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Article

Differential Long-Term Population Responses of Two Closely Related Human-Associated Sparrow Species with Respect to Urbanization

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Simple Summary: Sparrow species, especially the House Sparrow, live in a close association with people. Therefore, understanding their population status and trends will also help in monitoring the quality of environments where most people live. We studied population trends of the House Sparrow and the Eurasian Tree Sparrow in Europe, and in more detail in Finland. At the European level, population trends of both sparrow species differed between countries, although the decrease in the House Sparrow was quite clear. In many European countries, the population status of the House Sparrow is either threatened or still unknown. Our long-term (1991–2020) field study indicated that wintering populations of the House Sparrow have decreased, whereas the Eurasian Tree Sparrows have both expanded their wintering range and increased their population size in Finland. We did not find significant interspecific competition between the study species. The House Sparrow has suffered from decreased winter feeding activities and increased human population size within human settlements in Finland. To understand in more detail the population trends and habitat needs of sparrows, citizen science-based projects will be suitable tools.

Abstract: Urban planning and management need long-term population level studies for evaluating how urbanization influences biodiversity. Firstly, we reviewed the current population trends of the House Sparrow (*Passer domesticus*) and the Eurasian Tree Sparrow (*Passer montanus*) in Europe, and evaluated the usefulness of citizens' science projects to monitor these species in Finland. Secondly, we conducted a long-term (1991–2020) winter field study in 31 urban settlements along a 950 km north–south extent in Finland to study how latitude, weather and urbanization influence on sparrow's growth rates. The House Sparrow is declining in 15 countries, and increasing in 5, whereas the Eurasian Tree Sparrow is declining in 12 and increasing in 9 European countries. The trend of the House Sparrow was significantly negative in continental Europe. However, the trend of the Eurasian Tree Sparrow was not significant. Both species have declined simultaneously in six countries, whereas in four countries, their trends are opposite. Citizen-based, long-term (2006–2020) winter season project data indicated that House Sparrow has decreased, whereas Eurasian Tree Sparrow has increased in Finland. However, the short-term (2013–2020) breeding season citizen-based project data did not indicate significant changes in the occupation rate of sparrows. Our long-term (1991–2020) field study indicated that wintering populations of the House Sparrow have decreased, whereas the Eurasian Tree Sparrows have both expanded their wintering range and increased their population size. Based on our winter count data, latitude and weather did not significantly influence the growth rates of sparrows. When the human population increased within the study plot, House Sparrow populations decreased, and vice versa. There was also a trend that a decreasing number of feeding sites has decreased the House Sparrow numbers. Urban-related factors did not influence the growth rate of the Eurasian Tree Sparrow. Our results indicate that the colonization of a new, even closely related species does not influence negatively on earlier urbanized species. It is probable that the niches of these sparrow species are different enough for allowing them to co-occur. The House Sparrow mainly nests on buildings, whereas the Eurasian Tree Sparrow can easily accept, e.g., nest boxes.



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Urban planning should take care of both the food availability and nest sites availability for both sparrow species.

Keywords: *Passer domesticus*; *Passer montanus*; long-term study; winter; feedingsites; growth rate

1. Introduction

Increasing urbanization and human pressure on lands have important impacts on biodiversity, species distribution and abundances. For example, changes in bird communities and populations have been shown to be linked to urbanization [1,2], and several studies have indicated that populations of many species have declined due to urbanization [3]. However, at the same time, some synanthropic species thrive well within human settlements [4,5]. Many different mechanisms, such as human-induced food availability, milder micro-climate and reduced predator abundance, have been suggested to be responsible for positive changes in urban bird species richness and population abundances [1,3]. Especially during winter, high artificial food abundance and predictability through feeding sites may benefit those species that are able to use these resources [6–10]. In general, some species, known as “urban exploiters”, generally manage well in urban landscapes [11]. At the same time, reduced insect availability, e.g., due to the air pollution (see review for [12]), diseases [13–15] and toxins [12,16] as well as cats [17–19] may have negative impacts on birds. In general, cavity-nesters, grani- or omnivores and resident bird species have been reported to do well in urban environments [3,20]. Additionally, a wide distribution range and sociability of species have been suggested to favor the urbanization of bird species [21,22].

The House Sparrow (*Passer domesticus*) and the Eurasian House Sparrow (*Passer montanus*) are closely related and are well-known species for their habit of living in a close association with humans, their wide distribution ranges, resident way of life, cavity nesting breeding habits as well as their omnivorous/granivorous diet. Therefore, both species are predicted to do well in cities. The House Sparrow is one example of a very successful urban bird species, and except for a few cases, the House Sparrow does not breed away from human settlements [23]. Avery and Lockwood [24] have indicated that many different factors related, e.g., to their propensity to live with human settlements, good reproductivity ability, flocking behavior, boldness and general behavioral flexibility, are behind the House Sparrow’s successful and rapid introduction history in North America. However, the House Sparrow has shown a worldwide decline [25–30], whereas the population trends of the Eurasian Tree Sparrow are not so clear [31]. Despite the wide distribution range and large population sizes, the House Sparrow populations have especially been declining in Europe, in its native distribution area [26,27], but also in its non-native distribution areas in North America [30]. In Europe, the declines of the House Sparrow started firstly in rural areas [26,28]. However, the decline of House Sparrow populations since the mid-1990s has mainly occurred in urban areas, both in Europe [26] and in North America [30]. Unlike the farmland decline of the House Sparrow, the urban decline appears to be proceeding at an increasing rate and is showing no sign of stabilization [32]; but see [31]. As sparrows live in such close association with people, changes in their populations also indicate the living conditions of human beings. Therefore, sparrows are useful indicators of urban environments, and understanding their population trends will help to develop healthy urban environments. However, the primary causes of the decline of the House Sparrow, especially in urban habitats, are still inadequately understood [26]. It is important to determine why the House Sparrow abundances are still decreasing in urban landscapes, while their current rural populations have remained quite stable in recent years [30].

At the same time, a closely related species of the House Sparrow, the Eurasian Tree Sparrow, has been expanding its range in many European countries [31], as well as its non-native distribution area in the North America [33]. However, there is also some evidence that the Eurasian Tree Sparrow numbers have declined in some European countries [31].

In general, there seems to be no agreement as to why the Eurasian Tree Sparrow is decreasing in some areas, but expanding in some other areas. When studying sparrows' co-occurrence patterns, it is important to evaluate the mechanisms by which species can or cannot co-occur. According to Lepczyk et al. [20], one important urban bird research area is species interactions, since those interactions can influence species distribution. Some level of competition might also be apparent between the two closely related sparrow species [23]. It might be also possible that the Eurasian Tree Sparrow has filled the empty niches that the disappearances of the House Sparrow have caused.

Most of the earlier sparrow studies have been performed during the breeding seasons, despite the fact that winter conditions and the recent warming of winters may have important consequences for the distribution and abundance of resident sparrow species (see, e.g., [34,35]). Sparrows' winter distribution ranges, occupancy and abundance may be restricted by several factors, such as the temperature, food availability, behavioral adaptations and urbanization, which all may also interact [36,37]. Therefore, winter season studies may give new insights into the causes of the population change of sparrows. In addition, the results of resident species will give new insights into factors that operate at the given city scale, whereas conditions along a migratory route or at the long-distance overwintering areas might reduce the usefulness of migrants as city-scale indicators.

To understand in more detail how urbanization influences urban bird species, large-scale and multi-year studies that use similar study designs and methods are urgently needed (see, e.g., [20,38,39]). Partly due to practical reasons, researchers have normally monitored urban bird populations in a single town or few towns simultaneously, and only during a short term (normally 1–2 years; see reviews [38–40]), thereby partly neglecting especially temporal factors influencing urban bird populations [40]. To better understand urban species occupancy and population trends, and factors affecting them, a sound long-term monitoring of urban species is needed [40].

In many countries, long-term and large-scale bird monitoring work is based on observations made by voluntary bird watchers (amateur ornithologists) and by the use of citizen science. One challenge of these kinds of monitoring and data collection methods is related to possible variation of the data quality due to a non-standardized sampling effort, different detection abilities between observers and a lack of standard study protocols [41]. Long-term data sets collected with the exact same sampling design, methods and the same professional researchers will be needed to better understand long-term changes of animal populations. Even in the case of sparrows, urban and suburban populations are not currently adequately monitored, even if they are their main living habitats [26].

The conflicting results of the population trends and their causes between the two sparrow species, and between European countries, raise several questions. Why have these species declined in some places, but increased in some other areas? Is there competition between the two sparrow species or do their ecological niches differ? Do different factors influence the occurrence and abundance of the two sparrow species? To be able to answer these questions, we used multi-scale and long-term data.

We compared long-term population trends of the House Sparrow and the Eurasian Tree Sparrow across multiple scales; on a continental scale in Europe, and in more detail in Finland. Firstly, we extracted available data about the population trends of the two sparrow species in Europe. We evaluated whether the population trends of the two sparrows differed between countries. We predicted that some continental-level factor would be behind the changes of sparrow populations if the sparrow populations show similar trends in different countries. Alternatively, if population trends differed between countries, then local-level factors would be more important. Secondly, we extracted data collected by the different kinds of citizen-based projects in Finland to evaluate whether the results of these kinds of projects are useful to monitor the urban sparrow populations. Thirdly, we counted sparrows and their potential predators in 31 urban settlements during four winters along a long time period: 1991–2020, along a 950 km latitudinal gradient in Finland. Using our winter count data, we studied whether the latitude, weather conditions

and urbanization influences the population trends and population growth rates of the wintering House Sparrows and the Eurasian Tree Sparrows. We predicted that especially the southerly distributed Eurasian Tree Sparrow would benefit from the warming climate, and correspondingly, its range would expand towards the north. As a more urbanized species, the House Sparrow was not predicted to react to an increasing level of urbanization, whereas the Eurasian Tree Sparrow was predicted to suffer from urbanization [42]. Moreover, since the role of winter food availability was detected earlier to be important for wintering birds [6–8,10,43], we studied how the changes in numbers of winter feeding stations influenced population trends of the two sparrow species. As the data collected during 1985–2007 indicated that the amount of food (mainly sunflower seeds) offered for the birds increased in Finland, we predicted that overwintering sparrow species would benefit from the feeding [44]. However, there have been remarks that food offered for the birds later decreased, and at the same time, diversified. We predicted that a decrease in feeding was a disadvantage for the House Sparrow, whereas diversified food supply was beneficial, especially for the Eurasian Tree Sparrow [44]. Lastly, by using multiple data sets, we evaluated whether there was any indication about the possible interspecific competition or heterospecific attraction between the House Sparrow and the Eurasian Tree Sparrow. Only a few studies have analyzed interspecific strategies of how urban sparrows may interact (see [42,45–48]). We predicted that if interspecific competition between two closely related species explains population trends, then there would be a negative correlation between population growth rates between species. However, if there was a positive correlation between population growth rates between species, then there would be a positive attraction between species.

2. Materials and Methods

2.1. Study Species

Both of the study species belong to the Passeridae family. They are small-sized species (House Sparrow, average mass 24 g; Eurasian Tree Sparrow, average mass 22 g), and sedentary in most parts of their wide distribution ranges [49]. According to Cordero and Senar [45], the House Sparrow is a dominating species over the Eurasian Tree Sparrow. Both species are native in Europe, and live close to humans. Both the House Sparrow and the Eurasian Tree Sparrow are listed in Europe as SPEC3 species (i.e., species whose global population is not concentrated in Europe, but which is classified as regionally extinct, critically endangered, endangered, vulnerable, near threatened, declining, depleted or rare at European level; [31,49]).

According to the last Finnish Breeding Bird Atlas (2006–2010), the House Sparrow breeds in the whole country, although its distribution is not continuous in northern Finland (>65° N), where human population is also patchily distributed [50]. However, the continuous distribution area of the Eurasian Tree Sparrow is restricted to south-western Finland, and the species is absent from half of the country [50]. Currently, the House Sparrow is included in the Red List of Finnish Species as an endangered (EN) bird species, whereas the Eurasian Tree Sparrow was not included as a Red List species in Finland [51].

2.2. Study Areas and Materials

Population trends of the House Sparrow and the Eurasian Tree Sparrow in European countries (47 European countries, and the Faroe Islands, Gibraltar and Greenland) were extracted from country-based pages of the BirdLife International (2017) publication [31]. In this publication, there is a column that indicates the direction of the population trend (increase, decrease, stable, fluctuating or unknown) in each country since 2000. Later, we only used data from those countries (27 countries) from which trend data (indicated either an increase, decrease or stable) were available from both species for statistical testing.

We extracted raw data from the two Finnish citizen science-based bird projects led by BirdLife Finland; the Yard Birding Event arranged during mid-winter [52] and the Nest Box Twitching Event arranged during the breeding season [53]. Since 2006, the Yard Birding

Event has been arranged yearly during the last weekend of January. In this project, people record all species and individuals observed during one hour within or from their yard. The average number of participating yards per winter has been 10,752 (range 4646–15,923). From this data set, we extracted the percentage of yards from the total participating yards where the House Sparrow and the Eurasian Tree Sparrow were observed during different winters. Since 2013, the Nest Box Twitching Event has been arranged yearly during either the first or second weekend of June. In this project, participants report, for example, what kinds of nest boxes and how many of them they have in their study site, and which species are using these nest boxes. About 3000 sites have participated in this project yearly, and about 30,000 nest boxes are reported each year [53]. From this data set, we extracted the percentage of sites where the House Sparrow and the Eurasian Tree Sparrow were detected. In both citizen science projects, the study sites are quite evenly located though Finland. National Finnish population growth rate values (λ) of the House and Eurasian Tree Sparrow were extracted from the supplement of Fraixedas et al. [54].

Our winter field study data originate from 31 towns and villages located in the northern coniferous forest biome in Finland [55–57]. The study areas were situated relatively evenly along a 950 km north–south extent (60° N–68° N; [55]). Most of study plots were about 30 ha (mean \pm SD: 31.2 \pm 7.7 ha). The study areas included urban settlements, ranging from large towns to small villages, and both habitat types were located across Finland. The human populations in these communities ranged from 300 to 159,000 people (mean 21,694 \pm 34,018 (SD) inhabitants [55]). The variation in local habitat structure and edge effects were minimized by selecting each study plot from the most heavily urbanized area of each town or village. All study plots contained buildings, roads and scattered green areas between buildings [55]. More details of the study plots are given in Table 1.

Table 1. Amount of built area, number of buildings and inhabitants within the study plots; and winter temperature (average daily value of the Finnish winter months: December, January and February), permanent snow arrival and snow amount at the study region (1st of October is day 1). Differences between study winters is tested by the Friedman’s two-way ANOVA. Pairwise significance values have been adjusted by the Bonferroni correction for multiple tests, and different letters indicate differences between the study winters (at the $p < 0.01$ level).

		Year				Friedman Test		
		1990	2000	2009	2019	χ^2	df	p
Built area (ha)	Mean	1.5A	1.7B	1.8C	1.9C	69.04	3	<0.001
	SD	1.9	2.2	2.4	2.4			
Number of buildings	Mean	16.9A	17.4B	17.5B	17.5B	7.90	3	0.043
	SD	7.4	7.3	7.4	6.9			
Number of inhabitants	Mean	136.6	144.5	143.8	146.6	3.12	3	0.374
	SD	121.3	137.7	142.9	152.5			
Winter temperature (°C)	Mean	−4.4A	−6.8B	−11.8C	−2.5D	91.58	3	<0.001
	SD	2.2	3.3	2.0	3.1			
Snow arrival	Mean	76.4A	60.9B	51.6B	64.8B	23.74	3	<0.001
	SD	17.8	16.0	35.7	49.5			
Snow amount (cm)	Mean	18.8	24.4	17.2	22.2	4.78	3	0.189
	SD	11.7	16.3	7.3	22.9			

To evaluate the level of urbanization and their changes in the study plots, we estimated the average number of inhabitants, average area of buildings and number of buildings from each study site by using a 250 m \times 250 m square database (© SYKE and TK, 1990, 2000, 2009 and 2019; Table 1). As several (2–6) 250 m \times 250 m squares were inside or crossed our study plot squares, we used an average value of those squares to estimate the urbanization level in every bird survey study plot. The same squares were used in different study years. All of these urban indices were significantly intercorrelated (number of inhabitants vs. area of buildings ($r = 0.950$, $p < 0.001$), number of inhabitants vs. number of buildings

($r = 0.478$, $p = 0.006$) and area of buildings vs. number of buildings ($r = 0.394$, $p = 0.028$; $n = 31$) in all cases).

Meteorological data (winter temperature ($^{\circ}\text{C}$), arrival date of the permanent snow cover, and amount of snow (cm) during the 15 December) were extracted from the open-access database of the Finnish Meteorological Institute [58]. For the winter temperature, we used the average daily temperatures of all days of the Finnish winter months (December, January and February). When dating the arrival of the permanent snow cover, the 1st of October was indicated as the day 1, whereas the last day (29 February) obtained a value 152. The earlier the snow arrived, the smaller the number it received. By permanent snow cover, we mean a continuous snow cover (at least 5 cm) that stayed on the ground for at least 7 days. All meteorological data were extracted from the nearest meteorological station of each study site.

2.3. Winter Bird Counts

Wintering House Sparrows and Eurasian Tree Sparrows were counted by the single-visit study plot method, where all individuals seen or heard within the study plot were recorded [59]. Overflying individuals, which did not land and stay on the study plot, were excluded from the analyses. The earliest censuses were conducted during late December and the latest censuses were conducted during early February, i.e., during the mid-winter period in Finland. We counted the birds during four different winters: 1991–1992, 1999–2000, 2009–2010 and 2019–2020. We suppose that due to the long intervals between study winters, our winter bird samples are independent from each other. For example, according to the Finnish ring-marking data, the oldest recoveries of the House Sparrow have been 7–9 years, and the oldest recoveries of the Eurasian Tree Sparrow have been 5–6 years [60]. Twenty-nine study plots were censused during all four winters, whereas two study plots (Ruokolahti and Muhos villages) were not surveyed during the winter of 2009–2010. During the sparrow surveys, we also surveyed potential predators of the sparrows (Eurasian Sparrowhawk, *Accipiter nisus*; Northern Goshawk, *Accipiter gentilis*; Eurasian Pygmy Owl, *Glaucidium passerinum*; and cats) from the study plots. Additionally, the number of active feeding sites (i.e., sites that contained food during the surveys) located in the study plots was counted during the first and last survey years. The change of the number of feeding sites (delta number of feeding sites) did not correlate significantly with the changes in the area of buildings ($r = -0.018$, $p = 0.923$), the number of buildings ($r = -0.011$, $p = 0.954$) and the number of inhabitants in the study plot ($r = -0.121$, $p = 0.518$, $n = 31$) in all cases.

Of the total of 122 bird counts, J.J. conducted 41% and J.S. 37%, and the rest of the surveys were conducted by 15 ornithologists (most of them only conducted a single survey). Therefore, the observer of the study plot changed very rarely between the study winters, decreasing the possible bias caused by different detectability abilities of the observers. All of the researchers have tens of years' experience both in birding and bird surveys. Therefore, we assumed that the possible inter-observer bias was minimal in this study.

All surveys were conducted in good (windless and no rain/snowing) weather conditions at midday, when the light availability allowed one to detect birds (practically in our case only between 10.00 and 15.00). To avoid the possible effects of weekend vs. working days bias (e.g., traffic noise is greater during working days than weekends) on survey results, most of the surveys were conducted during working days, Monday through Friday. To avoid double counts of individuals, we used a relatively high census rate (30 ha/h). The surveys were not conducted along a single route through the plots but instead as a zig-zag walk through the plots. During the surveys, we also visited the backyards of the buildings. This kind of survey reduces many of the problems associated with counting birds in urban areas, e.g., varying visibility and noise [6]. As birds were not defending their winter areas by singing in our northern study latitudes, singing behavior did not affect species detectability. In the north, many wintering birds often forage on bird feeders, partly due to the low temperatures, a short daytime (4–6 h) and a snow cover. In general,

feeding sites are more abundant in urban than in rural or more natural forest areas [6,61]. Therefore, most overwintering birds within human settlements are concentrated in quite a few restricted feeding sites from where they are quite easy to detect. Additionally, a scarce vegetation cover during the winter, due to the absence of leaves on deciduous trees and shrubs, increases the visibility of birds, and thereby survey efficiency.

We used the single-visit survey method for practical reasons to obtain a sufficiently large number of spatial replicates for statistical analysis. In addition, due to the short mid-winter days with low light conditions at northern latitudes, the identification of birds is possible only during midday (4 h). Earlier studies have indicated that a single-visit census during winter enables the detection of approximately 90% of the species and 80% of the individuals in urban environments [6]; see also [62]. Therefore, we suppose that the efficiency and accuracy of the winter season bird surveys is high.

2.4. Data Analyses

We used long-term population trend data of the House Sparrow and Tree Sparrow from 27 countries in Europe [31]. We recorded population trends in each European country for our analyses in a following way: if sparrow population had decreased, then the trend was coded -1 , in a stable population size, the trend was coded as 0 and if the populations had increased, the trend was recorded as $+1$.

We used the One Sample t -test to analyze population trends of sparrow species in Europe. In the One Sample t -test, we used zero (0) as a reference number. This value indicates that population size was stable, and neither decreased nor increased during the study period. We used the Related-Samples Sign Test to analyze the between-species occurrence of sparrow species. When analyzing the trends of sparrow species observed in the Yard Birding [52] and the Nest Box Twitching Event [53], we used the Spearman Rank Correlation Coefficient. We used the Paired Sample t -test to analyze relationships between the proportional occupancy of the House Sparrow and the Eurasian Tree Sparrow in the sites of the Nest Box Twitching Event.

We estimated population growth rates (λ) with time interval corrected methods [63]:

$$\lambda = \log_{10} (N_{i+1}/N_i) / (\text{study interval}),$$

where study interval = $\sqrt{(t_{i+1} - t_i)}$, t_i = year of study winter; and N_i = number of individuals during study winter i and N_{i+1} = number of individuals during study winter $i + 1$.

If we did not find any sparrows either during a previous study winter or a later study winter within the same study area (i.e., in cases when $N_{i+1} = 0$ or $N_i = 0$), we added one 'unseen individual' for the data set; otherwise, it is impossible to calculate λ -value. Therefore, the method of calculating λ -values is conservative. We used an average λ -value of each study area as an independent observation for statistical tests. Eurasian Tree Sparrows were lacking from five study areas, and therefore, we were unable to calculate population growth rate values for those study areas.

We used the Friedman's two-way ANOVA to test differences in House Sparrow and Eurasian Tree Sparrow abundance between the four study winters. The study site was used as a "block" variable in Friedman's two-way ANOVA. In this analysis, we excluded two study sites (Ruokolahti and Muhos), which only had data in three winters. Friedman's test was also used to study differences of site-specific urban factors as well as climatic factors between the study winters.

After firstly checking that the assumptions of the parametric test were fulfilled, we used the Pearson correlation to examine the relationship between the population growth rate (λ), latitude and factors related to the urbanization level. Latitude was measured as kilometers from the most southern study area ($=0$ km) to most northern one ($=914$ km). We used the Spearman Rank Correlation to examine the relationship between the population growth rate (λ) of the sparrow species and the changes in the number of inhabitants, average area of buildings, number of buildings and number of feeding sites during the study winters because the data did not fulfill the assumption of the parametric statistical test.

All the data analyses were performed using the IBM SPSS statistical package, version 26.

3. Results

3.1. House and Eurasian Tree Sparrow Trends in Europe and Finland

Since 2000, the House Sparrow has had a declining trend in 15 European countries, an increasing trend in 5 countries, a stable population in 14 countries and the situation is unknown in 9 countries (Table S1). In general, the House Sparrow population has decreased (One Sample *t*-test; $t = -2.80$, $df = 26$, $p = 0.001$) in continental Europe. The Eurasian Tree Sparrow has had a declining trend in twelve countries, an increasing trend in nine countries, a stable population in nine countries and the situation is unknown in nine countries (Table S1). The Eurasian Tree Sparrow population size has been stable in continental Europe (One Sample *t*-test; $t = -0.24$, $df = 26$, $p = 0.814$). Both species have declined simultaneously in six countries, whereas there are four countries where the House Sparrow has had a declining trend, but the Eurasian Tree Sparrow has had an increasing trend (Table S1). However, the observed trend of the House Sparrow did not influence the observed trend of the Eurasian Tree Sparrow (Related-Samples Sign Test; $z = -0.75$, $p = 0.454$, $n = 26$).

According to the data of Yard Birding Event (2006–2020), the proportion of yards with House Sparrows decreased ($r_s = -0.902$, $p < 0.001$, $n = 15$), whereas the proportion of yards with Eurasian Tree Sparrows increased ($r_s = 0.873$, $p < 0.001$, $n = 15$) in Finland.

According to the data of the Nest Box Twitching Event (2013–2020), neither the proportion of sites with House Sparrows ($r_s = 0.357$, $p = 0.358$, $n = 8$) nor Eurasian Tree Sparrows ($r_s = 0.405$, $p = 0.320$, $n = 8$) changed significantly. However, the Eurasian Tree Sparrow occupied more study sites than the House Sparrow (Paired Sample Test; $t = 3.65$, $df = 7$, $p < 0.001$).

3.2. Winter Data and Sparrow Surveys

3.2.1. Background Variables

The built-up cover of the first and second study winters was lower than during the later study winters (Table 1). The total number of buildings was lower during the first study winter than the later winters (Table 1). There were no differences in the number of inhabitants in the study plots between the study winters (Table 1).

Winter temperatures differed between all study winters: the warmest winter was 2019/2020, followed by 1991/1992, 1999/2000 and 2009/2010 (Table 1). The snow arrived later on the study sites during the winter of 1990/1991 than the other winters (Table 1). There were no differences in the amount of the snow (cm) between the study winters (Table 1).

The total number of winter feeding sites was greater at the beginning of the study (1991/92; mean = 11.94, SD = 11.95, $n = 31$) than at the end of the study (2019/2020; mean = 6.55, SD = 6.01; Paired *t*-test, $t = 3.51$, $df = 30$, $p = 0.001$).

During the sparrow surveys, avian predator species were only detected during nine surveys (Eurasian Sparrowhawk: 1999–2000 in Turku and Rovaniemi; 2009–2010 in Kotka; Northern Goshawk: 2009–2010 in Kouvola, Turku, Jyväskylä, Oulu and Saarenkylä; Eurasian Pygmy Owl: 1999–2000 in Tapionkylä). No cats were observed in the study plots.

3.2.2. Population Trends during Winters

During the first study winter (1991/1992), the House Sparrow occurred in almost all study sites (30 out of 31), whereas the Eurasian Tree Sparrow was only found in four study sites. During the last study winter (2019–2020), both the House Sparrow and the Eurasian Tree Sparrow were found almost in all study sites (28 and 26 out of 31, respectively).

The abundance of House Sparrow decreased (Friedman's two-way analysis of variance, $\chi^2 = 8.67$, $df = 3$, $p = 0.034$; Figure 1a), whereas the abundance of Eurasian Tree Sparrow increased during the study period (Friedman's two-way analysis of variance, $\chi^2 = 34.68$, $df = 3$, $p < 0.001$; Figure 1b).

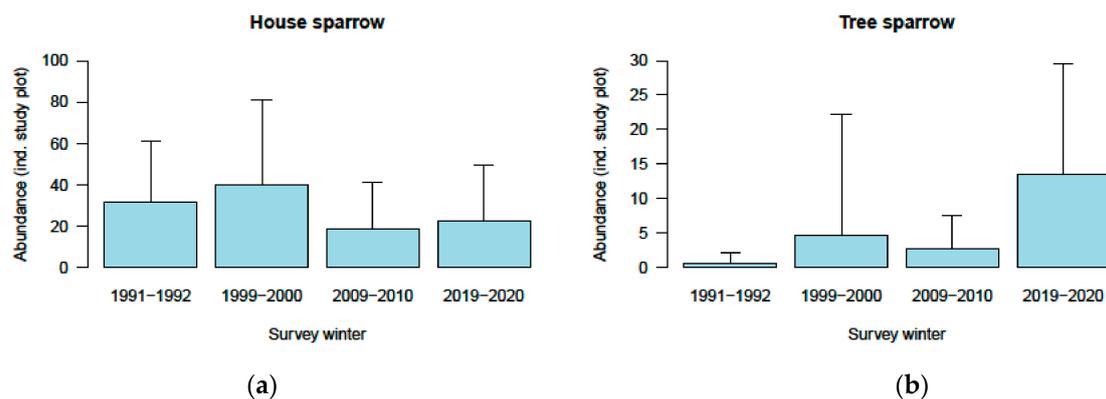


Figure 1. Average abundance ($\pm 95\%$ confidence intervals) of House Sparrow (a,b) Eurasian Tree Sparrow in 31 study sites during four study winters (1991–1992, 1999–2000, 2009–2010 and 2019–2020) in Finland.

The population growth rate (λ) of the House Sparrow, calculated to each study site separately, varied from -0.40 to 0.39 . The population growth rate (λ) was negative in over half of the study sites (17 out of 31; Figure 2a). However, the average population growth rate (λ) of the House Sparrow was -0.06 ($SD = 0.21$, $n = 31$), and it did not differ from zero (One Sample t -test, $t = -1.58$, $df = 30$, $p = 0.125$), indicating an only slight decrease during 1991–2020.

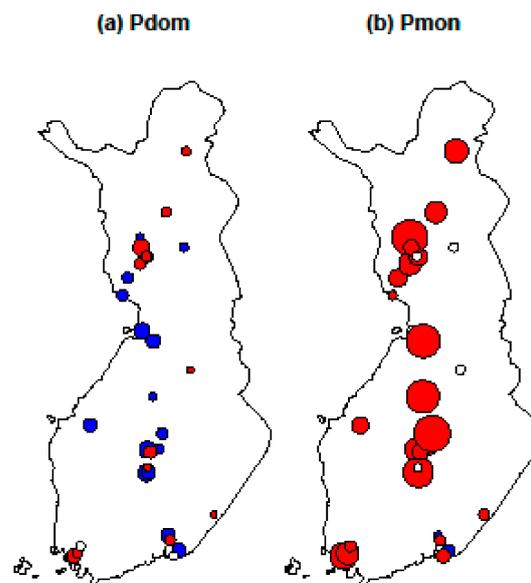


Figure 2. Population growth rates of House Sparrow (Pdom; a) and Eurasian Tree Sparrow (Pmon; b) in 31 study sites in between winters 1991–1992 and 2019–2020 in Finland. The size of the dot indicates the population growth rate (the larger the dot, the greater the change), and color of dot indicates direction (red positive, blue negative and open dot zero growth rates; or it was impossible to calculate the growth rate due to lack of species as in some cases of Eurasian Tree Sparrows).

The population growth rate (λ) of the Eurasian Tree Sparrow varied from -0.21 to 1.12 . The population growth rate (λ) was positive in almost all the study sites (23 out of 26; Figure 2b). The average population growth rate (λ) of the Eurasian Tree Sparrow was 0.46 ($SD = 0.37$, $n = 26$), and it was larger than zero (One Sample t -test, $t = 6.44$, $df = 25$, $p < 0.001$), indicating a clear increase in the Tree Sparrow population during 1991–2020.

Our data indicated a little bit of a greater decrease rate (mean $\lambda = -0.06$) of the House Sparrow than the Finnish bird monitoring work ($\lambda = -0.0189 \pm 0.0007$ (SD)), but the growth rates did not differ from each other (One Sample t -test; $t = -1.066$, $df = 30$, $p = 0.295$). Our data indicated a greater increase rate (mean $\lambda = 0.46$) of the Eurasian

Tree Sparrows than the Finnish bird monitoring work ($\lambda = 0.1248 \pm 0.0093$ (SD); One Sample *t*-test; $t = 4.697$, $df = 25$, $p < 0.001$).

3.2.3. Factors Affecting Wintering Sparrows

Neither the growth rates (λ) of the House Sparrow nor of the Eurasian Tree Sparrow correlated significantly with the latitude ($r = 0.10$, $p = 0.582$, $n = 31$; $r = 0.26$, $p = 0.193$, $n = 26$; respectively). The growth rate of the House Sparrow and the Eurasian Tree Sparrow did not correlate significantly with each other ($r = 0.03$, $p = 0.873$, $n = 26$).

The average growth rate (λ) of the House Sparrow did not correlate significantly with the average area of the buildings ($r = 0.003$, $p = 0.986$), number of buildings ($r = -0.052$, $p = 0.782$) and number of inhabitants in the study plot ($r = -0.006$, $p = 0.976$; $n = 31$ in all cases). The average growth rate of the Eurasian Tree Sparrow did not correlate significantly with the average area of buildings ($r = 0.026$, $p = 0.901$), number of buildings ($r = -0.197$, $p = 0.335$) and number of inhabitants in the study plot ($r = -0.041$, $p = 0.842$; $n = 26$ in all cases).

Changes in the number of inhabitants, average area of buildings and number of buildings in the study site did not influence the growth rates of the sparrow species during 1991–2020 (Spearman Rank Correlations; $p > 0.05$, results not shown), except that when the number of inhabitants increased within the plot during the study years, the House Sparrow populations decreased, and *vice versa* ($r_s = -0.418$, $p = 0.019$, $n = 31$ Figure 3).

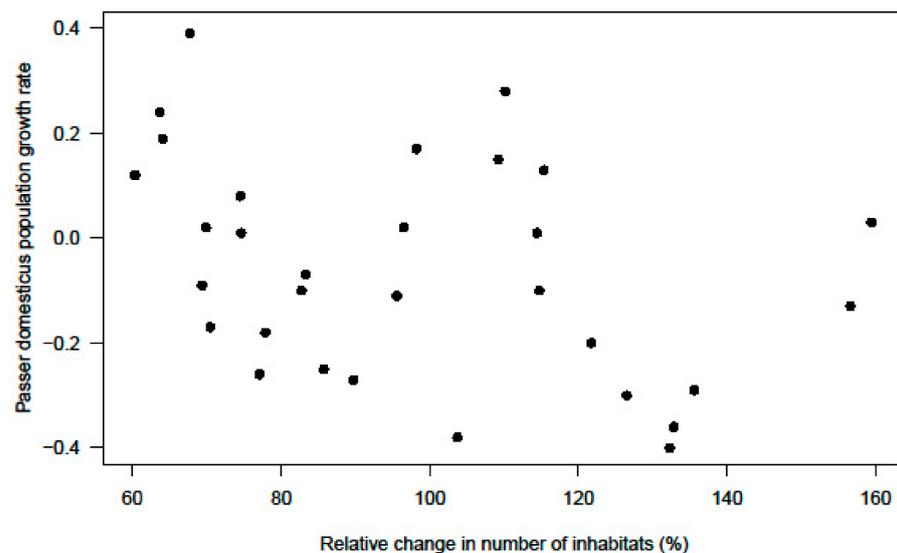


Figure 3. The relative change of number of inhabitants in each study area (%) in relation to population growth rates (λ) of House Sparrow in each of the 31 study sites between winters 1991–1992 and 2019–2020 in Finland. Values below 100% at the *x*-axis indicate that human population size was decreased and above 100% indicate that population was increased between study periods. The negative growth rate values (λ) indicate that the House Sparrow population size was decreasing and the positive values indicate that population size was increasing.

There was a tendency to observe that the decrease in winter feeding sites of birds during the study period (measured in changes in the number of feeding tables between winters 1991–1992 and 2019–2020) decreased the population growth rate of the House Sparrow ($r_s = 0.33$, $n = 31$, $p = 0.074$, $n = 31$), but no corresponding changes were observed in the case of the Eurasian Tree Sparrow growth rate ($r_s = 0.12$, $n = 26$, $p = 0.552$, $n = 26$).

4. Discussion

Our results indicate that there is great variability in the population trends of the House Sparrow and the Eurasian Tree Sparrow in Europe. This suggests that there is no single, common large-scale factor that has impacted their population trends. Citizen-based,

long-term (2006–2020) winter season Yard Birding Event data indicated that the House Sparrow has decreased, and Eurasian Tree Sparrow increased in Finland. However, the short-term (2013–2020) breeding season Nest Box Twitching Event data did not indicate significant changes in the occupation rate of sparrows. Our long-term (1991–2020) field study indicated that the wintering population of the House Sparrow has decreased, whereas the Eurasian Tree Sparrow has both expanded its wintering range and increased its population size. We did not find any data to suggest that interspecific competition or heterospecific attraction influenced the population trends or growth rates of sparrow species in Europe and Finland. However, there is a possibility that the Eurasian Tree Sparrow has benefited from the empty niches that the decline of the House Sparrow has caused in Finland. Our results indicate that the growth rate of the Eurasian Tree Sparrow has been very high. We did not detect any significant effects of the latitude or climate for the trends of the sparrow species. However, the House Sparrow populations decreased when the number of inhabitants in the study plots increased, and vice versa. Additionally, our results give some support that decreased winter feeding has been harmful for the House Sparrow.

4.1. Sparrow Populations in Europe

According to the most recent European Breeding Bird Atlas, the distribution of the House Sparrow has changed only a little, whereas the Eurasian Tree Sparrow has expanded its breeding range [64]. Our results indicate that the House Sparrow has declined in most European countries, whereas the Eurasian Tree Sparrow shows both declines and increases since 2000 (see also [31]). The populations of the House Sparrow have been reported to decline both in rural areas and cities in large parts of western Europe [25–29,65]. The decline of farmland birds in general was rapid in the last few decades of the 20th century [66,67]. This period coincides with changes in agricultural intensification practices that have been suggested to be behind the decline of farmland birds, such as sparrows.

According to Summers-Smith [26], the decline of the House Sparrow in built-up areas of the U.K. and western Europe has been massive since 1990, and it is still continuing with an increasing rate [32]; see also [34,48,68,69]. Many of the earlier studies were conducted during the breeding season. However, the decline of the House Sparrow in Valencia (Spain) was mainly observed during winter [34]. In Britain, the House Sparrow has declined by about over 50% since the mid-1970s, and the winter season decline has been more severe in urban (60%) than in rural habitats (48%; [28]). These results indicate that the recent decline of the House Sparrow has been widespread in Europe, and has been especially directed on birds living in urban habitats. Fortunately, the European level bird monitoring results give some indication that the decline of the House Sparrow seems to have stabilized a little bit during the 2000s in Europe.

In western Europe, a large decrease in Eurasian Tree Sparrow populations was observed during the 1950s and 1960s [70], and again during the 1980s and 1990s [71]. In Britain, the Eurasian Tree Sparrow has been decreasing in rural areas since the 1960s [72], but Gregory et al. [67] detected recovery and increasing population trends of the species since 1994. In the Netherlands, the Eurasian Tree Sparrow has declined at an annual rate of 5.0%, i.e., even at greater rate than the House Sparrow [48]. Graham et al. [73] suggested that the distribution range of non-native Eurasian Tree Sparrow will increase a lot in the USA, as far as the Pacific Northwest and Newfoundland, indicating the good dispersal ability of the Eurasian Tree Sparrow. Węgrzynowicz [74] indicated that the Eurasian Tree Sparrow has increased by 68% since the 1970s/1980s, but afterwards (2005–2012), the population has been stable or even declined. These results indicate that the population trends of the Eurasian Tree Sparrow differ a lot between European countries, indicating that there is no single, large-scale reason behind these changes.

It is worth noting that in nine European countries, the current status of both the species is unknown. This observation clearly indicates that the current bird monitoring work do not cover urban environments in Europe very well. For example, the British

Common Bird Census monitoring work is mainly concentrated on agricultural areas and woodlands, whereas urban areas are mainly neglected [26]. Therefore, we suggest that national bird monitoring programs should be enlarged so that urban sparrow habitats will also be covered more adequately.

4.2. Sparrow Populations in Finland

Our results indicate that the House Sparrow has decreased, whereas the Eurasian Tree Sparrow has increased in Finland during the last few decades. The decrease in the wintering population of House Sparrow has been about 30%, whereas the Eurasian Tree Sparrow population has increased about forty-fourfold during 1991–2020. Our winter bird survey data indicated that the House Sparrow populations firstly slightly increased (from 1991 to 1999), then decreased heavily (from 1999 to 2009), and thereafter (from 2009 to 2019) showed some recovery. The decrease in the House Sparrow started earlier than the expansion of the Eurasian Tree Sparrow in Finland.

Additionally, according to the Finnish breeding bird atlases conducted during 1974–1979, 1986–1989 and 2006–2010, the distribution range of the House Sparrow declined in Finland between 1974–1989 and 2006–2010 when the observation effort was considered [75]. The Eurasian Tree Sparrow is an exceptional species among Finnish birds, since its distribution range has increased much greater than in any other Finnish bird species [50].

According to the Finnish land bird monitoring work, the abundance of the House Sparrow has decreased by about half during 1983–2005, whereas no suitable data were available about the Eurasian Tree Sparrow from that time period [76]. The results of the Finnish winter bird monitoring work indicate that the House Sparrow numbers have decreased heavily from 1980–1999 (37.1 ind./census km) to 2010–2020 (8.6 ind./census km) [77]. During the same periods, the numbers of the Eurasian Tree Sparrow have increased enormously (from 2.4 individual to 11.0, correspondingly; [77]). According to the Finnish feeding site monitoring work, the occurrence of the House Sparrow has decreased about 20–40%, more deeply in southern than in northern Finland, during the years 1989–2005 [78]. At the same time, the abundance of the House Sparrow has decreased in feeding sites by about one tenth in southern, to one third in central, and to half in northern Finland, indicating a clear latitudinal difference. However, our winter census data did not indicate any latitudinal differences in population trends of the House Sparrow. One reason for the differences between our and citizen science-based data could be that the data collected by citizen scientists contain mostly sites located in rural and suburban residential areas (private yards), whereas our data are only from centers of cities and villages. More current feeding site data (2010–2020) indicate that the decrease in the House Sparrow and the range expansion of the Eurasian Tree Sparrow has continued heavily in Finland [79].

Our winter bird survey data indicates that the decline of the House Sparrow started between 1999–2009, corresponding well the results of the Finnish winter bird monitoring work [78,80]. However, according to the Finnish breeding season monitoring work, the deep decline of the House Sparrow already started at the end of the 1980s. These results indirectly suggest that the primary causes for the decline of the House Sparrow in Finland are related to factors operating during the breeding season, and, after a time lack, the winter population size of the House Sparrow also started to decrease.

Our winter bird survey data indicated that the Eurasian Tree Sparrow populations showed a small increase during 1991–1999, but the great increase in abundance and distribution ranges happened during 2009–2019. According to Väisänen [78], the increase in the Eurasian Tree Sparrow started in the mid-1990s, firstly in the south, and later (2010s) in the north. During the first Finnish breeding bird atlas (1974–1979), confirmed breeding of the Eurasian Tree Sparrow was detected only in 17 atlas grids (10 km × 10 km), whereas during the second (1986–1989) and the third (2006–2010), the number of squares were 74 and 996, correspondingly [50]. During the third atlas, the Eurasian Tree Sparrow was

detected about in one third of all atlas squares, and its breeding range was expanded from the sparsely occupied breeding areas in southeastern Finland (1974–1979) towards western and northern Finland [50]. However, it should be noted that the observation effort was also clearly the highest in the atlas of 2006–2010.

The results of the many different Finnish bird monitoring programs and our own winter bird survey results give a very consistent view about the decrease in the House Sparrow and the increase in Eurasian Tree Sparrow populations in Finland. These observations indicate that data collected by voluntary birdwatchers and citizens can be used as a reliable, additional estimate of sparrow population status and trends, and thereby also help the official monitoring and conservation of urban bird species. This observation is promising, because many current official land bird monitoring programs inadequately cover urban environments [26]. Additionally, researchers are not always allowed to go in several types of urban areas, such as private yards, which are important habitats for many birds, such as sparrows.

4.3. Sparrow Populations Growth Rates in Finland

Our data indicated a little bit of a greater decrease rate of the House Sparrow than the Finnish bird monitoring work, and the growth rate of the Eurasian Tree Sparrow was greater than reported in the Finnish bird monitoring work [54]. Probable reasons for these differences are related to temporal and spatial differences in data collection. The data of the Finnish land bird monitoring work [76] came from the breeding season, whereas our data were from winter; and our data were only collected from human settlements, whereas the Finnish land bird monitoring was based on data coming from all available habitats in Finland.

Despite the fact that the numbers of House Sparrows have decreased, the average negative growth rate (λ) of the House Sparrow did not differ from zero. This is due to the fact that the House Sparrow has increased in some of the study sites, but decreased in some other sites. Despite the fact that the numbers of Eurasian Tree Sparrows have increased in those sites where they have occupied a long time, the species is still absent from some large towns located in northern Finland (Jyväskylä, Kajaani, Oulu and Rovaniemi). Our results indicated that the expansion of the Eurasian Tree Sparrow has been sequential, both in relation to the latitude (from the south towards to the north) and urbanization level (from villages via small towns to large towns), probably due to the population pressure from the over-populated areas to the less populated areas.

4.4. Factors behind the Population Changes of the Two Sparrow Species

4.4.1. Latitude, Climate and Urbanization Level

According to our winter bird survey results, neither the latitude, climate nor urbanization level significantly influence the growth rate (λ) of the House Sparrow or the Eurasian Tree Sparrow. These results were partly against our predictions.

Climatic factors might impact the distribution and range shift of wintering bird species [36,37], especially the southerly distributed species, such as the Eurasian Tree Sparrow. For example, according to Burnett [33] the non-native Eurasian Tree Sparrow has extent of a great northward range expansion in USA, and Graham et al. [73] suggested that under projected climate change scenarios, the distribution and range of the non-native Eurasian Tree Sparrow will increase markedly in the USA in the near future. Wuczyński and Wuczyński [81] pointed out that the snow cover and temperature are important factors explaining winter bird abundance and the variability of sparrows during winter in agricultural areas in Poland. However, for example, Mohring et al. [69] did not detect influences of weather conditions for the House Sparrow population changes in Paris during 2003–2017. Additionally, our data collected during 1991–2020 does not give any indication that climatic change would have influenced the growth rates of the two sparrow species, even if we conducted our study in northern latitudes where climatic factors are estimated to be important factor affecting bird populations in natural habitats [36,37]. However,

the positive population growth rate of the House Sparrow was observed in some northern study sites, and population increase in the Eurasian Tree Sparrow seems to be greater in the north than in the south. These results indicate that the situation of both the sparrow species is better in northern than in southern Finland [78,79]. We assume that intensive winter feeding in the north is probably behind these differences. However, at the same time, climate warming has increased periods without snow in the northern latitudes, thereby making it easier for sparrows to also find food from natural habitats.

Basically, urbanization did not influence the growth rates of the sparrow species during 1991–2020. However, when the number of inhabitants increased during the study years, the House Sparrow populations decreased, and vice versa. Additionally, van Manen [48] indicated that the House Sparrow has currently declined most heavily in highly urbanized areas in the Netherlands, and in Spain, the species decrease has been linked with the high-impact urban development [82]. In general, changes in land use practices and local habitat characteristics may influence the sparrow's occurrence and abundance [42,83–87]. However, we are not able to study these topics in more detail, but obviously, there can be some differences between the sparrow's winter and breeding season habitat use that will serve further research.

4.4.2. Food Factor

We found that the House Sparrow has suffered from the decreased feeding activities in Finland. Both sparrow species are able to use food that are provided either accidentally (garbage) or intentionally (bird food in feeding sites). Galbreith et al. [10] demonstrated in their supplementary bird feeding experiment that feeding will restructure urban bird communities, and especially the House Sparrow will benefit from it (see also [8,35]). According to Tryjanowski et al. [61], urban and rural areas differ in the availability of winter food offered intentionally and unintentionally to birds by humans. However, in our case, changes in the numbers of feeding sites during the study period was not related to factors describing the urbanization level and changes in them.

Tomiałojć [88] suggested that a shortage of winter food may decrease adult survival, whereas a low abundance of animal-based breeding season food may lower the reproductive success of the Eurasian Tree Sparrow and cause their decline in central Europe. However, we did not find any significant effect of changes in feeding site numbers on the Eurasian Tree Sparrow, even if the species is one of the species that has obviously benefitted from the diversified winter food supply (from the dominating use of sunflower seeds to more diverse, and small-sized seeds that are more suitable for the Eurasian Tree Sparrow) in Finland [44]. Additionally, Plummer et al. [89] indicated that the diversity of food types available has increased in British gardens. The oat has been the one of the main food items for the House Sparrow a long time, both in agricultural and suburban areas [90]. Currently, only a few people feed birds with oats, whereas, e.g., the use of sunflower seeds without shells, peanuts and birdseed mixes increases at the feeding sites [78,79]. This has obviously been advantageous for the Eurasian Tree Sparrow, which is more flexible in its' food choice and feeding behavior than the House Sparrow. We suggest that the greater food supply diversity has been beneficial, especially for the Eurasian Tree Sparrow. Our results indicate that winter feeding in Finland has decreased during the recent decades. It might be possible that because of climate warming (snow comes later and melts earlier; temperature is milder), fewer people start winter feeding nowadays in Finland. If this is true, that might have an important consequence for the wintering bird assemblages in the north, and also for sparrow populations and their spatial distribution. Unfortunately, we have no opportunities to evaluate this topic in more detail, but a new ongoing survey about the possible decrease in winter feeding activities in Finland and its impacts for the wintering birds will give new insights for this. Additionally, in many cities, at least in their core areas and parks, feeding is forbidden due to possible rat problems and the spread of diseases. Currently, the Eurasian Tree Sparrow is already more common at feeding sites than the House Sparrow, also in northern Finland. The occupancy level and abundance of

the Eurasian Tree Sparrow in feeding sites has increased in Finland [78,79]. Additionally, Plummer et al. [89] noted that the proportion of gardens where the Eurasian Tree Sparrow use feeders increased during 1973–2012, but opposite trend was observed in the House Sparrow's case.

Feeder use of the two sparrow species might also differ between habitats. For example, in built-up areas, House Sparrows dominated feeders in Wrocław, Poland, whereas in green areas, the Eurasian Tree Sparrow was one of the most abundant species in feeders [91]. Feeders, and other supplementary food, may play an important role in the further urbanization processes of birds [92–94].

4.4.3. Inter-Specific Competition

We did not find significant negative correlation in growth rates between the study species, indicating that there is no competition between these species. This result is in accordance with the results of Węgrzynowicz [75] and Vepsäläinen et al. [46]. However, nesting niches of the House and Eurasian Tree Sparrow can overlap, and in some areas, these species compete for nest sites. A nest box experiment indicated that the House Sparrow is a dominant species over the Eurasian Tree Sparrow [45]. However, although the House Sparrow may decrease the breeding potential of the Tree Sparrow, the breeding plasticity of the Eurasian Tree Sparrow had allowed them to co-occur with the House Sparrow [45,46]. Unfortunately, our winter season data cannot be used to study the possible factors or processes of the co-occurrence of the two sparrow species in a very detailed manner.

4.4.4. Predation and Changes in Predator Communities

Additionally, predation might influence sparrow populations [66,88]. According to Mohring et al. [66], the decline of the House Sparrow population in Paris was mainly related to predation, i.e., a corresponding increase in the breeding Eurasian Sparrowhawk (see contrasting results from North America; [30,48]). Villén-Pérez et al. [95] reported that vulnerability to predators related to feeder location may play an important role for the foraging patch selection of wintering birds. Indeed, survival, as opposed to productivity, is implicated as one of the key factors in the population declines of seed-eating passerines, such as the House Sparrow [65,96]. However, we detected very few avian predators during our winter bird surveys, and no stray cats were observed in our study plots during the harsh northern winter season. Therefore, we suppose that the role of predators is minimal in our case. However, we cannot rule out the possible effect of predation outside the winter season.

4.4.5. Other Factors

There might be some other factors behind the changes in sparrow populations that we did not investigate in our winter season study. Many studies have indicated that the modernization of buildings has been disadvantage for the House Sparrow [47,68,97,98].

Whereas the House Sparrow uses nest boxes rarely, the Eurasian Tree Sparrow uses them very often [47,53]. Eurasian Tree Sparrow densities are positively correlated with the number of nest boxes, and the rate of nest box occupation decreases along an urbanization gradient in Warsaw, Poland. The rate of nest box occupation by the House Sparrow has decreased sharply since the 1980s, but the opposite trend has been detected for the Eurasian Tree Sparrow. In Poland, especially the Eurasian Tree Sparrow has benefitted from an increased number of nest boxes [47,68]. Additionally, according to the Finnish citizen science-based nest box monitoring work, the proportion of nest boxes and number of sites where the Eurasian Tree Sparrow occupies increased heavily, whereas the opposite was observed for the House Sparrow during 2013–2019 [47]. A flexible nest site selection of the Eurasian Tree Sparrow has probably also helped its expansion in Finland. For example, in our northernmost study town (Rovaniemi, Finland), where the Eurasian Tree Sparrow is

a newcomer, the species very often uses nest boxes and the horizontal poles of traffic signs as nesting places, whereas the House Sparrow rarely uses these sites for nesting [99].

Nest box availability is normally greater in suburban than in central parts of towns. Our study was directed on the centers of towns and villages and did not cover suburban private house areas that might be important habitats for the sparrows, especially for the Eurasian Tree Sparrow. However, our data agree well with the results of the Finnish citizen-science based Yard Birding Event performed during 2006–2020, which reported that the occurrence and abundance of the House Sparrow has decreased in private yards, whereas the opposite has been observed in the case of the Eurasian Tree Sparrow [52].

Shrub fences, especially hawthorn (*Crataegus grayana*) hedges, are important safe and escape places, especially for the House Sparrows. Mueller [35] indicated that House Sparrows benefitted from the occurrence of bushes around the winter feeding sites. During our field work, we observed that the House Sparrows escaped most often into shrub fences, whereas the Eurasian Tree Sparrows escaped most often on the upper parts of trees (pers. observations). Additionally, a study conducted in a city park in Crakow (Poland), indicated that the Eurasian Tree Sparrow uses higher vertical vegetation zones than the House Sparrow [100]. In addition, shrub fences were almost totally absent from the large-sized city centers (pers. observations), and we assume that this has been a disadvantage for the urban House Sparrows. Unfortunately, we do not have detailed information about the change of hawthorn hedges in our study sites during the study period. Other possible factors that might influence sparrow populations, but were not studied here, are, for example, noise, artificial light, pollution and diseases [26,101].

5. Conclusions

Our long-term winter season study indicates that the House Sparrow has slightly decreased, whereas the Eurasian Tree Sparrow has colonized many towns and increased its abundance in Finland. According to our results, the House Sparrow can be considered as an example of an urban exploiter species, whereas the Eurasian Tree Sparrow is still a suburban adapter species [11,102]. Urban habitats are important areas for both the sparrow species that are currently under threat in many European countries, and therefore, included in the threatened bird species lists in many countries. Therefore, urban habitats should be noted as important conservation sites for these sparrow species, and urban planning and architecture should pay more attention to the habitat needs of these species. Interspecific competition, latitude or their interactions did not explain the population trends of these two sparrow species. However, when the number of inhabitants increased within the plot during the study years, the House Sparrow populations decreased, and vice versa. This result indicates that even the House Sparrow does not thrive in very densely populated areas. Additionally, the House Sparrow numbers have decreased due to the decrease in winter feeding. An obvious reason behind the success of the Eurasian Tree Sparrow in Finland is its flexible nest site selection; the species easily accept, e.g., nest boxes and horizontal poles for nest sites. However, the House Sparrow prefers nesting in old buildings [42] with roof-tops, and this type of buildings normally decrease with urbanization. Changes in winter feeding food supply from oats and sunflower seeds to more diverse small-sized seeds have been probably beneficial for the Eurasian Tree Sparrow. Urban planning should consider both the nest site and food availability for both species. According to our results, establishing winter feeding sites in cities will especially benefit the House Sparrows. Also, planting shrub fences will offer safety places for sparrows against predators. We assume that the use of citizen science will help us to understand in more detail the population status and trends of sparrow species.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/birds2030017/s1>, Table S1: population trends of the House Sparrow and the Eurasian Tree Sparrow in European countries since 2000 based on the data of BirdLife International (2017). Countries (four) where the House Sparrow is decreased and the Eurasian Tree Sparrow is increased at the same time are in **bold**. Countries (six) where both sparrow species have declined are in *italics*.

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