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Urbanization and stability of a bird community in winter[1]

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Abstract: The main objective of this study was to analyze between-winter stability of bird communities along latitudinal (950 km) and urban gradients (from small village to towns) in Finland. Birds were surveyed at the same 30-ha study plots using the same methods in 31 villages and town centres in the winters of 1991-1992 and 1999-2000. Species richness did not differ between the 2 study winters, but variation in total abundance of birds increased with increasing urbanization. However, urbanization reduced variation in wintering bird community structure. Species richness, density of wintering birds, and dissimilarity of wintering bird communities did not vary with latitude. According to our results, the level of urbanization was a more important factor than latitude in explaining the structure of the bird community in winter. We assume that the presence of a continuous, rich, and diverse supply of food offered by humans with increasing urbanization may explain variation in species abundances and stability in urbanized ecosystems.
Keywords: Finland, latitude, persistence of community, species richness, stability of community, wintering bird assemblage.

Résumé : L'objectif principal de cette étude était d'analyser la stabilité hivernale des communautés aviaires le long de gradients latitudinal (950 km) et d'urbanisation (de petits villages aux villes) en Finlande. Des inventaires d'oiseaux ont été réalisés dans les mêmes parcelles d'étude de 30 ha avec les mêmes méthodes dans 31 villages ou centres-villes durant les hivers 1991-1992 et 1999-2000. La richesse en espèces ne différait pas entre les 2 hivers à l'étude, mais la variabilité dans l'abondance totale des oiseaux augmentait avec l'urbanisation. Cependant, l'urbanisation réduisait la variabilité dans la structure de la communauté aviaire hivernante. La richesse en espèces, la densité d'oiseaux hivernants et la dissimilarité entre les communautés aviaires hivernantes ne variaient pas avec la latitude. Selon nos résultats, le niveau d'urbanisation est un facteur plus important que la latitude pour expliquer la structure de la communauté aviaire en hiver. Nous supposons que la présence d'un approvisionnement alimentaire continu, riche et diversifié offert par les humains avec l'augmentation de l'urbanisation peut expliquer la variabilité dans l'abondance des espèces et la stabilité dans les écosystèmes urbanisés.
Mots-clés : assemblage d'oiseaux hivernants, Finlande, latitude, persistance de la communauté, richesse en espèces, stabilité de la communauté.

Introduction

The factors that affect urban bird assemblage stability have long been of interest to ecologists (Marzluff, 2001; Marzluff, Bowman & Donnelly, 2001). The spatial component of community variability, especially large-scale geographic patterns, is the object of considerable scientific interest, while temporal variation has mostly been ignored, especially in human-dominated landscapes (Marzluff, Bowman & Donnelly, 2001a). Several factors have been reported to affect avian community diversity and stability. Community persistence is likely to depend on the physical and temporal stability of habitats and on the interactions among the species in the community (Bengtsson, Baillie & Lawton, 1997; Gaston & Spicer, 1998). According to biogeographical theory, species richness decreases linearly with latitude (Gaston & Spicer, 1998, but see exceptions in Järvinen, Kouki & Häyrinen, 1987; Jokimäki & Suhonen, 1993; Kouki, Niemelä & Viitasaari, 1994), with communities in the northern hemisphere being less stable than those in the south (Järvinen, 1979). The instability of northern

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communities is assumed to be caused by reduced species richness, the increase in environmental unpredictability, and/or a decrease in environmental productivity (Gaston & Spicer, 1998). It has been predicted that increasing the number of interacting species in a community will increase the ability of populations to maintain their abundances (MacArthur, 1955). However, several theoretical models suggest that increasing community complexity may lead to instability (Haydon, 1994). Studies examining geographical gradients in community stability have also had conflicting results. Some studies suggest that the stability of species assemblages decreases with increasing latitude (Järvinen, 1979; Pianka, 1966), whilst others have not found any association between stability and latitude (Noon, Dawson & Kelly, 1985; Bethke, 1993; Bengtsson, Baillie & Lawton, 1997). At least one study found that stability increased with latitude (Virola *et al.*, 2001). Järvinen (1979) suggested that the poor predictability of weather conditions might be the reason for the instability of northern terrestrial bird communities. However, Pöysä (1989) pointed out that differences in environmental predictability between south and north may only partly explain the latitudinal gradient in the stability of Finnish waterfowl communities. According to Järvinen (1989) between-year temperature variability was higher in northern than in southern Finland (1000 km apart), whereas within-year predictability of temperature was better in the north than in the south. This result contradicts the conventional assumption that variable environments are unpredictable. Studies concerning the relationship between ecosystem productivity and community stability are scarce, and previous studies have not supported the hypothesis that ecosystem productivity increases community persistence (Järvinen, 1979; Bethke, 1993).

In this study, we measured the stability of wintering bird communities along an urban gradient (based on human population density) within a 950-km latitudinal range. This kind of gradient analysis offers a useful approach to test hypotheses on the impacts of urbanization on ecological processes, like latitudinal gradients. In an earlier study using the same study design and study sites, we showed that the species richness of wintering birds decreased toward the north but bird density did not (Jokimäki *et al.*, 1996). Species richness, however, did not decrease with latitude in heavily urbanized areas (Suhonen & Jokimäki, 1988; Jokimäki & Suhonen, 1993; Jokimäki *et al.*, 1996). Urbanization involves one of the most extreme forms of land-use alteration, generally leading to a complete restructuring of vegetation and species composition (Marzluff, Bowman & Donnelly, 2001b). During the last century, urbanization has led to a dramatic increase in the sizes of occupied cities at a global scale (Marzluff, Bowman & Donnelly, 2001b). Urbanization has increasingly altered natural environments and their dynamics (Clergeau, Jokimäki & Snep, 2006; Shochat *et al.*, 2006). In general, human activity has produced quite similar ecological structures in urban centres throughout the world (Clergeau, Croci & Jokimäki, 2004; Clergeau *et al.*, 2006). Urban environments also differ in many ways from more natural ecosystems; urban environments, for example, support more anthropogenic food resources, and the climate of urban areas may be more favourable for some bird species but also less favourable for others (Shochat *et al.*, 2006). Earlier studies have clearly demonstrated that urbanization reduces species richness, increases the total abundance of birds, and favours the occurrence of some superabundant bird species (Chace & Walsh, 2006). These strong competitors may benefit from the low-frequency resource fluctuations in urban environments (Anderies, Katti & Shochat, 2007). Most urban bird species generally have much higher population densities than rural populations (Batten, 1973), and urban exploiters are often resident species with omnivorous diets (Jokimäki & Suhonen, 1998; Kark *et al.*, 2007; Smith, 2007). These factors lead to a homogeneity in the overall structure of urban avian communities at a global scale (Blair, 2001; Clergeau *et al.*, 2006; McKinney, 2006; Devictor *et al.*, 2007; Sorace & Gustin, 2008).

Despite these changes in bird communities due to urbanization, almost nothing is known about their temporal stability. Devictor *et al.* (2007) found that specialist bird species in France had higher annual extinction and turnover rates than generalist species, and these differences increased with urbanization. In our earlier study we found that both between-year variation in species richness (CV was 10%) and total abundance of wintering species (CV was 22%) in a northern town centre (Rovaniemi, Finland) were low (Jokimäki & Suhonen, 1998). In addition, the temporal variation of urban bird communities may be affected by snow cover, temperature, and winter feeding resources. On an evolutionary time scale, urban environments are novel for birds. Urban areas thus represent a suitable model system for testing predictions as to community structure and dynamics (Fernandez-Juricic & Jokimäki, 2001).

We investigated the hypothesis that the stability of wintering urban bird communities across a geographical range is related to urbanization level. We recorded changes in the structure and the stability of wintering bird communities in 31 towns and villages in Finland along a 950-km latitudinal gradient at intervals of 8 y. To our knowledge, there have been no earlier studies dealing with the impact of geographical location and level of urbanization on the stability of wintering bird assemblages. The purpose of this study was to determine whether urbanization affects the latitudinal patterns of temporal variation of winter bird communities. We predicted that the favourable microclimate and the relatively rich, diverse, and continuous winter food supply available in a highly urbanized environment would mask the latitudinal patterns in community stability found in less urbanized ecosystems.

Methods

Description of study areas

Our data originate from 31 villages and towns in Finland (Jokimäki *et al.*, 1996). The number of wintering birds in forests (114 individuals·10 km^{-1} of survey route in northern Finland; 150 individuals·10 km^{-1} in southern Finland) is low compared with urban settlements (484 individuals·10 km^{-1} in northern Finland; 583 individuals·10 km^{-1} in southern Finland; Väisänen & Koskimies, 1989). In Rovaniemi (66° N) the number of wintering birds in forests can be as low as 43 individuals·10 km^{-1} of survey route (Jokimäki, 1982). Therefore, it was not practical to collect data from forests. The bird counts were made during 2 winters: 1991-1992 and 1999-2000. The study areas were situated at relatively even intervals along a 950-km north–south gradient. The map of the original study sites is shown in Jokimäki *et al.* (1996). The study area contained urban communities ranging from large cities to small villages, in both the south and the north of Finland. The human population in each community ranged from 300 to 159 000. The degree of urbanization was measured in terms of human population density (inhabitants·km^{-2}) in 2.5-km^2 squares in a uniform coordinate system around the study plots in the year 1980. Variation in local habitat structure, and any edge effects, were minimized by placing each study plot in the most heavily urbanized area of each village or town. Hence, the general habitat structures of the study sites did not change significantly between the study winters.

In general, adverse weather conditions, such as temperature (mean temperature during December 1991, $r_s = -0.81$, $P < 0.001$) and amount of snow (amount of snow [cm] at the end of December 1991, $r_s = 0.81$, $P < 0.001$; based on data obtained from the Finnish Meteorological Institute), increased northwards. Similar patterns were also apparent in 1999-2000 (for all, $P < 0.05$; data not shown). However, the month of December in the earlier winter (1991-1992) was slightly colder than in the later winter (1999-2000) (mean temperature [°C] –8.6 ± 2.3 *versus* –7.8 ± 4.11, $U = 77.5$, $P = 0.047$), but there was less snow (cm) at the end of December in 1991 (20.6 ± 11.2 versus 34.5 ± 13.9, $U = 81.5$, $P = 0.003$). Unfortunately, we did not have precise meteorological data along all of the urban gradients for all of the study sites. However, the temperature at night could be up to 5–7 °C warmer within a town (*e.g.*, Rovaniemi: 66° N; human population density 4000 inhabitants·km^{-2}) than in the surrounding agricultural areas (human population density 750 inhabitants·km^{-2}; J. Jokimäki, unpubl. data).

BIRD CENSUS WORK

The wintering birds were counted using a single-visit study plot method. A census did not consist of a single route through the plot, but rather a zigzag walk through the plot. We also inspected the backyards and gardens of houses. This kind of transect count reduces many of the problems associated with counting birds in urban areas, such as varying noise and visibility (Jokimäki & Suhonen, 1998). To avoid double counts of individuals, we used a high census rate (10 ha·20 min^{-1}). All birds were included in the survey except for overflying individuals that did not remain in the study plot. We omitted waterfowl and gulls from the analysis, since their occurrence is mainly related to open water. Most of the censuses in the 30-ha study plots, which were selected and marked beforehand, were carried out in December and early January. All censuses were conducted in the same study plots, and in most cases by the same person. In general, a single-visit census during wintering time detects about 90% of species and 80% of individuals (Jokimäki & Suhonen, 1998).

DATA ANALYSIS

We used the percentage dissimilarity index to measure the stability of wintering bird communities between the 2 study years (Helle & Mönkkönen, 1986) The percentage dissimilarity index (PDI) is PDI = 1 – PS, PS = $\Sigma \min (p_i1, p_i2)$, where p_i is the proportion of individuals of species i in year 1 and year 2. The index ranges from 0 to 1. The wintering bird community is stable when the PDI index is close to 0 and unstable when it is close to 1. We used paired t-tests (2-tailed) to test for differences in mean species richness and mean bird density between 1991-1992 and 1999-2000. The correlations in species richness and bird density between winter 1991-1992 and winter 1999-2000 were analyzed with Spearman's rank correlation. To test whether the stability of the wintering bird assemblage is affected by urbanization or geographical position, we used multiple regression, with the percentage dissimilarity index as the dependent variable and both human density and latitude as predictor variables. Latitude might correlate significantly with other variables, but we used it as an explanatory variable because its biological meaning is also related to winter harshness or other environmental features that may affect the stability of the bird communities. We used human population density as a measure of urbanization because it also indicates the level of human disturbance. In addition, the proportion of the built-up landscape in each study plot increased with human population density ($r_s = 0.60$, $P < 0.001$, $n = 31$), but not with latitude ($r_s = -0.34$, $P > 0.05$, $n = 31$). We $\log_{10}$-transformed the human population density data to normalize the error variances. All statistical tests were performed with SPSS for Windows Version 14.0, (SPSS Inc., Chicago, Illinois).

Results

We found a total of 31 wintering bird species in urban areas in Finland. Average species richness (8.6 ± 3.0 and 7.9 ± 1.9, mean ± SD; paired t-test, $t = 1.62$, df = 30, $P = 0.12$) and total average density (55.9 ± 55.7 and 57.9 ± 42.9 individuals·10 ha^{-1}; paired t-test, $t = 0.59$, df = 30, $P = 0.569$) did not differ between study winters. Species richness and bird density were high, and were significantly correlated within the same study area, in both winters ($r_s = 0.69$, $n = 31$, $P < 0.001$ and $r_s = 0.42$, $n = 31$, $P < 0.018$; Figure 1). Overall variation in species richness was low (CV = 7.7% ± 5.8) and was not associated with latitude or urbanization (Table I). Variation in wintering bird density, in contrast, was high, and increased with increasing urbanization (Table I; Figure 1b). The percent dissimilarity index of the bird assemblage between the 2 censuses averaged 41.8% ± 16.3 and was not associated with latitude (Table I). However, the stability of this winter bird community increased with urbanization (Table I; Figure 2).

Discussion

TEMPORAL VARIATION OF WINTERING BIRD COMMUNITIES IN RELATION TO LATITUDE

Our results are consistent with the hypothesis that urbanization is increasing the stability of the wintering bird community. However, it seems that latitude did not affect variation in species richness, density, or stability of the wintering bird community. Moreover, earlier studies examining geographical gradients of community stability of more natural communities have generated conflicting

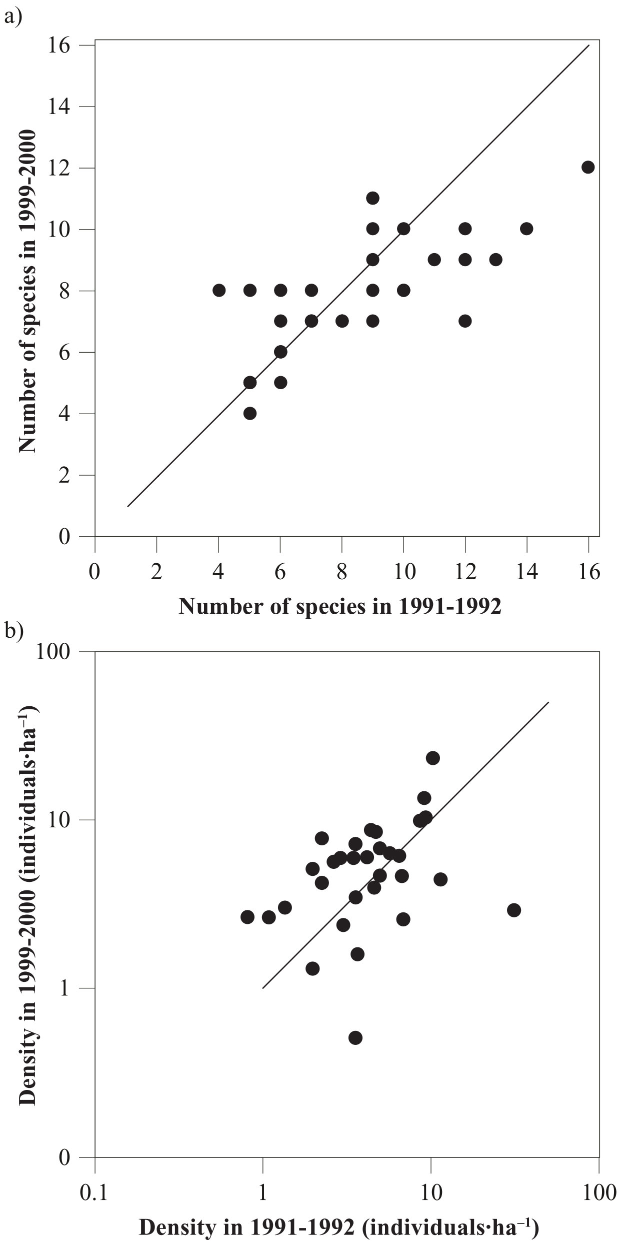

FIGURE 1. (a) The relationship between urban wintering bird species richness in 1991-1992 and 1999-2000. (b) The relationship between urban wintering density of birds (in $\log_{10}$ scale) in 1991-1992 and 1999-2000. The continuous line indicates that species richness or bird density were the same in both winters. Note that density is on a logarithmic scale.

TABLE I. Multiple regression models for wintering bird species richness and density in the winter of 1999-2000, and stability of the community estimated by the percentage dissimilarity index (PDI). Human density and species densities were $\log_{10}$-transformed.

Variable	Coefficient	SE	Test value (t)	P
Model for species richness 1999-2000			$F_{3, 27} = 9.92$	0.000
Constant	14.1	9.4	1.50	0.145
Latitude	–0.2	0.1	–1.16	0.254
Human density	0.1	0.5	–0.24	0.811
Species richness 1991-1992	0.4	0.1	3.58	0.001
Model for species density 1999-2000			$F_{2, 27} = 5.70$	0.004
Constant	2.3	1.4	1.66	0.108
Latitude	–0.04	0.02	–1.78	0.086
Human density	0.23	0.10	2.25	0.033
Species density 1991-1992	0.16	0.16	0.97	0.339
Model for PDI			$F_{2, 28} = 4.22$	0.025
Constant	158.4	76.9	2.06	0.049
Latitude	–1.2	1.1	–1.10	0.279
Human density	–15.5	5.3	–2.90	0.007

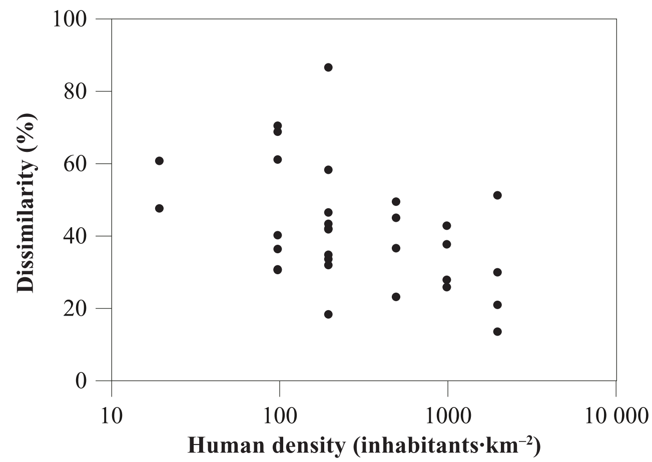

FIGURE 2. The relationship between human density (on a logarithmic scale) and percentage dissimilarity at each site in which birds were counted.

results. Some studies suggest that the stability of species assemblages decreases with increasing latitude (Pianka, 1966; Järvinen, 1979), while others have not found any correlation between stability and latitude (Noon, Dawson & Kelly, 1985; Bethke, 1993; Bengtsson, Baillie & Lawton, 1997). Unfortunately, neither we nor the Finnish Nation Wide Winter Bird Monitoring Network had corresponding winter bird data from more natural habitats.

With regard to studies of European terrestrial bird communities, Järvinen (1979) concluded that environmental unpredictability, for example variation in climate harshness, increases northward and causes a decrease in the stability of breeding bird communities. Our data from human-dominated environments support this prediction. We did not measure the effects of any human-related food on bird abundance in this study. Earlier studies have indicated that household density correlates significantly with spatial variation in the density of bird feeder provision by people, and the density of feeding stations across urban environments was positively correlated with avian abundance (Fuller *et al.*, 2008). This suggests that the provision of feeders may have contributed to the patterns we found.

URBANIZATION AND PERSISTENCE OF THE WINTERING BIRD COMMUNITY

We found that urbanization stabilizes the temporal variation of winter bird communities. This can be explained by at least 3 non-mutually exclusive hypotheses. First, environmental predictability may increase community stability (Järvinen, 1979). Winter conditions in towns, for example, may have more stable microclimates in winter because towns tend to have higher air and surface temperatures than their rural surroundings (Oke, 1997). During winter nights, the temperature of a town centre in northern Finland can be up to 5-7 °C higher than the surrounding forest areas (J. Jokimäki, unpubl. data). Thus, urban environments often have a longer growing season due to higher air temperatures and higher precipitation (Marzluff, 2001; Marzluff, Bowman & Donnelly, 2001b). Additionally, Bengtsson, Baillie, and Lawton (1997) found that the level of bird community stability was related to habitat variability. The stability of community structure among duck guilds, however, has been shown to be independent of both habitat variability and latitude (Bethke, 1993).

Second, bird communities may be stabilized by ecosystem productivity (Järvinen, 1979). However, neither Järvinen (1979) nor Bethke (1993) found a correlation between ecosystem productivity and the stability of bird communities. Urban areas are characterized by high resource abundance due to high primary productivity and the large amount of extra food provided by humans (Marzluff, Bowman & Donnelly, 2001b; Robb *et al.*, 2008). For example, most abundant wintering species are able to use both winter feeding sites and other anthropogenic food sources, which provide continuous, diverse, and abundant winter food resources for birds (Jokimäki & Suhonen, 1998; Jokimäki & Kaisanlahti-Jokimäki, 2003). Such food sources may increase the stability of bird communities (Fuller *et al.*, 2008). However, we found a high level of variation in total bird species densities in towns.

Finally, only a few species are well adapted to life in urban environments; these species outnumber others all over the world, causing increased community homogeneity (Blair, 2001; Clergeau *et al.*, 2006; McKinney, 2006; Sorace & Gustin, 2008). These generalist species, such as omnivore or seed-eating species using feeding tables and other anthropogenic food sources, may stabilize the variation in urban bird community structure between years (Devictor *et al.*, 2007).

Conclusion

According to our results, urbanization stabilizes between-winter variation in bird species communities. Thus, we did not observe latitudinal patterns of variation in species richness or stability of community composition in human-dominated sites. We assume that the presence a continuous, rich, and diverse food supply provided by humans may reduce between-year variation in wintering bird communities with an increasing urbanization level. Finally, only a few wintering species are likely to be well adapted to life in urban environments, and as a result populations of these few species tend to outnumber other species on a global scale. We suggest that this may also contribute to the overall factors that reduce temporal variation in wintering bird communities.

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