Long-term species richness-abundance dynamics in relation to species departures and arrivals in wintering urban bird assemblages

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ABSTRACT

Temporal dynamics of local assemblages depend on the species richness and the total abundance of individuals as well as local departure and arrival rates of species. We used urban bird survey data collected from the same 31 study plots and methods during three winters (1991–1992; 1999–2000 and 2009–2010) to analyze the temporal relationship between bird species richness and total number of individuals (abundance). We also evaluated local departures and arrivals of species in each assemblage. In total, 13,812 individuals of 35 species were detected. The temporal variation in bird species richness followed the variation in the total number of individuals. The numbers of local departure and arrival events were similar. Also, the mean number of individuals of the recently arrived species (8.6) was almost the same as the mean number of individuals of the departed species (8.2). Risk of species departure was inversely related to number of individuals. Local species richness increased by one species when the total abundance of individuals increased by around 125 individuals and vice versa. Our results highlight the important role of local population departures and arrivals in determining the local species richness-abundance dynamics in human-dominated landscapes. Local species richness patterns depend on the total number of individuals as well as both the departure-arrival dynamics of individual species as well as the dynamics of all the species together. Our results support the more individuals hypothesis, which suggests that individual-rich assemblages have more species.

KEYWORDS

Birds, Finland, more individuals hypothesis, species richness, urban environments, winter

INTRODUCTION

The variation in species richness in assemblages is one of the most studied patterns in ecology (Gaston, 2000; Evans et al., 2005c). The species richness in a local assemblage might be affected by the total number of individuals as well as the turnover species via immigrations (hereafter; arrivals) and extinctions (hereafter; departures). Therefore, it is important to take account of species arrivals and departures when studying the temporal relationship between species richness and total abundances. Several factors, such as productivity, spatial heterogeneity of the environment, and latitude, can influence the species richness-abundance relationship (Evans et al., 2005c). For example, the more individuals hypothesis (hereafter MIH) suggests that individual-rich areas have more species than the areas with fewer individuals partly due to greater productivity (Wright, 1983; Srivastava and Lawton, 1998; Storch et al., 2018). This relationship is based on the idea that a substantial resource abundance enables animals to attain larger population sizes, buffering them from departures. On the other hand, in sites with low total number of individuals, populations of most species are small, and local departures are common, leading to a reduction in species richness in low productivity areas (Evans et al., 2005a; Evans et al., 2005c; Evans et al., 2006; Mönkkönen et al., 2006; Carnicer et al., 2007; Yee and Juliano, 2007; Storch et al., 2018), although results from some empirical studies did not give support for the MIH hypothesis (Storch et al., 2018). Most of the earlier comparative studies have supported the idea that the most productive sites have high species richness (Wright, 1983; Srivastava and Lawton, 1998; Hurlbert, 2004; Evans et al., 2005a; Evans et al., 2005b; Evans et al., 2005c; Evans et al., 2006; Mönkkönen et al., 2006; Carnicer et al., 2007; Yee and Juliano, 2007; Chiari et al., 2010; Storch et al., 2018). However, the results of these studies are mainly based on the data collected from natural habitats and they are rarely considering the possible role of species departures and arrivals for the species richness-abundance relationship in the assemblage

(Magurran, 2007; Storch et al., 2018). Because disturbance dynamics, productivity and food availability, either intentional or unintentional, differ between natural and urban environments and urban heat island phenomena change the productivity and extend the growing season (Shochat et al., 2006; Francis and Chadwick, 2013); also, species richness-abundance dynamics may differ between natural and urban environments.

Urbanization has been cited as one of the most important threats to global biodiversity (Mennechez and Clergeau, 2006; Grimm et al., 2008). Generally, urbanization decreases bird species richness, but at the same time, it can increase the total number of individuals and abundance of some human-tolerant species (Chace and Walsh, 2006; Shochat et al., 2010; Tryjanowski et al., 2015b; Saari et al., 2016). Therefore, against the prediction of the MIH, there is a paradox, since even if urbanization increases the total number of individuals, urbanization decreases species richness. However, one study has indicated that there is a positive relationship between breeding season species richness and assemblage abundance for the urban areas in Italy (Chiari et al., 2010). Many of the earlier urban ecological studies have been restricted at the spatial scale (McPhearson et al., 2016). In general, the results of single-site snapshot studies may give a misleading picture in terms of the species richness-abundance dynamics and species persistence within environments (Wiens, 1989). However, long-term studies will give more detailed insights into the dynamics of assemblages, for example, from species departures and arrivals (Wiens, 1989). Earlier, urban studies that addressed departure-arrival dynamics were focused on fragmentation effects of natural-like habitats (e.g., urban woodlots and parks). These studies indicated that the same factors, such as patch size and isolation, are influencing patch occupancy in urban and natural environments (Fernandez-Juricic and Jokimäki, 2001; Smith, 2007; Beninde et al., 2015). However, the urban matrix is not an unsuitable living environment for all species (Hodgson et al., 2007). Therefore, enlarging the view from the patch level to the entire urban environment might help us to understand the factors influencing urban biodiversity and assemblage dynamics in more detail.

Towns represent the most human-influenced landscapes across the world. Towns could be seen as habitat islands surrounded by the more-or-less natural matrix (Fernandez-Juricic and Jokimäki, 2001). In addition to species-related factors (e.g., migratory habit or food preference), human-related changes such as artificial feeding and land cover changes may influence species occurrence, departures and arrivals in an assemblage (Marzluff, 2005; Huste and Boulinier, 2007; Jokimäki et al., 2016). Also, the many factors affecting species richness may differ between natural and human-dominated landscapes. For example, due to the urban heat island phenomena (Roth, 2007), cities are not as harsh on an environment; food resources are substantial and predictable (general productivity is high) due to the birds' artificial feeding (Lawson et al., 2018); towns are young habitats in the evolutionary sense; disturbances are abundant in urban habitats; and urban areas are relatively similar in their habitat structure all over the world (Francis and Chadwick, 2013).

Therefore, urban environments are excellent model systems to test the species richness-abundance relationship, species departure-arrival dynamics and assumptions of MIH. Earlier winter ecological studies have indicated that total number of individuals is greater in urban than in rural environments (Tryjanowski et al., 2015b); assemblage structure differ almost totally between urban and rural areas (Tryjanowski et al., 2015b); bird biomass is about tenfold in the city than other habitats (Nuorteva, 1971); wintering bird species richness varies only slightly between winters (Suhonen et al., 2009; Suhonen et al., 2010); winter bird assemblages are dominated by only a few (2–7) species that constitute a high proportion of the entire assemblage (> 70%; Jokimäki et al., 1996); between winter variation, in the total, abundance of birds (22%) and single species (20–40%) are low; most abundant species occur at the most sites (Jokimäki and Suhonen, 1998; Suhonen and Jokimäki, 2019), and urbanization increases the abundance of omnivore (Smith, 2003) and feeding table species (Jokimäki and Suhonen, 1998).

In this study, we analyzed the temporal bird species richness-abundance dynamics across several generations in the local assemblages in Finland. In particular, we considered how single species departure-arrival dynamics are influencing local species richness-abundance patterns in the assemblage. One question related to temporal species richness-total abundance dynamics in local assemblages and MIH is how many new individuals are needed so that species richness will increase or how many individuals should be lost so that species richness will decrease in local assemblage. Several studies conducted in natural habitats have tested spatial (geographical) variation in the species richness of the assemblages (Wright, 1983; Hurlbert, 2004; Evans et al., 2005a; Evans et al., 2005b; Evans et al., 2005c; Evans et al., 2006; Mönkkönen et al., 2006; Carnicer et al., 2007; Yee and Juliano, 2007; Chiari et al., 2010) and only a few experimental studies have been conducted (Srivastava and Lawton, 1998, see review Storch et al., 2019). It has been suggested that assemblages that have more disturbances and greater resource availability will be better established and able to receive invaders (Colautti et al., 2006). However, local species richness might also vary across temporal scales due to species departures and arrivals (Evans et al., 2005c; Carnicer et al., 2007). To understand species richness-abundance pattern in more detail, long-term studies are urgently needed. For example, it would be important to know if there is any balance between departures and arrivals of species in human-dominated landscapes (Marzluff, 2005; Huste and Boulinier, 2007; Suhonen et al., 2009; Suhonen et al., 2010).

We used long-term data (1991–2010) collected by the same study methods from three winters (intervals 8 and 10 years between survey times) collected from the same 31 human settlements located along a 950 km north-south gradient to study species-richness temporal dynamics in Finland. According to our best knowledge, this is the first long-term study

analyzing species richness-abundance dynamics in relation to species departure-arrival dynamics in urban assemblages during winter. The winter season is an ideal period to conduct these kinds of studies, because all the species and individuals are mainly residents, and the results might not be affected by factors relating to the migratory habits of species and factors that operate far away from the study sites.

The local arrival and departure of species in relation to the number of individuals can be tested by using the repeated census data from the same study plots (Pimm et al., 1988). We estimated the local number of individuals of each wintering bird species from each study site. Thus, our long-term data allow us to test the effect of local number of individuals on departures of species (local extinction risk) and the effects of number of individuals on the arrivals of new species. We expected that less abundant species would depart more often from the same study plots than the more abundant species, as expected by the MIH (Pimm et al., 1988; Legendre et al., 1999;). On the other hand, if local wintering bird assemblage is in balance, then the number of individuals of arrival species will be similar as local departure species. According to the MIH, it could be predicted that if the local assemblage lost individuals, then it would likely also lose species and vice versa.

1. MATERIALS AND METHODS

1.1. Study area
Our data originate from thirty-one villages and towns in the northern coniferous forest biome in Finland (Jokimäki et al., 1996; Suhonen et al., 2009; Suhonen et al., 2010). Most of the study plots were 30 ha (mean ± SD: 31.2 ± 9.4 ha, range: 13–62 ha) and size of the individual study plots were constant across the study winters. From each study plot, we estimated the wintering bird species richness and abundance of each species. The study areas were situated at relatively even intervals along a north-south gradient that was 950 km in length (60˚N-68˚N; Jokimäki et al., 1996). The study areas included urban settlements, ranging from towns to villages, both less and more-urbanized habitat types were located evenly across the latitudinal gradient. The human populations in these communities ranged from 300 to 159,000 people (mean 21,694 inhabitants; Jokimäki et al., 1996). The variation in local habitat structure and edge effects were minimized by selecting each study plot from the most heavily urbanized area of each village or town. All the study plots contained houses, roads and scattered green area between the houses (Jokimäki et al., 1996). Since our study plots were located in the most urbanized parts of each study area, we assumed that the general habitat structures of the study sites did not significantly change between the study winters and study sites. A more detailed description of the study sites and methods is available in Jokimäki et al. (1996).

Study winter (December–February) 2009–2010 was warmer and its winter-season rainfall was lower than during the other study winters (1991–1992 and 1999–2000; Finnish Meteorological Institute; data bases; Table 1). Correspondingly, winter 2009–2010 climate was milder than on average (1981–2010) in Finland (Finnish Meteorological Institute; data bases; Table 1). The snow depth (cm) of the study winters was lower than on average both in southern (Helsinki 60°N; 15. December 1991, 1992 and 2009; snow depth 0; 0 and 2 cm) and northern Finland (Rovaniemi 66°N; 15. December 1991, 1992 and 2009; snow depth 8; 16 and 5 cm; Finnish Meteorological Institute; data bases). The corresponding long-term average (1981–2010) depth of snow in Helsinki was 8 cm and in Rovaniemi was 19 cm (Finnish Meteorological Institute; data bases).

1.2. Winter bird surveys
Winter birds were surveyed by the single-visit study plot method (Bibby et al., 1992). Most of these censuses were made in late December or early January for each study plot. We counted the birds during three different winters; t_0 = 1991–1992, n = 31, t_1 = 1999–2000, n = 31, t_2 = 2009–2010, n = 29. Because of the relatively large time difference between the survey periods (8 and 10 years), we considered that the independence of observations was fulfilled. This factor is very important and was seldom controlled in earlier studies.

The census work in each case was done by one person (mainly the same person during each period) in good weather conditions at midday, when the light-availability allowed for surveys (i.e., between 10.00 and 14.00). Most of the surveys were conducted during working days, Monday through Friday. The surveys were not conducted along a single route through the plots but instead as a zig-zag walk through the plots. To avoid double counts of individuals, we used a relatively high census rate (10 ha/20 min). We also included the backyards and gardens of houses in these surveys. This kind of a transect count mitigates many of the problems associated with counting birds in urban areas, for example, varying noise level and visibility (Jokimäki and Suhonen, 1998). It is important to note that winter-time territorial behavior by singing in northern latitudes is lacking. Thus, singing behavior did not affect species detectability in our study. During winter season, at least in the northern areas as in our case, wintering birds do not move a lot, partly due to the low temperatures, during a short day-time (4–6 hours) and a snow cover. Most overwintering individuals are concentrated in quite a few restricted areas where food is available (Jokimäki and Suhonen, 1998; Tryjanowski et al., 2015a, b). Also a scarce vegetation cover, due to the absence of leaves on deciduous trees and shrubs in winter, increases the validity of results collected by the single-visit method. In general, a single-visit census during wintering enables the detection of approximately 90% of the species and 80% of the individuals in urban environments (Jokimäki and Suhonen, 1998). Therefore, our species richness, total number of individuals as well as species departure and arrival estimates are reliable. All birds were included in the survey, except for overflying individuals, which did not land and stay on the study plot. We excluded aquatic bird species such as the mallard (*Anas platyrhynchos*), the herring gull (*Larus argentatus*),

and the common gull (*L. canus*) from these analysis, since their occurrence is mainly related to open water. We also excluded one large flock (over 800 individuals) of the Bohemian waxwing (*Bombycilla garrulus*) flock from the Saarenkylä (Jokimäki et al., 1996; Suhonen et al., 2009) survey area during the first winter 1991–1992, because the flock was a migratory flock.

1.3. Statistical methods

The local population size for each bird species was counted during the three study winters. The data consisted of 778 records of local wintering bird population sizes from 35 species. All together, we had local departure data from 30 species. Correspondingly, we had local arrival data from 30 species. We used the Kruskal-Wallis ANOVA to test differences in number of individuals per species arrived to local assemblages between the three study periods ($t_1 - t_0$, $t_2 - t_1$ and $t_2 - t_0$). The local departure of wintering bird species populations were counted on each study plot. The presence or absence of each species in each study plot was compared to the data of next winter. In other words, a species was present in t_0 (or t_1), and the same species has at least one individual in the following winter (t_1 or t_2) (presence). If we did not find any individuals from the species, which was observed during the previous counting periods (winters t_0 or t_1), we assumed that the species had departed from the local assemblage. We tested the effect of the number of individuals of each species in each study area on the risk of local departure by means of a binary logistical regression. If we did not find a particular species during the later survey period on the same study area, we assumed that this species had departed locally (coded as 1 in the binary logistic regression analysis). On the other hand, if we found the species again in the same study area during later census periods in the same study area, we assumed that this species survived (coded as 0 in the binary logistic regression analysis). The local number of individuals of each species in the previous census periods in each study area was used as a covariate in the binary logistic regression.

For the temporal change in the abundance-species richness relationship in the MIH, we calculated the change in species richness (ΔS) and the change in total abundance of birds (Δ total abundance of birds) between two survey periods (later census – earlier census in the same survey area). In the statistical test, we used all the possible differences in species richness and abundance of wintering birds in each of the sur-vey areas. The three differences for wintering bird assemblage abundance and species richness were (*i*) $\Delta_1 = t_1 - t_0$ (9 years between the censuses), n = 31, (*ii*) $\Delta_2 = t_2 - t_1$ (10 years), n = 29, and (*iii*) $\Delta_3 = t_2 - t_0$ (19 years) n = 29. We used the Friedman ANOVA to test the differences in the species richness and abundance between winters, and each study area was used as a block in the analyses. Because we did not count birds from the two study areas during the last winter, the sample size was reduced from 31 to 29. According to the prediction of the MIH, if the assemblage total abundance increases between the two surveys, then the species richness would increase and *vice versa*. Therefore, we expected that the relationship between the change in species richness (ΔS) and the change in abundance (Δ abundance) to be positive. We tested this idea with regression analysis. The dependent variable was the change in species richness (ΔS), and the independent variable was the change in abundance (Δ abundance). We did not calculate intercept in the regression analysis, because we used the delta values for the abundance and species richness instead of the original numbers. Moreover, we expected that if total abundance did not change between the two time periods, then species richness also did not change. Each delta value was used as an independent data point in the statistical tests. Mean values and their standard deviations (SD) are reported in the results section. The statistical tests in our study were performed using the IBM SPSS 22.0 statistical package.

2. RESULTS

2.1. Species richness and total abundance

In total, we observed 35 (26 species in 1991–1992, 23 species in 1999–2000 and 26 species in 2009–2010) wintering bird species. A total of 13,812 (4,334 individuals in 1991–1992, 5,144 individuals in 1999–2000 and 4,334 individuals in 2009–2010) individuals were observed. The average number of individuals in each species in each assemblage was 17.8 ± 16.9 individuals (range 1–230; n = 778; Fig. 1).

The mean abundance (total number of individuals) in the assemblage did not differ between the study periods (151.8 ± 82.0; Friedman ANOVA, χ^2 = 2.33, df = 2, P = 0.311, n = 29). However, the number of species differed between winters (Friedman ANOVA, χ2 = 8.88, df = 2, P = 0.012, n = 29). The high-

Table 1. Average winter (months: December, January and February) temperatures (°C) and rainfalls (mm) during the study winters in southern (Helsinki) and northern Finland (Rovaniemi) during study winters and their long-term (1981–2010) values (Finnish Meteorological Institute; data bases)

Location	Helsinki (60°N)		Rovaniemi (66°N)	
Winter	Temperature	Rainfall	Temperature	Rainfall
1991–1992	-2.4	132.9	-10.1	87.7
1999–2000	-4.2	213.3	-12.1	115.9
2009–2010	-1.7	116.0	-7.9	75.0
1981–2010	-3.5	146.2	-10.6	109.5

est number of species (9.2 ± 2.6; n = 29) was observed during the last winter (2009–2010), and the lowest one (7.9 ± 2.0; n = 29) was observed during the first winter (1991–1992). In the winter of 1999–2000, the average species richness in the study plot was 8.5 ± 2.9 (n = 29).

2.2. Species departures and arrivals

Local departure and arrival rates were estimated for 721 out of the 778 local species populations. In total, 168 out of 721 (23.5%) local wintering bird species populations departed between the two survey periods (Fig. 2). The average number of individuals of the departed bird species was 8.2 (± 11.8) and ranged from one to 56 individuals (Fig. 2). About one fifth of the local bird species departed from the assemblages between the study winters (between the winters of 1991–1992 and 1999–2000, 26.0% [number of departures, n = 262]; 1999–2000 and 2009–2010, 19.8% [n = 227] and 1991–1992 and 2009–2010, 23.7% [n = 232]). Because the number of departures did not differ between the study periods (Kruskal-Wallis ANOVA, χ^2 = 2.59, df = 2, P = 0.274), we pooled the data from the different periods for the next analyses. The risk of local departure of species was inversely related to the number of individuals (logistic regression, χ^2 = 53.15, df = 1, p < 0.001; Fig. 3).

New species arrived in the local urban wintering bird assemblages 214 times (Fig. 4). The average number of arrived species had 8.6 ± 14.7 individuals (n = 214) ranged from 1 to 104 (Fig. 4). There were differences in the number of arrivals to the local wintering bird assemblages between the study periods (Kruskal-Wallis ANOVA, χ^2 = 10.83, df = 2, P = 0.004). The lowest number of arrivals was observed between the winters of 1999–2000 and 1991–1992 (number of arrivals, n = 49), and the highest number of arrivals was observed between the winters of 1991–1992 and 2009–2010 (n = 86). Intermediate numbers of arrivals were observed between the winters of 1999–2000

and 2009–2010 (n = 79). However, there were no differences in the number of individuals arrived per species between the study periods (Kruskal-Wallis ANOVA, H = 0.50, df = 2, P = 0.975).

2.3. Temporal change in total abundance and species richness
The average change in species richness (mean ΔS) between the study periods was 0.5 ± 2.5 (n = 89). In the extreme case, one local assemblage lost six bird species (Fig. 5). On the other hand, two assemblages gained six new species (Fig. 5). The average change in the total abundance (mean Δ abundance) was 5.6 ± 88 individuals and ranged from -215 to 251 individuals (Fig. 5). When the total abundance of birds (Δ abundance) increased between the two survey periods, the species richness (ΔS) also increased and *vice versa* (regression analysis, $F_{1,87}$ = 6.62, P = 0.012, r^2 = 0.07; Fig. 5).

3. DISCUSSION

3.1. Species departures and arrivals
Both species richness and number of individuals varied between the study winters in the Finnish urban settlements. First, the new species arrived, and some species departed from the local assemblages. Second, almost one fourth of the local wintering bird species departed between the survey periods. Despite differences in winter weather conditions between the study winters, we did not observe any differences in the departure rates between winters. Therefore, winter conditions did not seem to be very harmful for species wintering within human settlements, probably due to human-derived inputs in the form of supplementary feeding of birds, waste food sources (Jokimäki and Suhonen, 2008; Fuller et al., 2008; Robb et al., 2008; Oro et al., 2013; Tryjanowski et al., 2015a) and higher temperature in urban areas than their surrounding landscape
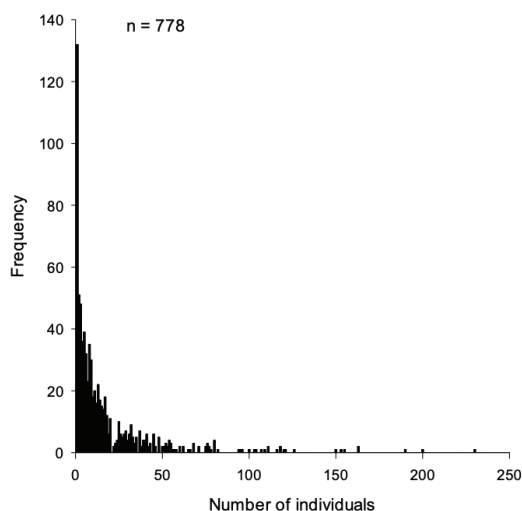

Figure 1. The frequency distribution of number of individuals in each species in each local wintering bird assemblages. Pooled data from three winters (1991–1992, 1999–2000 and 2009–2010). Total 778 observations from 35 species in 31 urban centers in Finland.
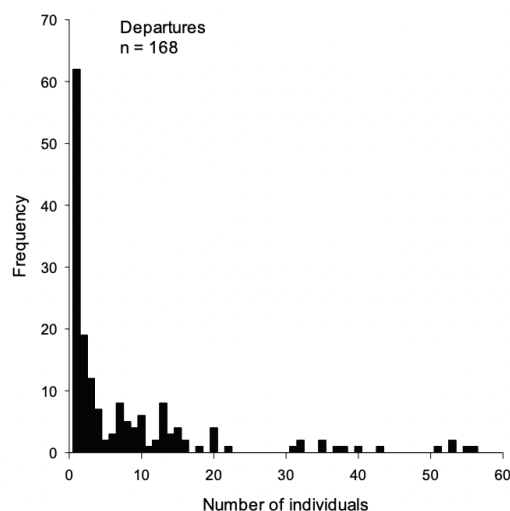

Figure 2. The frequency distribution of number of departures (n = 168) in relation to the number of individuals per species in previous censuses in the same local urban wintering bird species assemblages in Finland. Pooled data from three winters (1991–1992, 1999–2000 and 2009–2010).
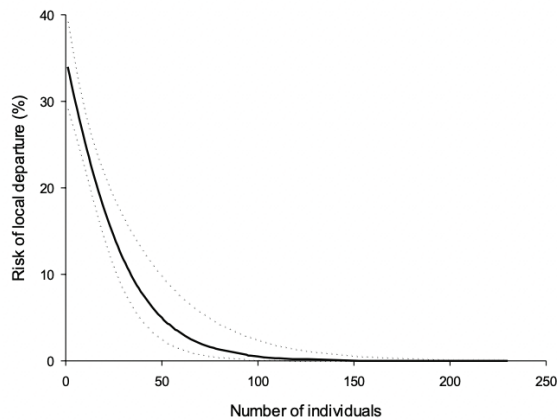
Figure 3. The predicted risk of local departure of species (continuous line) (%) in relation to the number of individuals in the previous census period was observed in the same study area. If we did not find a species during the later survey period on the same study area, when the species had occurred in previous census period, we assumed that this species had locally vanished (the value was 1 in the logistic regression analysis). If we found the species again in the same study area during the later census periods, we assumed that this species survived (0). Pooled data from three winters (1991–1992, 1999–2000 and 2009–2010) from 31 wintering bird assemblages. (Dotted lines are 95% confidence intervals.)

Figure 4. The frequency distribution of bird species arrived (n = 214) to the urban wintering bird assemblage in relation to the number of individuals arrived from each species to the local wintering bird assemblages. Pooled data from three winters (1991–1992, 1999–2000 and 2009–2010) from 31 wintering bird assemblages.

Figure 5. The relationship between the change in bird species richness (later census − earlier census) (Δ species richness) and the change in total abundance (later census − earlier census) (Δ total abundance of birds) of the wintering bird assemblages. The continuous line was fitted with a regression analysis (F1,88 = 6.62, P = 0.012; Δ S = 0.008* Δ Abundance; r² = 0.07).

(urban heat island; see, e.g., Shochat et al., 2006). Third, the risk of local departure of bird species was inversely related to the number of individuals. Fourth, the average number of individuals per species that arrived into the assemblage was almost equal to the average number of individuals that departed from the assemblage. Fifth, the temporal variation in the local species richness followed the temporal variation in the total number of individuals in the same assemblage as predicted by MIH (e.g., Storch et al., 2018).

Local departures were common and inversely related to the number of individuals in an urban wintering bird assemblage during the previous census period. One third of the species (34.4%) with only one individual departed between the two survey periods. However, the risk of local departure decreased to 4.8% if the species had more than 50 individuals. These results agree with the previous local extinction risk studies of birds (Thomas, 1990). It seems that a large number of individuals reduces the risk of local departure, and thereby, promotes a high species richness in the assemblages. The local extinction rate in relation to population size (number of individuals) is one key assumption for the five causal mechanisms of the species energy relationship: (*i*) increased population size, (*ii*) dynamic equilibrium, (*iii*) niche position, (*iv*) niche breadth, and (*v*) consumer pressure (Evans et al., 2005c). Therefore, our results from wintering urban bird assemblages highlight the important role of the number of individuals in determining the risk of local departure rate (Pimm et al., 1988; Legendre et al., 1999). The lack of migratory birds from the wintering community in the northern areas may be one possible reason for the relatively low numbers of departures in this study. However, resident birds live in the same areas year-round, and therefore,
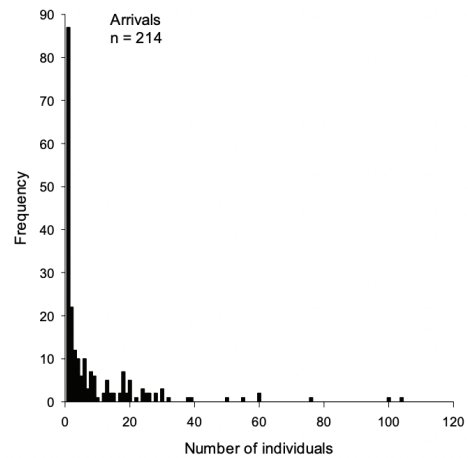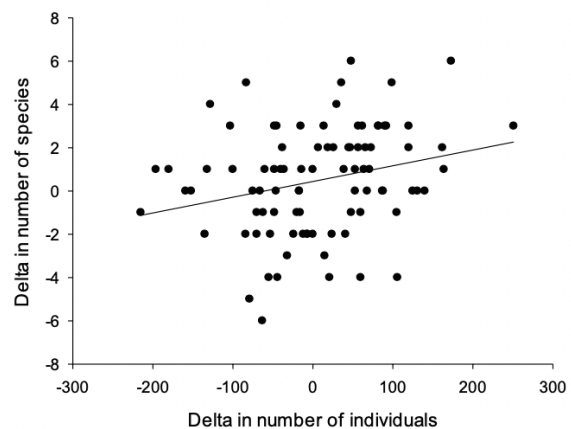
their occupancy in assemblages is dependent only on factors operating at the local site. It might also be that sedentary winter birds are better adapted to live in urban winter conditions with substantial and predictable food resources (Tryjanowski et al., 2015a, b), and therefore, less local departures occur (Jokimäki and Kaisanlahti-Jokimäki, 2012). In addition, high availability of food offered intentionally and unintentionally to birds by humans is great in urban areas (Tryjanowski et al., 2015a) and might buffer against species departures. However, a previous study found that the local departures of breeding birds were almost twice as common as arrivals in urban forests and parks (Crooks et al., 2001), suggesting a high departure of bird species in urban habitats. This mechanism may also partly explain why urbanization decreases species richness (Jokimäki and Suhonen, 1993; Chiari et al., 2010).

It is also possible that sampling artefact may cause local departures of rare species. The sampling of locally rare species is a potential problem in the studies of local departure of bird assemblage if locally rare species are not detected, although they actually occur at a study site (Evans et al., 2005a, b, c; 2006). It is thus highly likely that some locally rare bird species were not detected at every site where they actually occurred. This seems to increase our estimate from bird species risk of local departure. However, although such sampling problems likely occurred, they are unlikely to be the sole underlying factor behind the survival of common species population in local assemblage. To facilitate our comparison, we standardize our bird survey time to 1 h per 30 ha. Also, samples from large areas are more heterogeneous than samples from smaller areas, but our study sites were almost equal in size and we surveyed birds only from the centers of each human-dominated areas to decrease habitat heterogeneity between the study sites. Moreover, in most of cases, the same person surveyed exactly the same study sites in each study winters, which decreased the variations in bird detectability. Thus, the possible role of sampling artefact on results is only marginal.

In our study, the number of local arrivals and the number of local departures were approximately the same, 214 and 168, respectively. This observation is in accordance with the bird data collected from residential habitats in northern Finland during 1998/1999–2003/2004 (Jokimäki and Kaisanlahti-Jokimäki, 2012). Moreover, the average number of individuals of the new species was very small, but it was approximately the same size as the average number of individuals of the departed species, 8.6 and 8.2, respectively. We found that the number of arrivals differed between winters, being greatest between the winters 1991–1992 and 2009–2010. This is understandable because during this long period, many new bird species (e.g., the Greenfinch *Carduelis chloris*; the Blue tit *Cyanistes caeruleus*) have expanded their distribution ranges in the north and settled in our study site (Suhonen et al., 2009; Jokimäki and Kaisanlahti-Jokimäki, 2012). The arrivals of new species in urban wintering bird assemblages is a common pattern at least in northern countries like Finland (Suhonen et al., 2009; Suhonen et al., 2010; Suhonen and Jokimäki, 2019). Probably winter feeding in urban areas is the most plausible reason why some bird species, like the Mallard *Anas plartyrhynchos;* Pulliainen, 1963) and the Blackbird (*Turdus merula*; Møller et al., 2014) have changed their migratory status from migratory via partial migratory to resident way of life, and settled in new wintering areas.

3.2. Temporal change in species richness and total abundance
We also found that wintering species richness differed between the study winters, being greatest during the warm winter 2009–2010. It would be interesting to know, how many new individuals are needed to result in an assemblage gaining one new species (Cassey et al., 2004; Lockwood et al., 2005; Colautti

et al., 2006; Blackburn et al., 2009; Lockwood et al., 2009). We found that the variation in species richness followed the variation in the total number of individuals in the assemblage. When the total abundance of birds increased, the species richness increased and *vice versa* (Fig. 5). This finding is consistent with the MIH (Wright, 1983; Chiari et al., 2010; Storch et al., 2018). At the assemblage level, the average number of species change was only 0.5, and the average change in abundance was 5.6 individuals. Our results indicated that, on average, the same number of species vanished that had arrived in the local assemblage. Also, the same number of individuals per species disappeared that had arrived in the assemblage. We found that if the local assemblage lost 125 individuals, then it would likely lose one wintering bird species. This rate is over two times larger than our estimated local departure (extinction risk) for a single species. Previous studies have indicated that introduction success for birds increased with the number of individuals released (Green, 1997; Cassey et al., 2004; Lockwood et al., 2009). For exotic bird species, introduction success was high (over 80%) if more than 100 individuals were released in New Zealand (Green, 1997). This finding agrees with our estimation that about 125 individuals are needed, when one new species arrived in the urban wintering bird assemblage at northern latitudes. This is much larger than the average number of individuals of the arrived species. The arriving and departing species were in most cases rare species with restricted distribution area and low abundances, as predicted by the broad general patterns of species abundance (e.g., Magurran, 2007; Storch et al., 2018; Suhonen and Jokimäki, 2019). However, we noted that sometimes very abundant species (up to 104 number of individuals of single species) also arrived at the local wintering bird species assemblage (Fig. 4).

Thus, at the local assemblage level, the relationship between the total abundance of individuals and species richness do not depend on single species departures (Fig. 2) or arrivals (Fig. 4). However, species richness increases only if several species arrive and fewer species depart the assemblage (see also Evans et al., 2005c), and simultaneously, the number of individuals in the assemblages increases about 125 individuals (Fig. 5). On the other hand, the species richness decreases only if several species depart and fewer species arrive into the assemblage, and simultaneously, the number of individuals in the assemblages decreases to about 125 individuals (Fig. 5). Therefore, our findings give support for the soft formulation of the MIH that suggests that number of individuals is determines species richness, at least partly, although also some other mechanisms may also influence the observed species richness pattern (Storch et al., 2018). Also, the earlier urban ecological studies have found that species turnover is relatively high, and assemblages simultaneously loose or gain several species (Suhonen et al., 2009; Suhonen et al., 2010). It is possible that the temporal variability, for example, in food resources, affects the population variability of species and turnover rates of the assemblage (Jokimäki and Kaisanlahti-Jokimäki, 2012).

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4. CONCLUSIONS

This is the first urban ecological empirical study addressing the temporal dynamics in wintering bird assemblage species richness-abundance relationships with a large number of temporal and spatial replicates, and this study also considers the role of species departures and arrivals in species abundance-richness dynamics (e.g., Storch et al., 2018). Our results from temporal abundance species richness patterns indicate that individual rich assemblages are also species rich and vice versa, giving support to the soft formulation of the MIH (Evans et al., 2005c; Storch et al., 2018). Worldwide, these kinds of large-scale analyses are needed to understand the assemblage dynamics not only in urban environments but also more natural habitats (see also Clergeau et al., 2006a; Clergeau et al., 2006b; Pautasso et al., 2011; Aronson et al., 2014; Storch et al., 2018). We encourage scientists to conduct further research by also using other groups than birds in urban environments, to understand more detailed temporal species richness and abundance relationships. Moreover, we need more studies to understand how common the pattern is that urbanization increases the total abundance of individuals, but at the same time, decreases species richness (Shochat et al., 2010; Saari et al., 2016). This pattern goes against the common expectation that species richness increases with the number of individuals (Wright, 1983; Srivastava and Lawton, 1998; Storch et al., 2018). Our results show that species richness-abundance relationship dynamics in local assemblages depend on both the dynamics of single species as well as the arrivals and departures of all the species together, given support on the soft formulation of the MIH (e.g., Storch et al., 2019). However, more studies are needed to determine the temporal dynamics of abundance on total species richness in bird assemblages during breeding season. Moreover, it would be expected that species richness may be sensitive to temporal variation in abundance in disturbed environments other than urban habitats (Pimm et al., 1988; Green, 1997; Legendre et al., 1999).

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