeding tables. Our study demonstrated that carefully planned winter feeding programmes can enhance the wintering possibilities for birds, and thus promote the biodiversity in urban ecosystems at northern latitudes.

Introduction

Urbanization involves one of the most extreme forms of land-use alteration, and generally it leads to the complete restructuring of vegetation and species composition. Urbanization is recognized as one of the main threats to biodiversity on the global scale (Wilcox & Murphy 1985). In addition, urban environments differ in many ways from more natural ecosystems; for example, they support more anthropogenic food resources and the microclimate in urban areas can be more favourable for wintering species (Gilbert 1989, Rebele 1994). Urban areas are also characterized by high levels of disturbance and environmental modifications, which can affect bird populations and community patterns (Gilbert 1989, Blair 1996, Fernandéz-Juricic & Jokimäki 2001).

Breeding season studies have demonstrated that urbanization decreases species richness, increases the total abundance of birds, and favours the occurrence of some superabundant bird species (Bezzel 1985, Marzluff 2001, Chace & Walsh 2006). However, species richness in urban environments can also peak at intermediate levels of development (e.g. Jokimäki & Suhonen 1998, Marzluff, 2001, Chace & Walsh 2006, Lepczyk et al. 2008). Urban bird communities are usually characterized by the dominance of a few species, these being mainly generalists (Beissinger & Osborne, 1982, Bezzel, 1985, Marzluff 2001). These strong competitors can benefit from the low-frequency resource fluctuations in urban environments (Anderies et al. 2007). In addition in such environments, population densities of many urban bird species are usually higher as compared with those of rural birds (Batten 1973, Bezzel 1985), and often these urban exploiters are resident species with omnivorous diets (Jokimäki & Suhonen 1998, Chace & Walsh 2006, Kark et al. 2007, Croci et al. 2008).

Urban environments are not homogeneous and urban bird communities can differ between land-use types and practices (e.g. DeGraaf & Wentworth 1986, Jokimäki et al. 1996, Germaine et al. 1998, Jokimäki 2000, Savard & Falls 2001, Jokimäki et al. 2002, Hostetler & Knowles-Aanez 2003, Jokimäki & Kaisanlahti-Jokimäki 2003, Rodewald 2003, Palomino & Carrascal 2006, Caula et al. 2008). Suburban areas with residential developments, parks and gardens have been reported to be species-rich areas (Cannon 1999, Fernández-Juricic & Jokimäki, 2001, Jokimäki & Kaisanlahti-Jokimäki 2003, Leveau & Leveau, 2005, Chamberlain et al. 2007, Goddard et al. 2010, Gaston & Gaston 2011). The likelihood of species presence in suburban gardens can depend on factors such as garden characteristics (Daniels & Kirkpatric 2006, Parsons et al. 2006), surrounding habitats (Chamberlain et al. 2004), network of gardens (Goddard et al. 2010) as well as winter feeding (Jokimäki & Suhonen 1998, Jokimäki & Kaisanlahti-Jokimäki 2003, Atchison & Rodewald 2006, Jones & Reynolds 2008). Factors such as size of woodlands and building density immediately adjacent to woodland areas have been found to affect the bird species richness in

woodlands in America (Tilgman 1987) and in Britain (Chamberlain *et al.* 2007).

However, many bird species have broader use of the urban landscape in winter than during the breeding season (Caula et al. 2008), and therefore the results between breeding time and winter time can differ (Atchison & Rodewald 2006). In addition, winter is the most critical season for many birds, and this also includes urban areas (see e.g. Doherty & Grubb 2000), and especially at northern latitudes, and therefore the occurrence of resident species and their abundance can be affected by the winter conditions. Indeed, many bird species in urban environments are resident species (Jokimäki & Suhonen 1998, Chace & Walsh 2006, Kark et al. 2007). This being so, urban planners need knowledge of the habitat needs of wintering birds in order to create or maintain appropriate biodiversity in residential areas.

Winter season ecological studies conducted urban environments are rare (Marzluff et al. 2001a). According to results obtained in connection with large-scale biogeographical studies, bird species diversity and richness were found to be lower in the city of Québec (Canada) than in the city of Rennes (France; Clergeau et al. 1998), and the species richness of wintering birds was higher in the urban areas in France than in the urban areas in Finland (Jokimäki et al. 2002). The urbanization level was found to impact on bird community composition more in northern Finland than in France (Jokimäki et al. 2002). Along a 950-km-long latitudinal gradient in Finland, species richness, but not bird density, were found to decrease northwards in urban environments (Jokimäki et al. 1996). These results reflect the harsher winter conditions in northern regions. For example, the winter climate in northern Finland imposes significant constraints (e.g. snow cover and low temperatures) also on birds in urban areas.

Only few studies have focused on the winter bird assemblages of different types in residential areas (DeGraaf 1991, Jokimäki & Kaisanlahti 2003, Smith 2007, Suhonen *et. al.* 2009, Jokimäki & Kaisanlahti 2012), while at the same time taking into account the regional species pool. In addition, in most cases, the results of such studies are based on studies spanning one or two years. A short-term study based on single-year results will give a misleading picture of density and bird-habitat relationships (Wiens 1981). Therefore, urban winter-ecological studies spanning several years are urgently needed. In addition, the characteristics of species adapted to using residential urban environments during the winter are relatively poorly known (see e.g. Jokimäki & Suhonen 1998, Marzluff et al. 2001a, Smith, 2007). This is mainly due to the lack of corresponding information about the regional pool of wintering species. It has been suggested that urban constraints appear to act as a filter that selects which kinds of species from the regional species pool are able to colonize urban environments (Croci et al. 2008). The objectives of the present research were to study (1) which species from the regional species pool are able to inhabit residential areas during the winter and what characteristics distinguish urban species from non-urban species; (2) if residential area types (apartment-building areas, single-family house areas, and villages) have any effect on the structure of the wintering bird communities: and (3) what factors affect winter bird abundance and distribution in residential areas.

Urban areas are characterized by a high and predictable amount of food that allows some bird species to live in towns (Shochat 2004, Andreies et al. 2007). Following the ideas of this "credit card" hypothesis, we predicted that the resident species that are able to use urban-related "extra" resources, e.g. wintertime feeding tables, are better able to settle in residential areas from the regional species pool than other species. Despite the global habit that people have of feeding birds, very little is known about the outcomes and implications of supplementary feeding on bird assemblages and species (Jones & Reynolds 2008). Because the resource availability can differ between residential area types, we predicted that a residential area type with additional winter resources could be more favourable in providing wintering sites for the birds than residential areas with few feeding sites (e.g. Jokimäki et al. 2002). Brittingham and Temple (1988) indicated that birds that have access to supplementary food had higher overwinter survival rates than birds without such access. Because of the harsh winter conditions (cold climate, lots of snow, short daylight during winter) in our northern study area in northern Finland, we predicted that the availability of feeding sites would affect the abundance of wintering bird species in residential areas (e.g. Chamberlain *et al.* 2005, Fuller *et al.* 2008).

Material and methods

Description of the study areas

The study was conducted during 1998/1999-2003/2004 in Rovaniemi, northern Finland, in the vicinity of the Arctic Circle (66°N, 25°E). The land area of the study region is 7601 km² and the human population is 60 000 (Statistics Finland). Most of the human population (approx. 83%) is concentrated in the town of Rovaniemi (population approx. 49 000 inhabitants). There are about 20 small villages from some hundreds up to a thousand inhabitants in the Rovaniemi area. Because of the large land area, the average human population density is very low, about 8 inhabitants per km². The general structure of the study plots did not change during the study period (Jokimäki & Kaisanlahti 2012). In general, natural forest patches and coniferous forests were located either within or very close (200 m) to the study plots.

The matrix around the human settlements is mainly covered by forests (over 60%), and the proportion of agricultural land is small (< 1%) and it is restricted to the surroundings of villages and riversides. Most of the forests (86%) are dominated by Scots pine (*Pinus sylvestris*). Snow falls in this area between October and November and the temperature falls below 0 °C at the beginning of November (Finnish Meteorological Institute). The average temperature in December is about -10 °C and in January it is -11.7 °C. The average thickness of the snow cover is 29 cm in December and 46 cm in January.

We selected three types of homogenous residential areas in the Rovaniemi area: apartmentbuilding areas, single-family house areas, and villages (Fig. 1 and Table 1). Each habitat type had five replicates. The apartment-building areas consisted of buildings of 3–6 storeys, their park-

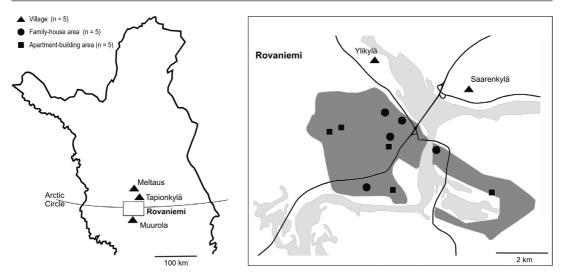


Fig. 1. Location of the study plots. In the right-hand-side panel urban areas are in dark grey, thick solid lines are main roads, and light-grey areas are main rivers. Other areas are mainly conifer-dominated forests.

ing areas, and shoping centres. The family-house areas consisted of small buildings with gardens, and the villages consisted mainly of scattered houses surrounded by agricultural fields. The coverage of apartment-buildings was lower in the villages and in the family-house areas while the coverage of parks was higher in the villages and of family-house areas (Table 1). In addition, wintertime feeding was very rare in the apartment-building areas. The apartment-building and family-house areas were located in the urban core of the town with a population density of about 370 inhabitants per km², while the villages were located in the peripheral area with

Sites	Number of inhabitants	Dist. from town centre	Cover (%)					Number of	
	2001/2004	(km)	Apartment buildings	Family houses	Parks	Open areas	Roads	feeding stations 1998/2003	
Apartment-building	areas								
Ounasrinne	1341/1363	3.8	58	0	8	10	23	3/1	
Rantavitikka	1021/1063	1.9	43	1	7	14	34	1/4	
Asemieskatu	590/642	1.2	53	3	10	12	22	2/0	
Sudentie	1055/1009	3.9	44	0	10	10	36	0/0	
Hillapolku	1029/1005	2.8	52	0	7	12	28	6/3	
Family-house areas	6								
Katajaranta	352/349	1.2	0	61	8	12	18	5/5	
Viirinkangas	330/314	2.4	4	48	14	4	30	10/8	
Ounasjoentie	341/355	1.1	0	56	19	2	32	8/3	
Jokkatie	218/253	1.3	2	51	12	3	31	11/5	
Rakkatie	368/356	1.9	0	51	17	3	29	12/1	
Villages									
Muurola	1096/1033	21.3	14	20	30	6	30	3/5	
Saarenkylä	980/1137	2.7	0	40	5	25	30	3/3	
Ylikylä	1381/1221	3.7	3	40	20	15	22	3/2	
Tapionkylä	337/328	25.7	0	10	10	70	10	3/5	
Meltaus	229/212	49.0	0	20	30	40	10	5/5	

Table 1. General description of the apartment-building areas, family-house areas, and villages.

a human population density of about 3 inhabitants per km² (Statistics Finland). The matrix of apartment-building and family-house areas was urban-dominated, whereas the immediate matrix of the villages was composed of either agricultural land or forest areas. The study sites were selected so that both apartment-building and family-house areas were located about 500 m from one another, and the distance between these (with individual study sites of block of flats as well as single-family house areas) were designed to be over 3000 m. The nearest villages were located at a distance of about 3.5 km from the town centre with the furthermost village being located at a distance of about 50 km.

Each study plot (30 ha) was estimated as regards its proportion of apartment-building areas (with buildings three or more storeys high), the proportion of family-house areas, wooded parks, open areas, and roads. These estimates were made using town maps (scale 1:4000). We also carried out ground-level checks during the bird surveys. The number of inhabitants was derived from the statistics of the town of Rovaniemi. The distance of each study-plot centre from the urban core (i.e. the most urbanized area of the Rovaniemi, which is also the historical centre of the town) of the town of Rovaniemi was measured using maps. Active feeding stations (i.e. feeding tables with food) were counted during every bird survey. According to the general guidelines about wintertime feeding of birds in Finland (www.birdlife.fi/lintuharrastus/talviruokinta.shtml [in Finnish]), no changes in the abundance of food at the wintertime feeding stations was assumed to occur during the 2-month survey period. The amount or quality of food offered was not evaluated, but according to nationwide surveys on wintertime feeding of birds in Finland, most feeding tables in our study area provide sunflower seeds (Väisänen & Hildén 1993, Väisänen 2008). Therefore, the availability of different food types among the study sites was not considered to be an important factor affecting the results when comparing the different types of residential areas. The basic features of each study site are given in Table 1. Based on the habitat structure, the apartmentbuilding areas were the most urbanized, the family-house areas were moderately urbanized, and

the villages were the least urbanized (Table 1). The general structure of the study plots did not change during the study period.

The rowanberry (Sorbus aucuparia) crop size can affect frugivorous species such as the waxwing (Bombycilla garrulous) (Fox et al. 2009, Lehikoinen et al. 2010). However, because during our survey period (all surveys were conducted in mid-winter) the rowanberry trees were practically void of berries, this factor had no effect on our results (Jokimäki & Kaisanlahti-Jokimäki 2012). The situation was also the same for the other tree-seed-preferring species [like the siskin (Carduelis spinus) or the redpoll (Carduelis flammea)]. Anthropogenic food availability was measured by counting the number of active feeding stations (i.e. feeding tables with food) during each bird survey. Unfortunately, we do not have data on the quality or amount of food at these feeding stations. According to Väisänen (2001), most feeding stations in the Rovaniemi area have either one large feeding table or 2-3 smaller ones. Thus in the residential areas, food was offered either moderately or in large quantities, and the most common food consisted of sunflower seeds (at 97% of the feeding stations) and fat (at 88% of the feeding stations).

Potential predators within the study area were the red squirrel (*Sciurus vulgaris*), the Eurasian sparrow hawk (*Accipiter nisus*), the northern goshawk (*Accipiter gentilis*), and the pygmy owl (*Glaugidium passerinium*). Because of harsh winter conditions, domestic cats are not considered important wintertime predators. In addition, the abundances of the sparrow hawk, the goshawk and the pygmy owl are so low, that their possible role in modifying the winter bird assemblages in these northern latitudes is minimal.

Bird census

The wintering birds were counted by using a single-visit study-plot method and applying a rate of 1 hour/per 30 ha study plot. All the plots were surveyed each year, and the surveys were carried out in mid-winter (December–January) in good weather (no strong wind or rain), and early in the day (10:00–14:00). All the birds encountered within the study plots were counted; overflying birds that did not land on the study plot were ignored. The surveys were not conducted along a straight route, but instead the entire plots were walked along a zigzag line. Therefore, all sites, including the feeding stations for birds, were accessible and visible to the surveyor. The detectability of the species could differ among the habitats. Because of our comprehensive study plot survey method, we assumed that we were able to observe all individuals present on the study plot during the survey period. Therefore, the possible habitat-related differences in the detectability of the species did not significantly influence our results. To eliminate possible observer bias, the same person carried out most of the surveys (95% by JJ). We used a fairly high census rate (10 ha/20 min) to avoid counting the same individuals twice. According to our earlier results from the same study region, the efficiency of this type of survey method is high, and its efficiency does not markedly vary among the residential area types (Jokimäki & Kaisanlahti-Jokimäki 2003, 2012).

Since the direct winter-bird atlas data were not available at national, regional or local level, we used district-based (municipality of Rovaniemi; 8000 km²) winter data collected by local ornithologists as indicators of the district's regional winter species pool per study winter (www.lly.fi [in Finnish]). These data provide a comprehensive picture of the district's species pool in the study area per study year.

We classified the bird species according to their migratory habits and habitat preferences in Finland according to Väisänen *et al.* (1998). The bird species were classified as feeding-table species if they were observed at over 50% of the feeding stations, and if their relative abundance within the study area (the average number of individuals per fortnight) was over 1.5 (Väisänen 2001). The species groups used in this study and their characteristics are given in Appendix 1.

Statistical analyses

Because we used a fixed sampling design (fixed study plot size, fixed survey speed, and the same number of samples from the different types residential areas each winter as well as having just one observer collecting most of the samples), there was no need to use the rarefaction method.

In our analyses, we used non-parametric statistical tests only. However, before the testing an arcsin-square-root transformation was applied to percentages. This was done in order to normalize the data, and was also expected to help in the interpretation of the results even when applying a non-parametric approach. The G-test was used for comparisons of the bird guilds of the regional and residential bird communities, 'average abundance of species belonging to different guilds' being the dependent variable, and 'habitat type' being the independent, nominal variable. A Kruskall-Wallis test was used when comparing the bird communities among the types of residential areas. Subsequently, a non-parametric Tukey-type a-posteriori test (Zar 1984) was used for paired comparisons. The variables were species richness, total abundance of individuals, abundance of single species, and the abundance of individuals belonging to different guilds. It should be noted that even if we report some of our results in terms of proportions, all statistical tests were done using ordinal-scale variables.

The correlation analyses were conducted using Spearman's rank correlation. Because proportions of different habitat components within a study plot were highly inter-correlated, in the correlation analysis - in addition to the human population, the number of feeding stations per study plot, and the distance of the study plot from the urban core of the town of Rovaniemi – we used the proportion of apartment buildings (instead of other land-cover variables) as it correlated the least with the other variables. In addition, the proportion of apartment-building area had earlier been found to be an important variable explaining winter bird abundances at northern latitudes (Jokimäki & Kaisanlahti 2003), and it is a very good indicator of the level of urbanization of the study plots (Suhonen et al. 2009). In order to avoid misleading results, the analyses were restricted only to the most common bird species, i.e. species occurring at least 18 times over 75 possible occurrences. Consequently, the analyses were done for only 11 species out of 21 species detected in the residential areas.

Before the analyses, we carried out a test to see if the abundance of individuals differed in the study winters by using the pooled data for all study sites. Because abundances did not differ in the study years ($\chi_4^2 = 7.86, p > 0.05$), as dependent variables we used in our analyses the average values of bird variables from the five study winters.

Results

Regional species pool vs. bird species wintering in residential areas

In total, the regional species pool in the study area included 67 wintering species, and 21 wintering species (31.3% of the species pool) were found within the residential areas of Rovaniemi (Appendix 1). However, 19 species (e.g. *Grus grus* and *Phalacrocorax carbo*) of the regional species pool were observed only during one winter in the Rovaniemi area. Twelve species (25.0% of the regional species pool) of regularly overwintering species were observed in the apartment-building areas, 17 species (35.4%) in the single-family house areas, and 16 species (33.3%) in the villages.

The proportions (%) of species belonging to different migratory ($G_3 = 13.1$, p = 0.004) and habitat guilds (*see* species grouping in Appendix 1; $G_6 = 16.7$, p = 0.020) differed between the residential and nonresidential areas. Most of the species that were not observed within the residential

areas were short-distance or long-distance migrators (Table 2 and Appendix 1). The proportions of forest specialists (mainly coniferous or oldgrowth forest species) were 58.7% and 33.3%, in residential and nonresidential areas, respectively. (Table 2 and Appendix 1). Many species observed in the nonresidential areas were water birds, birds of prey, game birds, owls, woodpeckers, species favouring old-growth-forests, or late migrants (Appendix 1).

Species richness, total abundance, and species composition in the types of residential areas

There were 6.5 ± 2.2 (SD) species per plot. The average species richness differed between the habitats ($\chi^2_2 = 16.1, p < 0.001$). The species richness in the family-house areas and villages was higher than that in the apartment-building areas (Table 3). In the residential areas, we observed a total of 5125 individuals (68.3 \pm 112.0 individuals per plot). The average number of individuals differed between the habitats ($\chi^2_2 = 25.45, p <$ 0.001). The number of individuals in the villages and family-house areas was higher than that in the apartment-building areas (Table 3). There was a positive correlation between the abundance of bird species and the number of sites where a species occurred ($r_s = 0.866$ for pooled data; $r_s =$ 0.983 for the apartment-building areas; $r_s = 0.41$

Table 2. Proportions (%) of species belonging to different migratory and habitat guilds in the residential areas and the study district. In the case of the study district, only species absent from residential areas (but belonging to the regional species pool) are considered.

	Residential areas	Study region
Migratory status		
Resident	57.1	41.3
Partly migratory	28.6	13.0
Invasive	14.3	15.2
Short- or long-distance migrant	0.0	30.5
Preferred habitat		
Human-associated species	42.9	10.9
Forest-generalist species	19.0	8.7
Deciduous-forest species	4.8	10.9
Coniferous-forest species	23.8	30.4
Old-growth-forest species	9.5	17.4
Oligothrophic-lake species	0.0	13.0
Others: mire, mountain and archipelago species	0.0	8.7

for the family-house areas, and $r_s = 0.898$ for the villages; in all cases n = 21 and p < 0.001).

The bird species composition differed between the habitats (Table 3 and Appendix 1). All species observed in the apartment-building areas (with the exception of Columba livia domestica, which was not observed in the villages) were also observed in the other habitats. Nucifraga caryocatactes, Passer montanus, Loxia curvirostra, and Emberiza citrinella were observed only in the family-house areas. Glaucidium passerinum, Turdus pilaris, Parus cinctus and Garrulus glandarius were observed only in the villages. Many species, including Dendrocopos major, Parus montanus, Parus major, Pica pica, and Passer domesticus, were less abundant in the apartment-building areas than in the other two types of residential areas (Table 3). The villages had fewer Corvus corone cornix than the family-house and apartment-building areas.

Ecological groups in residential areas

The proportions of individuals belonging to resident bird species ($\chi_2^2 = 10.70$, p = 0.005), partlymigratory bird species ($\chi_2^2 = 8.49$, p = 0.014), invasive bird species ($\chi_2^2 = 11.34$,, p = 0.003), feeding-table species ($\chi_2^2 = 14.58$, p = 0.001), and coniferous-forest bird species ($\chi_2^2 = 7.55$, p = 0.023) differed significantly between the types of residential areas.

The proportion of individuals belonging to resident birds was higher in the apartment-building areas (mean \pm SD = 84.1% \pm 16.0%, *n* = 25) than in the family-house areas (mean \pm SD = 69.4% \pm 16.4%, *n* = 25; Tukey-type *a-posteriori* test: *p* < 0.001) and in the villages (mean \pm SD = 74.4% \pm 21.5%, *n* = 25; *p* < 0.05). The proportion of individuals belonging to partly-migratory birds was higher in the family-house areas (mean \pm SD = 28.2% \pm 17.2%, *n* = 25) than in the

Table 3. The total and mean (\pm SD) abundances of the species, the total numbers of individuals and species richness in different habitats for all study winters. Statistically significant differences (Tukey's paired comparison; *p* < 0.05) between the apartment-building areas (B), family-house areas (S) and villages (V) are indicated in the last column. The species grouping is shown in Appendix 1.

	Apartment-building areas (B)		Family-house areas (S)		Villages (V)		Paired comparisons	
	Total	Mean ± SD	Total	Mean ± SD	Total	Mean ± SD		
Columba livia	68	2.72 ± 4.77	17	0.68 ± 1.25	0		B > V	
Glaucidium passerinum	0		0		1	0.04 ± 0.20		
Dendrocopos major	1	0.04 ± 0.20	9	0.36 ± 0.57	19	0.76 ± 1.09	V > B	
Bombycilla garrulus	10	0.40 ± 2.00	35	1.40 ± 4.32	831	33.24 ± 164.54		
Turdus pilaris	0		0		17	0.68 ± 3.40		
Parus montanus	1	0.04 ± 0.20	22	0.88 ± 1.23	46	1.84 ± 3.10	V > B; S > B	
Parus cinctus	0		0		2	0.80 ± 0.40		
Parus caeruleus	32	1.28 ± 1.51	105	4.20 ± 2.61	65	2.60 ± 3.23	S > B; S > V	
Parus major	187	7.48 ± 4.12	384	15.36 ± 6.47	365	14.60 ± 8.56	S > B; V > B	
Garrulus glandarius	0		0		4	0.16 ± 0.47		
Pica pica	93	3.72 ± 2.15	177	7.08 ± 3.53	170	6.80 ± 4.07	S > B; V > B	
Nucifraga caryocactes	0		1	0.04 ± 0.20	0			
Corvus corone cornix	36	1.44 ± 1.26	44	1.76 ± 1.59	7	0.28 ± 0.61	S > V; B > V	
Passer domesticus	240	9.60 ± 10.77	477	19.08 ± 12.21	576	23.04 ± 21.14	V > B; S > B	
Passer montanus	0		2	0.80 ± 0.28	0			
Carduelis chloris	49	1.96 ± 3.46	244	9.76 ± 14.77	177	7.08 ± 10.64	S > B	
Carduelis flammea	28	1.12 ± 3.35	270	10.80 ± 15.95	208	8.32 ± 13.03	S > B	
Carduelis hornemanni	0		2	0.80 ± 0.40	3	0.12 ± 0.60		
Loxia curvirostra	0		1	0.40 ± 0.20	0			
Pyrrhula pyrrhula	3	0.12 ± 0.44	27	1.08 ± 3.28	58	2.32 ± 4.31	V > B	
Emberiza citrinella	0		11	0.44 ± 1.45	0			
Total no. of indiv.	748	9.92 ± 17.03	1828	73.12 ± 33.84	2549	101.96 ± 185.76	V > B; S > B	
Richness	12	5.32 ± 1.43	17	7.40 ± 2.43	16	6.72 ± 2.01	S > B; V > B	

apartment-building areas (mean \pm SD = 15.1% \pm 15.5%, n = 25; p < 0.001). The proportion of individuals belonging to invasive birds was lower in the apartment-building areas (mean \pm SD = 0.8% \pm 3.0%, n = 25) than in the villages (mean \pm SD = 5.1% \pm 16.7%, n = 25; p < 0.001) or in the family-house areas (mean \pm SD = 2.4% \pm 5.9%, n = 25; p < 0.05).

The proportion of individuals belonging to feeding-table birds was higher in the villages (mean \pm SD = 94.0% \pm 16.8%, n = 25) than in the apartment-building areas (mean \pm SD = 86.3% \pm 11.7%, n = 25; p < 0.001) or in the family-house areas (mean \pm SD = 93.4% \pm 6.3%, n = 25; p < 0.05). Moreover, the proportion of individuals belonging to feeding-table birds was higher in the villages than in the family-house areas (p < 0.05). The proportion of individuals belonging to coniferous-forest birds was higher in the villages (mean \pm SD = 6.7% \pm 17.4%, n = 25) than in the apartment-building areas (mean \pm SD = 1.0% \pm 3.1%, n = 25; p < 0.05).

Factors affecting winter bird communities in residential areas

The bird species richness and the total number of individuals increased with increasing number of feeding tables ($r_s = 0.743$, p = 0.002; and r_s = 0.698, p = 0.004; n = 15 in both cases) and decreased with increasing proportion of apartment-building areas ($r_s = -0.565$, p = 0.028, n= 15 and $r_s = -6.33$, p = 0.011; n = 15 in both cases). In the pooled data (n = 75), the number of feeding stations within the study plot had a positive effect on the abundance of Parus montanus $(r_{s} = 0.436)$, Parus major $(r_{s} = 0.496)$, Parus caeruleus ($r_s = 0.437$) Passer domesticus ($r_s =$ 0.397), and Carduelis flammea ($r_s = 0.521$) (p <0.001 in all cases). The increase in the proportion of apartment-building areas affected negatively the average abundance of *Parus major* (r_s = -0.623, p = 0.013), Passer domesticus ($r_s =$ -0.568, p = 0.027) and Carduelis flammea (r_s = -0.669, p = 0.006), and positively Columba livia domestica ($r_s = 0.723, p = 0.002$) (n = 15in all cases). The number of inhabitants affected negatively two species: Dendrocopos major (rs = -0.590, p = 0.021, n = 15) and Carduelis flammea ($r_s = -0.652$, p = 0.008, n = 15). The distance from the urban core of the town of Rovaniemi had a negative effect on the abundance of *Corvus* corone cornix ($r_s = -0.585$, p = 0.022, n = 15).

Discussion

Regional species pool *vs*. bird species composition in residential areas

According to our pooled results from multiple study winters, a high proportion of the species belonging to wintering species were observed in the residential areas. According to the data on pooled species richness, and if only the species observed during every study winter in the region (30 species) were taken into account, the proportion was as high as 70%. However, there were year-to-year changes in the residential-area winter bird assemblage, with some species arriving in the study area and others disappearing (Jokimäki & Kaisanlahti-Jokimäki 2012). Indeed, our results indicate that residential areas with gardens have highly diversified bird communities (Edgar & Kershaw 1994, Goddard et al. 2010, Gaston & Gaston 2011) and they are important wintering areas for many species (Jokimäki & Kaisanlahti-Jokimäki 2012). However, our results also pointed out that some species (e.g. birds of prey, owls, game birds), especially species favouring old-growth coniferous forests, were almost absent from the residential areas even though they were regularly observed in the nonresidential areas. For these species, residential areas seem to be unsuitable or sub-optimal wintering habitats (Appendix 1; "urban avoiders" according to Blair 1996). However, it is a well-known fact that many waterfowl species (e.g. Anas platyrhychos) benefit from urbanization due to the anthropogenic feeding.

It is quite understandable that species sensitive to disturbance caused by human activities, e.g. Aquila chrysaetos, large boreal owl species (Strix spp.), and game birds, did not occur in the residential areas. The absence of other birds of prey may be due to sampling bias because Accipiter gentilis (especially juvenile individuals) and Accipiter nisus frequently use urban areas as foraging sites, including the urban core areas of Rovaniemi (pers. obs.). Indeed, according to Rutz (2008), an increase in the abundance of avian prey has been one of the most obvious reasons for the rapid colonization of the town of Hamburg by Accipiter gentilis. According to Solonen (2008), the brood size of Accipiter gentilis was smaller in rural than in more urbanized areas in southern Finland. One explanation for this could be that the forests within urban areas may not be so intensively managed as the adjacent forests (Solonen 2008). This could be due to the high recreational value of the forests located near human settlements. In addition, many avian predators, among them Accipiter gentilis, Accipiter nisus, Falco tinnunculus, Falco peregrinus and Strix aluco (Marzluff et al. 2001a, Sorace 2002, Chace & Walsh 2006), have nowadays established their territories even within heavily urbanized areas partly due to the good and predictable food conditions that prevail there. In years when vole populations crash, wintering owls, such as Strix aluco and Asio otus, occupy urban areas. However, the winter distribution areas of these species do not extend to our northern study area.

The almost total absence of Parus cinctus and Perisoreus infaustus, i.e. species that are certain to be also able to use feeding tables (Väisänen 2001), from residential areas is interesting. Both of these old-growth forest coniferous taiga species easily colonize winter feeding stations established in forests (the authors' unpublished material). In addition, these two species can also be found at many feeding stations located on the outskirts of villages (Väisänen 2001, our personal observations). Why do these two resident northern bird species not colonize the winter feeding stations located in residential urban areas as do their close relative, Garrulus glandarius and other Parus spp.? Unfortunately, our data do not provide a direct answer. We propose that either (i) some essential resource needs of these species are not met in residential areas, or (ii) inter-specific competition could hinder their colonization of residential areas. Studies about species interactions in urban landscapes are rare, but an Australian study revealed that the presence of noisy miners (Manorina melenocephala), a species that is capable of aggressively excluding other species from its territories, has an important effect on other species in suburban areas (Parsons *et al.* 2006). Other obvious explanations for the lack of old-forest specialist species, such as *Parus cinctus* and *Perisoreus infaustus*, in residential areas may be that urban landscapes do not include enough natural forest areas and that the patch size of these remnants are too small for resident species not adapted to the urban environment (Mörtberg 2001). To fulfil the habitat needs of forest passerines, urban planners should strive to retain large natural forest patches within residential areas (Fernández-Juricic 2004).

Many of the species that avoided residential areas were coniferous-forest species. It may be that the habitat needs of these coniferous-forest bird species are not met in highly urbanized landscapes where deciduous plants are favoured over evergreen plants (Gilbert 1989, Edgar & Kershaw 1994). Indeed, according to the results obtained by Jokimäki and Suhonen (1998), most of the bird species in Finland that avoid urban areas are coniferous-forest bird species. To support the existence of these species and to increase biodiversity in residential areas, planting more coniferous trees in residential areas is a good option (see also Savard & Falls 2001). Evergreen trees provide food and shelter for birds also during winter. Coniferous trees are important for birds especially in northern latitudes, where deciduous trees lose their leaves in autumn (Jokimäki & Suhonen 1998). Smith (2003) indicate that the percentage of insectivorous birds is very low (1.5%) in the cities of Canada in winter. According to our results, urbanization favours omnivorous bird species over insectivores and (coniferous-) forest species (see also Lancaster & Rees 1979, Smith 2003).

The core species in residential areas (Appendix 1, "suburban-adaptable species" according to Blair 1996) at northern latitudes during winter were *Pica pica*, *Parus major*, *Passer domesticus*, *Parus caeruleus* and *Carduelis chloris*. These species are mainly the same as the most abundant species found in the European wintergarden survey (Thompson *et al.* 1993). Interestingly, all these species belong to the group that commonly used the winter feeding stations in our study area (Väisänen 2001). Earlier results demonstrated that urban birds appear to have markedly broader environmental tolerances than their rural congeners, and this broad environmental tolerance may predispose some birds to thrive in urban habitats (Bonier *et al.* 2007). Species with broad environmental tolerances are less sensitive to human disturbance than those with narrower environmental tolerances (e.g. generalists *vs.* specialists; omnivores *vs.* insectivores). According to our results, the features of the common species wintering in residential areas include broad environmental tolerance and the ability to use winter feeding stations. It is probable that abundant food resources and their low frequency of fluctuation favour these core species (*see* Anderies *et al.* 2007).

Influence of type of residential area on wintering bird communities

Only few bird species were detected in the apartment-building areas. This result corresponds well to that of Smith (2003), who indicated that wintertime bird diversity was at its lowest in the most urbanized areas of Ontario, Canada. Some species observed in the villages or familyhouse areas were not detected in the apartmentbuilding areas. These species were mainly scarce winter species. In addition, some species were less abundant in the apartment-building areas than in the family-house areas or villages (e.g. *Dendrocopos major, Pyrrhula pyrrhula, Parus montanus, Carduelis flammea*) (Appendix 1; "suburban-adaptable species" according to Blair 1996).

No single species was more abundant in the apartment-building areas than in the other two residential-area types. In general, the bird community structure of the apartment-building areas resembled that of bird communities in urban-core areas of towns and cities (Jokimäki & Kaisanlahti-Jokimäki 2003). The low abundance of birds in the apartment-building areas indicates the low value of these areas for wintering birds (*see* also Jokimäki *et al.* 2002, Jokimäki & Kaisanlahti-Jokimäki 2003). Winter-feeding studies indicate that the areas surrounding apartment buildings are of poor quality for wintering birds (Jokimäki *et al.* 1996, Jokimäki & Suhonen 1998). However, *Columba livia domestica* was missing from villages, and *Corvus corone cornix* overwintered in low numbers and only occasionally in some villages (Appendix 1; "urban exploiters" according to Blair 1996). One obvious reason for the avoidance of villages by these species might be the lack of anthropogenic food sources. In general, the number of species benefiting from urban habitats (i.e. species whose abundance was higher in the apartment-building areas) was lower than the number of urban-avoiders (i.e. species whose abundance was lower in the apartment-building areas than in other habitats): two and nine, respectively (*see* also Palomino & Carrascal 2006).

The proportion of individuals of resident bird species was higher in the apartment-building areas than in the other two types of residential areas. This result supports the earlier observation that urbanization favours resident species (Jokimäki & Suhonen 1998, Chace & Walsh 2006, Kark et al. 2007). However, the proportion of individuals of feeding-table species was higher in the villages than in the apartmentbuilding or family-house areas. We propose that in less urbanized habitats such as villages, feeding tables are more important for overwintering species than they are in towns where the microclimate is warmer. However, this requires more research. The proportion of individuals of coniferous-forest bird species was lower in the apartment-building areas than in the villages, which supports the observation that coniferousforest species avoid urban environments (Gilbert 1989, Jokimäki & Suhonen 1998, Savard & Falls 2001).

Factors affecting bird species abundance in residential areas

Our results demonstrate that winter feeding could play an important role in structuring and transforming of winter bird fauna at least in northern regions (*see* also Jokimäki & Suhonen 1998, Parsons *et al.* 2006, Fuller *et al.* 2008). We found that the bird species richness and the numbers of birds increased with increasing numbers of winter feeding stations. Especially *Parus montanus*, *Parus major*, *Parus caeruleus*, *Passer domesticus*, and *Carduelis flammea* benefited from increased numbers of feeding stations. All of these species were classified by Väisänen (2001) as being the most common and abundant winter-feeding-site species within the study area. Winter feeding of birds increased greatly in Finland during the years 1989-2007 (Väisänen 2008). At the same time, food offered to birds has become more diverse. In fact, intensified and diversified winter feeding has been reported to be the foremost factor affecting long-term changes in Finland's winter bird fauna (Väisänen 2001, 2003). Also in Britain, over half of the studied species increased their occurrence in feeding places in gardens between the years 1970 and 2000 (Chamberlain et al. 2005). In the recent decades, the distribution ranges of many winter bird species (e.g. Parus caeruleus and Carduelis chloris) have expanded towards to the north and the abundance of these species has increased in Finland mainly because of intensified feeding with energy-rich sunflower seeds (Väisänen 2001, 2003, 2008). Our results indicate that intensified winter feeding has enabled range expansions of southern bird species towards the north rather than increased the survival possibilities of already common species. Although birds of towns and cities in the world are now provided with supplementary food, quite little is known about benefits or disadvantages of this practice (Jones & Raynolds 2008). Recently, there has been discussions as to whether winter feeding is actually beneficial to birds (Shochat 2004). It has been suggested that feeding birds promotes the spread of diseases (Brittinham & Temple 1988), favours aggressive species (Parsons et al. 2006), and results in malnourishment (Cannon 1999). Winter feeding of birds has been reported to increase the reproductivity of birds in the subsequent breeding season (Robb et al. 2008). However, according to results obtained in Finland, the average clutch and fledgling production of Parus major and Parus caeruleus urban populations were lower than in rural populations (Solonen 2001). Most probably, poor quality of food before the breeding season in urban habitats was responsible for the low breeding success of urban tits.

According to our results, bird species richness and the total number of individuals decreased with elevated levels of urbanization. At the species level, the proportion of apartment-building areas affected negatively the average abundances of Parus major, Passer domesticus, and Carduelis flammea, and positively Columba livia domestica. Hence in northern Finland, only few species (e.g. Columba livia domestica) appear to benefit during winter from heavily-urbanized landscapes. According to our results, even a globally-urbanized species like Passer domesticus appears to avoid apartment-building areas. However, we did not directly analyse the effects of parks, woodlands or more natural areas on wintering urban bird communities. The distance from the urban core of the town of Rovaniemi has a negative impact on the abundance of Corvus corone cornix. It is possible that crows do not find enough anthropogenic food (household refuse) in villages and other less-urbanized areas. Indeed, many corvids, e.g. Pica pica, have been reported to benefit from these anthropogenic food resources (Jerzak 2001, Marzluff et al. 2001b).

The abundance of the human population had a negative effect on two species: *Dendrocopos major* and *Carduelis flammea*. This result is quite difficult to interpret. Perhaps the fact that trees, whose seeds those species depend on in winter (coniferous and deciduous trees, respectively), are scarce in highly populated areas, is the reason for the afore-mentioned effect. Thus, for a bird to have a specialist way of life is disadvantageous when living in urban environments (Devictor *et al.* 2007).

We are aware of the potential limitations of a single-visit method (Wiens 1981, Jokimäki & Suhonen 1998, Jokimäki & Kaisanlahti-Jokimäki 2003) which, for practical reasons (short midwinter days, long distances, and single observer), we were forced to use. However, the results of Jokimäki and Kaisanlahti-Jokimäki (2003) obtained when conducting a five-visit winter study in residential areas in northern Finland demonstrated relatively low variation (CV%) of species richness in apartment-building (8%) and family-house (5%) areas; the variations in the total numbers of individuals were 25% and 16%, respectively. Of course, no survey method is free from sampling errors, but we assume that the census efficiency in residential areas is relatively high and does not vary greatly between habitats (Jokimäki & Kaisanlahti-Jokimäki 2003).

Conclusions

According to our results, residential areas in northern latitudes are important wintering habitats for many bird species. Winter feeding is one of the main factor attracting birds to residential areas during the winter. Another possible positive factor could be the milder micro-climate in residential areas when compared with that of the surrounding natural habitats. However, the value of the site for bird species differed between the types of residential area (see also Smith 2003). Apartment-building areas had fewer overwintering species and individuals than family-house areas or villages. This partly indicates that highly urbanized areas with many high buildings are disadvantageous for wintering birds. In addition, the increasing proportion of apartment-building areas within the study area resulted in a decrease in bird species richness and abundance. The species composition within the apartment-building areas was a subset of the species composition of other habitat types. Bird species richness and total number of individuals increased with increasing number of feeding stations, which is indicative of the importance of winter feeding in residential areas in northern latitudes. Most of the common and abundant species observed in the residential areas were resident, human-associated or forestgeneralist species able to access winter feeding stations. Winter feeding may increase both the species richness as well as the number of individuals in residential areas in northern latitudes. Therefore, winter feeding could be a good option for increasing urban-bird diversity during winter at least in northern latitudes. Some species commonly observed in the study area, but which were absent from residential areas, were coniferousforest bird species. The use of evergreen coniferous plant species could improve the overwintering possibilities of bird species belonging to this guild. We recommended carefully planned winter feeding programmes, saving natural-forest remnants, and increasing the number of coniferous trees as means towards increasing overwintering possibilities of birds in northern latitudes, and thus increasing the biodiversity of residential areas. However, in larger towns and cities, factors such as distance from the urban centre may be more powerful explanatory variables than was

found in this study. Indeed, the size of the urbanized area has proved to have an effect on bird communities (Jokimäki & Kaisanlahti-Jokimäki 2003, Garaffa *et al.* 2009). For example, in cities with human populations in excess of one million (Fuller *et al.* 2008), the distance from the urban centre is a modifying factor.

Our results clearly show that residential areas attract bird species because of their high and predictable amount of food during the winter season. However, more detailed predictions related to the credit card hypothesis (Shochat 2004), require further species-level survival and reproduction studies both during the winter and breeding seasons.

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Appendix 1. Numbers of winters (December–January, max = 5) the species were detected in different habitats and in the entire study area. Groups (based on Väisänen *et al.* 1998): RE = resident, PA = partly migratory, IN = invasive, S1 = short-distance migrant, and S2 = long-distance migrant. Preferred habit associations (based on Väisänen *et al.* 1998): HA = human associated, FG = forest generalist, FD = forests, deciduous, FC = forests, coniferous, FO = forests, old-growth, MO = mountains, LO = lakes, oligothrophic, MI = mires, and AR = archipelago; FS (feeding site) = species commonly using feeders in the study area.

	Groups	Apartment- building areas	Family- house areas	Villages	Entire study area
SPECIES OBSERVED IN RESIDENTIAL AREAS					
Residential-area core species					
Pica pica	RE HA FS	5	5	5	5
Parus major	RE FG FS	5	5	5	5
Passer domesticus	RE HA FS	5	5	5	5
Parus caeruleus	RE FD FS	5	5	5	5
Carduelis chloris	PA HA FS	5	5	5	5
Town species					
Corvus corone cornix	PA HA	5	5	3	5
Columba livia	RE HA	5	4	0	5
Species avoiding apartment-building areas					
Carduelis flammea	PA FG FS	3	5	5	5
Parus montanus	RE FG FS	1	5	5	5
Dendrocopos major	IN FG	1	5	5	5
Pyrrhula pyrrhula	PA FC FS	2	4	5	5
Winter birds scarce in residential areas		_	-	-	-
Bombycilla garrulus	IN FC	1	2	4	5
Emberiza citrinella	PA HA FS	0	4	0	5
Garrulus glandarius	RE FC FS	0	0	3	5
Passer montanus	REHA	0	2	0	2
Carduelis hornemanni	PAMO	0	1	1	5
Glaucidium passerinum	RE FO	0	0	1	3
Turdus pilaris	S1 HA	0	0	1	3
Parus cinctus Boddaert	RE FO	0	0	1	5
Nucifraga caryocactes	RE FC	0	1	0	4
Loxia curvirostra	IN FC	0	1	0	2
SPECIES AVOIDING RESIDENTIAL AREAS	INTO	0	I	0	2
Species always wintering in the region					
Anas platyrhynchos	S1 LO	0	0	0	5
Accipiter gentilis	PA FO	0	0	0	5
Accipiter nisus	PA FC	0	0	0	5
Bonasa bonansia	RE FC	0	0	0	5
Lagopus lagopus	RE MI	0	0	0	5
Tetrao tetrix	RE FG	0	0	0	5
Tetroa urogallus	RE FO	0	0	0	5
Dryocopus martius	RE FO	0	0	0	5
Cinclus cinclus	RE LO	0	0	0	5
Parus cristatus	RE FC	0	0	0	5
Certhia familiaris	PAFO	0	0	0	5
Perisoreus infaustus	RE FO	0	0	0	5
Corvus corax	RE FG	0	0	0	5
Species observed in the region during severa		ũ	5	ũ	Ũ
winters, but rarely overwintering there	-				
Aegithalos caudatus	RE FD	0	0	0	5
Picus canus	RE FD	0	0	0	4
Parus ater	IN FC	0	0	0	4
Cygnus cygnus	S1 LO	0	0	0	4
Bucephala clangula	ST LO	0	0	0	3
	51 LU	0	0		ontinued
				C	onunued

Appendix 1. Continued.

	Groups	Apartment- building areas	Family- house areas	Villages	Entire study area
Aquila chrycaetos	PA FO	0	0	0	3
Aegolius funereus	IN FC	0	0	0	3
Picoides tridactylus	RE FO	0	0	0	3
Turdus merula	S1 FD	0	0	0	3
Sitta europea asiatica	IN FD	0	0	0	3
Lanius excubitor	S1 MI	0	0	0	3
Corvus frugilegus	S1 HA	0	0	0	3
Loxia leucoptera	IN FC	0	0	0	3
Pinicola enucleator	RE FO	0	0	0	3
Species observed in the region					
only occasionally during winters					
Larus argentatus	S1 LO	0	0	0	2
Surnia ulula	IN FC	0	0	0	2
Sturnus vulgaris	S1 HA	0	0	0	2
Fringilla coelebs	S1 FG	0	0	0	2
Loxia pytyopsittacus	IN FC	0	0	0	2
Phalacrocorax carbo	S1 AR	0	0	0	1
Mergus merganser	S1 LO	0	0	0	1
Phasianus colchicus	RE HA	0	0	0	1
Grus grus	S2 MI	0	0	0	1
Streptopelia decaoto	RE HA	0	0	0	1
Bubo bubo	RE FC	0	0	0	1
Stix uralensis	RE FC	0	0	0	1
Stirx nebulosa	IN FC	0	0	0	1
Dendrocopos minor	RE FD	0	0	0	1
Erithacus rubecula	S2 FC	0	0	0	1
Turdus iliacus	S2 FG	0	0	0	1
Regulus regulus	PA FC	0	0	0	1
Carduelis carduelis	PA HA	0	0	0	1
Carduelis spinus	PA FC	0	0	0	1