The role of residential habitat type on the temporal variation of wintering bird assemblages in northern Finland

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Wintertime ecological studies conducted in different kinds of residential areas over several winters have thus far been lacking. The objective of this study was to analyze if the between-winter variability of bird communities differs between urban residential habitat types. The study was conducted in five blocks of flats areas, five single-family house areas, and five villages in Rovaniemi, northern Finland, during five winters. Birds were surveyed using a single-visit study plot (30 ha) method. The average between-winter variation (CV%) in bird species richness was 27% and in bird abundance was 53%, and these values did not differ between the three types of residential areas. Temporal variation of species in residential areas was species-specific. The lowest between-winter variation was observed for omnivore or feeding table species such as the Great tit *Parus major* (50%), Magpie *Pica pica* (53%) and House Sparrow *Passer domesticus* (76%). The highest variation was observed for berry-eating species, such as the Bullfinch *Pyrrhula pyrrhula* (196%) and Waxwing *Bombycilla garrulus* (192%). The between-winter variation (CV%) of abundance of most species was greater in the blocks of flats areas than in the other residential-area types. The between-winter average qualitative similarity was 76.1% in the blocks of flats areas, 80.0% in the single-family house areas, and 78.0% in the villages, and these values did not differ between types of residential areas or between study winters. Stability of winter communities decreased from the centre to the periphery of Rovaniemi. We suggest that the stabilizing, warmer microclimate near the urban core of the town partly explains this result. The average species turnover rate (%) in the block of flats areas was 22.8, in single-family house areas was 20.5, and in the villages was 21.6. In general, the lowest between-winter similarities, highest species turnover rates, and the highest between-winter variation of abundance of individual species were observed in areas of blocks of flats. Our results suggest that single-family house and village areas are better overwintering areas for wintering birds than areas of blocks-of-flats. Intensive winter feeding might stabilize the between-winter variation of bird assemblages especially in single-family house areas. In addition, the warmer microclimate near the urban core might probably also stabilizes variation in residential bird assemblages.

1. Introduction

Large areas have come under a strong human influence through urbanization, and even larger areas will be affected in the future. Hence the various ways of how urbanization affects ecosystems and the ecology of animals becomes increasingly important. Many ecological effects of urbanization have been recognized, including changes in resources, disturbance regimes, habitat distribution, and species composition (Rebele 1994, Turner *et al.,* 2004, Alberti 2005).

Urban environments differ from more natural ecosystems in many ways. For example, microclimatic conditions in urban areas can be more favorable than in rural areas for animals living there (Gilbert 1989, Rebele 1994). Urban areas are also characterized by high levels of disturbances and environmental modifications, which can affect bird populations and characteristics of communities (Gilbert 1989, Blair 1996, Fernandéz-Juricic & Jokimäki 2001). These factors can cause both spatial and temporal variation in bird communities.

During the breeding season, urbanization can decrease bird species richness (Beissinger & Osborne 1982, Bezzel 1985, Marzluff 2001; for a review, see Chace & Walsh 2006). Occasionally, however, species richness can peak at intermediate levels of development (e.g., Jokimäki & Suhonen 1998), increase the total abundance of birds, and favor the occurrence of some superabundant bird species, causing a general homogenization of communities (e.g., Clergeau *et al*. 2006). The structure of urban bird communities can differ between land-use types and practices (DeGraaf & Wentworth 1986, DeGraaf 1991, Jokimäki *et al*. 1996, 2002, Germaine *et al*. 1998, Hostetler & Knowles-Aanez 2003, Jokimäki & Kaisanlahti-Jokimäki 2003, Caula *et al*. 2008, Fuller *et al*. 2008). Suburban areas with residential developments and gardens in general are particularly species-rich areas (Leveau & Leveau 2005, Chamberlain *et al*. 2007).

While breeding bird communities have received research attention in urban environments (Marzluff *et al*. 2001), wintertime bird studies are scarce (but see DeGraaf 1991, Jokimäki *et al*. 1996, 2002, Jokimäki & Suhonen 1998, Chamberlain *et al*. 2005, Smith 2007). This is surprising, as

winter is the most critical season for many birds, and the primary goal of birds in winter is to find most favorable conditions or sites for survival, especially at high latitudes. Indeed, human settlements attract birds in winter time (Nuorteva 1971, DeGraaf & Wentworth 1986, Jokimäki *et al*. 1996, Jokimäki & Suhonen 1998). Another shortcoming of urban bird research is that, although the spatial component has received considerable attention (Marzluff *et al* 2001), temporal patterns, i.e., between-year variation of urban winter bird communities, have seldom been studied (but see Väisänen & Solonen 1997, Jokimäki & Suhonen 1998, Väisänen 2000, 2001, 2003, 2008, Cannon *et al*. 2005, Suhonen *et al*. 2009).

Several factors have been reported to affect community stability, which is likely to depend on the physical and temporal habitat changes and on the interactions between species in a community (Bengtsson *et al*. 1997, Gaston & Spicer 1998). Also the unpredictability and productivity of the environment can affect community stability (Gaston & Spicer 1998). Järvinen (1989) noted that variable environments are not necessarily unpredictable. Studies concerning the relationship between ecosystem productivity and community stability are rare, but their results do not support the hypothesis that ecosystem productivity increases community stability (Järvinen 1979, Bethke 1993).

Urban areas, with their anthropogenic food resources, low species richness with dominance of a few species, warmer microclimate, high levels of disturbance, and environmental modifications can provide insights on factors affecting temporal stability of communities (Shochat *et al*. 2006). Because urban environments are novel for birds, considering the evolutionary time scale, urban areas provide a suitable model system for testing evolutionary hypotheses as well as for modeling community structure and dynamics (Fernandez-Juricic & Jokimäki 2001).

The main objectives of the present study were (1) to analyze between-winter variation of overwintering bird assemblages (CV% values between winters, between-winter similarities and turnover rate, including extinction ["departures"] and colonization rates ["arrivals"]), and (2) to determine whether the residential-area type impacts the temporal variation of overwintering bird communi-

Table 1. Characteristics of the blocks-of-flats areas, single-family house areas, and villages studied in this research.

Area/ Site name	No. inhabitants 2001/2004	Distance to town centre (km)	% cover					No. feeders 1998/ 2003
			Blocks-of-flats	Single-fam. houses	Wooded parks	Open areas	Roads	
Blocks-of-flats areas								
Ounasrinne	1,341/1,363	3.8	58	0	8	10	23	3/1
Rantavitikka	1,021/1,063	1.9	43	1	7	14	34	1/4
Asemieskatu	590/642	1.2	53	3	10	12	22	2/0
Sudentie	1,055/1,009	3.9	44	0	10	10	36	0/0
Hillapolku	1,029/1,005	2.8	52	0	7	12	28	6/3
Single-family house areas								
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	1,096/1033	21.3	14	20	30	6	30	3/5
Saarenkylä	980/1137	2.7	0	40	5	25	30	3/3
Ylikylä	1,381/1,221	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

ties. Because of intensive winter feeding and other anthropogenic food sources, residential areas may be productive and predictable environments for wintering birds. Hence, we predicted that the residential winter-bird communities would be relatively stable (e.g., Suhonen *et al.* 2009). However, resource availability, and therefore also the stability of the winter-bird assemblages, might differ between types of residential areas. We predicted that residential areas with many feeding stations might have lower between-winter variability of bird assemblages than areas with few feeding stations. Because the microclimate of residential areas might depend on the distance to the urban core of the town (more favorable conditions near the urban core), the variation of bird assemblages may be lower in residential areas located nearer the urban core than in areas located further away. We also predicted that the between-winter variation in abundances of urban-adapted generalist species should be lower than the variation of other species.

2. Material and methods

2.1. Study area

The study was conducted during 1998/1999–2003/2004 in Rovaniemi, northern Finland (66°N, 25°E). The land area of the study region is 7,601 km^2, with about 60,000 inhabitants throughout the study period (Statistics Finland 1998, 2003). Eighty-three percent of inhabitants (about 49,000) were concentrated in the urban city of Rovaniemi, and there were about 20 small villages with a few hundred to a thousand inhabitants in the Rovaniemi area. Because of the large land area, the average human population density was only about eight inhabitants/km^2. The matrix around the human settlements is mainly covered by forests (over 60%), and the proportion of agricultural areas is low and restricted around the villages. Most of the forests (86%) are dominated by the Scots Pine (*Pinus sylvestris* L.).

In the area of Rovaniemi, we selected three types of residential areas: blocks-of-flats areas, single-family house areas, and villages. Each habi-

Table 2. Average monthly temperature (°C) and snow depth (cm) in Rovaniemi during the five study winters. Data from the Finnish Meteorological Institute 1998–2004.

Month	1971–2000		1998/1999		1999/2000		2000/2001		2002/2003		2003/2004	
	Temp	Snow	Temp	Snow	Temp	Snow	Temp	Snow	Temp	Snow	Temp	Snow
October	0.2	2	1.2	0	1.7	0	4.7	0	–2.4	0	0.5	0
November	–6.1	4	–8.0	38	–3.2	10	–1.4	0	–10.3	7	–3.0	1
December	–10.0	29	–9.6	33	–12.4	37	–7.7	17	–13.6	31	–8.1	8
January	–11.7	46	–14.6	62	–10.1	63	–6.3	44	–17.2	59	–9.7	31

tat type had five replicates. The blocks-of-flats areas and single-family house areas are located within the urban city core with a population density of about 370 inhabitants/km^2, whereas the villages are located in the rural area with human population density of about 3 inhabitants/km^2 (Statistics Finland 1998, 2003). The matrix surrounding the blocks-of-flats and single-family house areas were urban-dominated, whereas the matrix surrounding villages was either agricultural or forest land.

For each study plot (30 ha in area), we estimated the proportion of the area of blocks of flats (with buildings ≥ three stories), the proportion of single-family house areas, wooded parks, open areas and roads, using town maps (scale 1: 4,000) and field notes. The number of inhabitants was derived from the statistics of Rovaniemi. The distance between the center of each study plot to the urban core of Rovaniemi (i.e., the most urbanized area, which is also the historical centre of the town) was measured using the maps. Basic features of each study site are given in Table 1. Based on habitat structure, the blocks-of-flats areas were most urban, the single-family house areas were moderately urban, and villages were the least urban (Table 1). The general structure of the study plots did not significantly change during the study period.

Snow fall begins in the study area between October and November, and the temperature drops below 0°C at the beginning of November (Table 2; Finnish Meteorological Institute 1998–2004). The average temperature during December is about –10.0°C and –11.7°C during January (Finnish Meteorological Institute data base). The average snow depth is on average 29 cm during December and 46 cm during January (Finnish Meteorologi-

cal 1998–2004). According to the meteorological data, winter weather stabilizes to mid-winter conditions at the beginning of December.

Rowanberry (*Sorbus aucuparia*) crop size may affect wintering bird assemblages (Fox *et al.* 2009, Lehikoinen *et al.* 2010). Therefore, we obtained data of the early autumn (September–October) and mid-winter (25.12.–7.1.) rowanberry crops for the study area from the national winter-bird monitoring database (Finnish Museum of Natural History, University of Helsinki, Finland). These data come from seven winter-bird survey routes located in residential areas of Rovaniemi. A median value of rowanberry abundance in different routes surveyed per winter was used as an estimate of early-autumn and mid-winter (i.e., our survey period) abundance of rowanberry crop (0 = no data; 1 = no berries; 2 = very few berries; 3 = few berries; 4 = quite many berries; 5 = abundant berries; and 6 = superabundant berries).

2.2. Bird surveys

The over-wintering birds were surveyed using the single-visit study plot method, with fixed 30-ha plots. All surveys were carried out during December–January in good weather, and during the part of the day when the light level allowed doing surveys, i.e., during 10:00–14:00. December–January represented the mid-winter season for birds, because the average monthly temperature is below –10°C, snow depth is at least 30 cm, and the rowanberry crop is basically depleted before the survey period. Therefore, no major changes in the wintering conditions of birds (e.g., climate, rowanberry crop) are predicted to occur during the survey period. The number of winter-feeding sta-

tions with available bird food ('active feeding stations') were counted during each survey for each study plot. According to the general guidelines about winter feeding of birds in Finland – which encourage people to continue feeding thorough the winter once it has been started – no significant changes in the abundance of active feeding stations should occur during the survey period.

We repeated surveys during five winters, i.e., during winters of 1998/1999–2003/2004. All bird individuals were identified to species level and counted, except over-flying birds that did not land in the study plot. The surveys were not fixed routes within the plots, but rather zig-zag walks covering the whole plot. Therefore, all sites, including backyard feeding stations, could be detected and observed by the surveyor. Because of the full coverage survey method, we assume that the detectability of species did not differ markedly between habitats or species. We used a consistent census rate of 10 ha/20 min to avoid double counts of individuals. The author JJ carried out 95% of surveys.

According to Jokimäki and Kaisanlahti-Jokimäki (2003), between-winter variation in the wintering bird species richness is 5–8%, and in the total number of individuals is 16–25% in northern Finnish residential areas. Although single-visit census studies have certain limitations (Wiens 1981, Jokimäki & Suhonen 1998, Jokimäki & Kaisanlahti-Jokimäki 2003), we used the method for practical reasons, i.e., to obtain sufficiently high number of spatial replicates for statistical analysis, the short mid-winter days, long distances between study plots, and the fact that most bird data were collected by a single observer. We believe that the method did not severely bias our results, as the short-term fluctuation during one winter are relatively low in Finnish town centers in terms of species richness and number of individuals (15% and 24%, respectively; Jokimäki & Suhonen 1998). Our census efficiency in residential areas was relatively high (see above) and did not vary markedly between the residential habitat types (Jokimäki & Kaisanlahti-Jokimäki 2003).

2.3. Statistical methods

Percentage variables were arcsin-transformed in order to normalize residuals. Because we used a fixed sampling design (fixed study-plot size, fixed survey speed, and a constant amount of samples from different residential areas within winters), there was no need for transformations for the species richness estimate, e.g., by using rarefaction method. We used the coefficient of variation index (CV%) to study the between-year variation in urban bird populations. For CV%, the standard deviations of bird numbers of different study years are divided by their average numbers and multiplied by 100. Higher index values indicate higher variability in bird abundance or species richness. Only species with >25 individuals were used in statistical tests when analyzing between winter variation in the abundances of the most abundant bird species.

Species turnover (ST) was calculated by using the following formula:

$$ST = (I + E)/(S1 + S2) \qquad (1)$$

where I and E are the number of species immigrations and extinctions, respectively (arrivals and departures) between study winters, S1 is the number of species in sample 1, and S2 is the number of species in sample 2 (Magurran 1988).

Sörensen qualitative community similarity (SI) was calculated by using the following formula:

$$SI = 2c/(a+b) \qquad (2)$$

where c = number of shared species, a = total number of species in community a and b = total number of species in community b (Magurran 1988).

Kruskall-Wallis test was used to compare bird communities between residential habitat types. Tukey-type a posteriori tests were used for paired comparisons (Zar 1984). Correlation analyses were conducted using Spearman rank correlation tests. Values in brackets are mean ± SD. Linear regression was used to study the relationship between bird richness or abundance and winter conditions (temperature, snow depth) or the amount of rowanberry crop. All analyses were performed with SPSS for Windows version 14.0. Detailed survey data are available from the authors upon request.

Table 3. Bird species with over 5% of the total abundance of all observed birds in the blocks-of-flats areas, single-family house areas, and villages. Numbers in the columns are percentages of the total abundance of birds in different residential-area types.

Species	Blocks-of-flats	Single-f. houses	Villages
House Sparrow	32.1	26.1	22.6
Great Tit	25.0	21.0	14.3
Magpie	12.4	9.7	6.7
Feral Pigeon	9.1	<5.0	<5.0
Greenfinch	6.6	13.3	6.9
Redpoll	<5.0	14.8	8.2
Blue Tit	<5.0	5.7	<5.0
Waxwing	32.6	<5.0	<5.0

3. Results

A total of 21 species with 5,125 individuals were detected during the study winters. Twelve species (748 individuals) were observed in the blocks-of-flats areas, 17 species (1,828 individuals) were observed in the single-family house areas, and 16 species (2,549 individuals) were observed in the villages. The number of dominant bird species (at least 5% of the total number of individuals) varied between five and six, and they made up between 85.2 and 91.3% of the total number of individuals (Table 3). The House Sparrow *Passer domesticus*, Great Tit *Parus major*, Magpie *Pica pica* and Greenfinch *Carduelis chloris* were among the numerically dominant bird species in all three types of residential area (Table 3).

No significant differences in winter temperatures, snow depth, number of feeding stations per study plot and rowanberry crop size was observed between the study winters ($P > 0.05$). However, the number of active feeding stations was higher in the single-family house areas (6.36 ± 2.80) than in the blocks-of-flats areas (1.40 ± 1.61) or in the villages (3.92 ± 1.85) ($F_{2,72} = 33.4$, $P > 0.001$).

3.1. Between-winter variation in species richness and total abundance

The average species richness differed between the five winters ($\chi^2 = 14.60$, df = 4, $P = 0.006$). More species were observed during 2002/2003 than during 2003/2004 and 1999/2000 (8.13 ± 1.99, 5.47 ± 2.13 and 5.73 ± 1.91, respectively; $P < 0.05$). The average number of individuals was only slightly different between the five winters ($\chi^2 = 7.86$, df = 4, $P = 0.097$). Winter temperatures or snow depth did not significantly affect species richness or total abundance (linear regression; $P > 0.05$). The abundance of rowanberry crop before (September–October) and during (25.12.–7.1.) the bird survey had a detectable albeit slight impact on the species richness of wintering birds ($F_{1,3} = 5,85$, $P = 0.094$ and $F_{1,2} = 11.95$, $P = 0.041$, respectively).

In the pooled data, CV% in bird species richness was 27 ($n = 15$) and in total bird abundance was 53 ($n = 15$). CV% of the species richness and total abundance of birds did not significantly vary between the three types of residential areas ($P > 0.05$). Characteristics of the survey plots (human population size, distance to the town centre, proportion of blocks-of-flats, number of active feeding stations) did not significantly affect between-winter variation in species richness or total number of individuals (Table 4).

3.2. Between-winter variation in the abundance of individual bird species

According to the pooled data with the most abun-

Table 4. Spearman rank correlations between study-plot characteristics and CV% of the bird community. *N* = 15 in all cases, * = *P* < 0.005. See text for details.

Variable	Richness	Abundance	Similarity	Turnover
Human population	−0.082	0.050	0.300	0.263
Distance from town centre	0.281	0.288	0.597*	0.002
Proportion of blocks of flats	−0.009	−0.107	−0.041	−0.225
Number of feeding stations	−0.036	0.009	−0.406	−0.066

dant bird species (>25 individuals), the highest CV%'s were observed for the Bullfinch (196) and Waxwing *Bombycilla garrulus* (192), and the lowest values were observed for the Great Tit (50%), Magpie (53), and House Sparrow (76). CV% values for the other species varied between 102 and 179. Between-winter CV% of all abundant bird species decreased with the mean abundance of active feeding stations per study plot. However, this result was statistically significant only for the House Sparrow and Blue Tit *Parus caeruleus* (r_S = –0.561, P = 0.029, n = 15 and r_S = –0.601, P = 0.023, n = 14, respectively).

CV% values of many species were higher in the blocks-of-flats areas than in the other types of residential areas (Appendix 1). The CV% differed between types of residential areas for the House Sparrow (χ^2 = 6.21, df = 2, P = 0.045), Blue Tit (χ^2 = 5.87, P = 0.053) and Redpoll *Carduelis flammea* (χ^2 = 4.71, P = 0.095). However, the a posteriori comparisons revealed statistically significant differences between residential-area types only for Blue Tit, its abundance variation being greater in the blocks-of-flats areas than in the single-family house areas (P < 0.05).

3.3. Between-winter similarities of bird communities

The between-winter SI was 76.1% ($\pm$ 11.0; n = 20) in the blocks-of-flats areas, 80.0% ($\pm$ 8.1; n = 20) in the single-family house areas, and 78.0% ($\pm$ 12.2; n = 20) in the villages. The three area types did not differ from each other statistically significantly (χ^2 = 0.95, df = 2, P = 0.622) and neither did the five winters (χ^2 = 3.27, df = 3, P = 0.351). According to the linear regression, neither species richness nor the total abundance of birds impacted the SI value ($F_{1,58}$ = 0.367, P = 0.547 and $F_{1,58}$ = 2.090, P = 0.154, respectively). The CV% of the SI index increased with increasing distance to the town centre (Table 4).

3.4. Between-winter species turnover rates in bird communities

The average species turnover rate (ST%) in the blocks-of-flats areas was 22.8% ($\pm$ 10.3, n = 20), in the single-family house areas was 20.5% ($\pm$ 7.72, n = 20), and in the villages was 21.6% ($\pm$ 11.0, n = 20). ST% did not show statistically significant differences between the three types of residential areas (χ^2 = 0.409, df = 2, P = 0.815) or between the five winters (χ^2 = 2.078, df = 3, P = 0.556). According to the linear regression, neither the species richness nor the total abundance of birds significantly impacted on the ST ($F_{1,58}$ = 0.094, P = 0.760 and $F_{1,58}$ = 0.877, P = 0.353, respectively). Plot characteristics did not significantly affect CV% of the ST index (Table 4).

3.5. Species departures and arrivals

A total of 27 species departures were observed in the blocks-of-flats areas, 39 in the single-family house areas, and 27 in the villages (Appendix 2). A total of 26 species arrivals were observed in the blocks-of-flats areas, 30 in the single-family house areas, and 30 in the villages. The highest numbers of departures and arrivals (at least 15 observations) were observed for the Hooded Crow (*Corvus corone cornix*), Redpoll, Feral Pigeon (*Columba livia domestica*), Willow Tit (*Parus montanus*), Blue Tit, Bullfinch and Greenfinch (Appendix 2). The largest numbers of departures were observed for the Redpoll, Hooded Crow, Willow Tit, and Bullfinch. No departures or arrivals were observed for the Great Tit and the Magpie.

4. Discussion

Our results indicate that the stability of winter-bird communities decreased from the centre of the town towards the periphery of the town, i.e., urbanization might reduce variation in wintering bird assemblages (Suhonen *et al.* 2009). This can be partly due to the more favorable micro-climatic conditions (higher temperature and less snow) nearer the city center. For example, during winter nights, temperatures at the centre of Rovaniemi can be 6°C higher than in peripheral areas of the town (J. Jokimäki, unpubl. data). Perhaps also abrupt snowfalls or low temperatures might have more severe impacts on wintering birds in more southern areas than in our study areas located at

northern latitudes. Yet another factor is winter feeding (see below).

Neither temperature nor snow depth during and before the survey period had a significant impact on the species richness or abundance of wintering birds in the study area. This might be partly an artifact related to our study design. We did not have plot-specific data about temperature and snow depth, and our meteorological data included only five winters. In a farmland area in Poland, the number of wintering species and the total number of birds were negatively correlated with snow depth (Goławski & Kasprzykowski 2010).

Interestingly, the total abundance of individuals did not markedly differ between the study winters, whereas more species were observed during 2002/2003 than during 1999/2000 and 2003/2004. This finding might be partly explained by richness variation in berry-eating specialists: the crop size of rowanberry during both early autumn (superabundant) and the survey period (abundant) was greater during winter 2002/2003 with high species richness than during the low species-richness winters 1999/2000 and 2003/2004 (very few or no berries). Rowanberries appear important sources of food for Finnish berry-eating bird species, such as the Bullfinch and Waxwing (Fox *et al.* 2009, Lehikoinen *et al.* 2010). Regrettably we were unable to directly study this topic, because our bird data consisted of material from a spatially restricted area, whereas the rowanberry data came from a much larger area.

The average between-winter variation (CV%) in bird species richness was 27% and in bird abundance was 53%. These values are higher than those reported in a nation-wide study conducted in Finland (10% and 22%, respectively; Jokimäki & Suhonen 1998). However, Jokimäki and Suhonen (1998) considered mainly town centers, while we focused on a variety of residential areas. As only a few bird species are adapted to the most urban areas, the variation in avian assemblage structure in urban cores may be lower than in the residential suburbs with more overwintering species.

We did not observe significant temporal variation either in species richness or in the total abundance of birds between the types of residential areas. However, within the area types, variation in both species richness and the total number of individuals was high. In addition, the species turnover rate varied greatly within the types, being 7.7–45.5% in the blocks-of-flats areas, 7.6–38.5% in the single-family house areas, and 0–41.7% in the villages. These results indicate that local characteristics of residential areas (e.g., abundance of feeding stations) might have an important influence on the temporal variation of residential bird communities (see also Daniels & Kirkpatrick 2006, Murgui 2007).

Our results suggest that winter feeding stabilizes the between-winter abundance variation for many species of northern latitudes, particularly the Blue Tit and House Sparrow. However, the between-winter variability of species in residential areas was species-specific. Our data support the hypothesis that specialist bird species show greater between-winter variation in abundance, and have higher annual departure and turnover rates than have omnivorous or generalist bird species. Indeed, species with many departures were mainly seed-eating specialists or berry eaters, whereas species with a more constant presence were omnivores and such that are able to use feeders, such as the Blue Tit, Great Tit, Magpie, and House Sparrow. On the other hand, the high departure and arrival numbers of the Hooded Crow, Feral Pigeon, Blue Tit and Greenfinch might be related to fact that these species rarely over-winter at the Arctic circle, and all are currently trying to expand their current regional or local distribution ranges from their "source" town area towards villages and other residential areas located at the periphery of Rovaniemi (authors' pers. obs.).

Specialist bird species may thus have higher annual departure and turnover rates than generalist bird species have, but these differences may also depend on the level of urbanization (cf. Devictor *et al.* 2007). Correspondingly, powerful urban competitors can benefit from the low-frequency resource fluctuation in urban environments (Anderies *et al.* 2007). It is notable that species showing least abundance fluctuations in our data are common and abundant winter birds in urban areas around Europe (Thompson *et al.* 1993, Konstantinov *et al.* 1996, Jokimäki *et al.* 2002). However, the between-winter variation of many species, such as the House Sparrow, Blue Tit and Redpoll, differed between residential area types, and this variation was greater in the blocks-of-flats areas than in the other area types. Blocks-of-flats areas

may thus be suboptimal overwintering areas for many bird species.

The detected assemblage structure was relatively constant between study years and residential area types, which may have resulted from several reasons. The between-winter average qualitative similarity was 76–80% and the average species turnover rates in the residential areas were only about 20%. These values did not markedly vary between study winters or residential area types, agreeing with the results of a larger-scale study conducted in urban cores of human-dominated settlements in Finland (Jokimäki & Kaisanlahti-Jokimäki 2003). This low temporal variation in winter bird assemblages may have resulted from several reasons, of which the most obvious is that only a few species are adapted to life in urban habitat types. The numbers of such species outnumber other species all over the world, thus leading to homogenization of assemblages (Clergeau *et al.* 2006, Blair 2001, Sorace & Gustin 2008). These ubiquitous generalist species undergo little variation in population size and are more likely to be present in a community than are highly variable species, which contributes to the low variability in community turnover (Devictor *et al.* 2007).

Another important factor stabilizing the residential winter-bird communities is winter feeding (Suhonen *et al.* 2009), which increases the "productivity" and correspondingly the predictability of the residential-area environment for over-wintering. Urban areas are characterized by abundant, diverse and predictable winter-time resources partly due to the extra food provided by humans (Jokimäki & Suhonen 1998, Marzluff *et al.* 2001, Jokimäki & Kaisanlahti-Jokimäki 2003, Chamberlain *et al.* 2005, Jones & Reynolds 2008, Robb *et al.* 2008). These resources might decrease the temporal variation in urban bird communities. In Finland, the most abundant over-wintering species are able to use winter feeders (Jokimäki & Suhonen 1998, Jokimäki & Kaisanlahti-Jokimäki 2003), and wintertime feeding significantly shapes the winter-bird fauna (Jokimäki & Suhonen 1998; Parson *et al.* 2006, Fuller *et al.* 2008). Indeed, our results support this suggestion, as the between-winter variation of species seemed to decrease with increasing amount of active feeding stations. We also observed the lowest between-winter similarities and highest turnover rates in the abundance of individual species in apartment block areas, which had the least feeding stations. These results suggest that single-family house areas and villages are better over-wintering areas for birds due to resource predictability. That the stability of residential winter-bird assemblages decreased outwards from the town centre supports this pattern at least indirectly; also the microclimatic conditions might impact the between-winter variability of wintering bird assemblages (e.g., Goławski & Kasprzykowski 2010).

As we have demonstrated above, urbanization and development of residential areas may stabilize winter-bird assemblages. The Finnish long-term winter bird monitoring program suggests that the annual population fluctuations of many species are relatively similar in different parts of Finland (Väisänen 2000). Hence the fact that our data come from a geographically restricted area (7,601 km^2) may only slightly limit the generality of our findings at the national scale. The between-winter variation of bird assemblages in residential areas varies according to the type of residential areas, as well as with the distance from the urban core of the town. Variation in resource availability due to, e.g., the density and quality of feeding stations may partly explain this result.

The low turnover rate and high similarity in the winter bird assemblage structure between winters indicate that residential areas are predictable overwintering habitats for these birds. We suggest that the high amount and predictability of food due to the winter feeding, and favorable micro-climatic conditions in residential areas located near the town centre, at least partly explain these results. More importantly, our results also indicate that factors other than resource availability are important.

Asutustaajaman tyyppi vaikuttaa linnuston talvienväliseen vaihteluun

Talvilinnuston vuosien välistä vaihtelua asutustaajamissa tutkittiin Pohjois-Suomessa Rovaniemellä. Talvilinnut laskettiin viitenä talvena (1998/1999–2003/2004) viideltä omakotitalo-, kerrostalo- ja kyläalueelta. Vakioiduilla koealoilla havaittiin kaikkiaan 21 lajia (5 125 yksilöä). Kerrostaloalueilla havaittiin kaikkiaan 12 lajia (748), omakotitaloalueilla 17 lajia (1 828) ja kylissä 16 lajia (2 549).

Asutustaajamien talvilinnuston vuosienvälinen vaihtelu oli vähäistä: kokonaisyksilömäärän vaihtelu oli 53 % ja kokonaislajimäärän 27 %, eivätkä ne eronneet tilastollisesti talvien tai asutusaluetyyppien välillä. Havainto viittaa asutustaajamien mahdollisuuksiin tarjota vakaita talvehtimisympäristöjä talvilinnuille. Talven lämpötila- tai lumiolosuhteilla ei ollut merkitsevää vaikutusta talvilinnuston vuosienväliseen vaihteluun. Lajeilla, jotka hyödyntävät ruokintapaikkoja, talvienvälinen runsausvaihtelu oli vähäisempää kuin esim. erityisravintoa käyttävillä marjalinnuilla. Monien lajien talvienvälinen runsausvaihtelu oli suurempaa kerrostalo- kuin omakoti- tai kyläalueilla. Lisäksi lähempänä kaupungin keskustaa sijaitsevilla koealoilla vaihtelu talvilinnustossa oli vähäisempää kuin kauempana sijaitsevilla koealoilla.

Tutkimuksen tulokset osoittavat, että sekä asutusalueen tyypillä (kerrostaloalue, omakotitaloalue tai kylä), asutusalueen etäisyydellä kaupungin keskustasta, ruokintapaikkojen määrällä että pihlajamarjasadolla on vaikutusta asutusalueiden talvilinnuston vuosienväliseen vaihteluun. Tulosten mukaan omakotitalo- ja kyläalueet ovat parempia talvehtimisympäristöjä linnuille kuin kerrostalolähiöt. Intensiivinen talviruokinta etenkin omakotitaloalueilla näyttää vähentävän talvien välistä runsausvaihtelua sellaisilla lajeilla, jotka pystyvät hyödyntämään lintulautoja.

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Appendix 1. Minimum (Min), maximum (Max), mean values (Mean) and number of winters (n) of between-year variation in abundance (CV%) of bird species in different types of residential areas. – = species was not detected in a given residential type.

Species	Blocks-of-flats				Single-f. houses				Villages			
	Min	Max	Mean	n	Min	Max	Mean	n	Min	Max	Mean	n
Columba livia domestica Gmelin	125	197	160	4	139	224	195	5	–	–	–	–
Glaucidium passerinum L.	–	–	–	–	–	–	–	–	224	224	224	1
Dendrocopos major L.	136	136	136	1	91	224	150	4	37	137	88	3
Bombycilla garrulus L.	224	224	224	1	121	224	173	2	137	223	194	3
Turdus pilaris L.	–	–	–	–	–	–	–	–	224	224	224	1
Parus montanus Condrad	224	224	224	1	100	224	144	5	71	224	122	4
Parus cinctus Boddaert	–	–	–	–	–	–	–	–	224	224	224	1
Parus caeruleus L.	71	224	145	5	31	97	64	5	87	108	96	4
Parus major L.	32	74	57	5	26	63	42	5	20	108	51	5
Garrulus glandarius L.	–	–	–	–	–	–	–	–	148	224	186	2
Pica pica L.	42	109	58	5	34	52	41	5	41	80	58	5
Nucifraga caryocatactes L.	–	–	–	–	224	224	224	1	–	–	–	–
Corvus corone cornix L.	34	224	99	5	29	149	92	5	100	224	183	3
Passer domesticus L.	57	141	105	5	35	73	54	5	52	91	69	5
Passer montanus L.	–	–	–	–	137	137	137	1	–	–	–	–
Carduelis chloris L.	100	153	124	5	58	129	99	5	65	154	102	4
Carduelis flammea L.	163	224	204	3	85	224	132	5	107	172	143	5
Carduelis hornemanni Holboell	–	–	–	–	224	224	224	1	224	224	224	1
Loxia curvirostra L.	–	–	–	–	224	224	224	1	–	–	–	–
Pyrrhula pyrrhula L.	224	324	274	2	156	224	201	3	64	224	161	
Emberiza citrinella L.	–	–	–	–	146	224	185	2	–	–	–	–
Total no. individuals	46	55	51	5	18	55	49	5	21	149	68	5
Species richness	16	40	26	5	13	63	30	5	13	39	26	5

Appendix 2. Number of observed departures (D) and arrivals (A) in blocks-of flats areas, single-family house areas, villages during and in the pooled data during study winters. – = species was not detected in a given residential-area type.

Species	Blocks-of-flats		Single-f. house		Villages		Pooled	
	D	A	D	A	D	A	D	A
Corvus corone cornix L.	4	5	5	4	2	4	11	13
Carduelis flammea L.	3	1	4	2	6	5	13	8
Columba livia domestica Gmelin	3	5	5	5	–	–	8	10
Parus montanus Condrad	1	1	6	5	2	3	9	9
Parus caeruleus L.	3	4	3	2	1	4	7	10
Pyrrhula pyrrhula L.	2	2	2	1	5	3	9	6
Carduelis chloris L.	5	4	2	1	1	2	8	7
Dendrocopos major L.	1	1	4	4	1	3	6	8
Bombycilla garrulus L.	1	1	2	2	3	2	6	5
Passer domesticus L.	4	2	1	0	0	0	5	2
Garrulus glandarius L.	–	–	–	–	2	2	2	2
Glaucidium passerinum L.	–	–	–	–	1	1	1	1
Emberiza citrinella L.	–	–	2	1	–	–	2	1
Nucifraga caryocatactes L.	–	–	1	1	–	–	1	1
Turdus pilaris L.	–	–	–	–	1	1	1	1
Carduelis hornemanni Holboell	–	–	1	0	1	0	2	0
Loxia curvirostra L.	–	–	1	1	–	–	1	1
Parus cinctus Boddaert	–	–	–	–	1	0	1	0
Passer montanus L.	–	–	0	1	–	–	0	1
Parus major L.	0	0	0	0	0	0	0	0
Pica pica L.	0	0	0	0	0	0	0	0
Total	27	26	39	30	27	30	93	86