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# Snow depth drives habitat selection by overwintering birds in built-up areas, farmlands and forests

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## Abstract

**Aim:** Abundances of animals vary according to species-specific habitat selection, but habitats are undergoing rapid change in response to anthropogenic alterations of land use and climate. The long-term decline of snowfall is one of the most dramatic abiotic changes in boreal regions, with potential to alter species communities and shape future ecosystems. However, the effects of snow cover on habitat-specific abundances remain unclear for many taxa. Here we explore whether long-term declines in snow cover affect the abundances of overwintering birds.

**Taxon:** Fifty bird species.

**Location:** Finland, Northern Europe.

**Methods:** We used generalized linear mixed models to analyse citizen-led monitoring data from 196 transects over a 32-year period to assess whether abundances of birds have changed in built-up areas, farmlands and forests, and whether these covary with warming temperatures and decreasing snow. We then explored if changes in abundance can be explained by body mass, migration strategy or feeding guilds of the species.

**Results:** Over the study period, the abundance of overwintering birds increased. This increase was most pronounced in farmlands (69.6%), where abundances were positively associated with decreasing snow depth. On the other hand, while abundances in built-up habitats (19.5%) decreased over the study period, they increased in periods of high snow depths. Finally, we found that the short-distance migration strategy explains changes in bird abundances with snow. In farmlands, ground feeding birds and heavier birds also show a positive trends in abundance with decreasing snow depths.

**Main conclusions:** Local snow conditions are driving habitat selection of birds in the winter; birds in farmlands were most responsive to a decrease in snow depth. Changing snow depths can affect bird movements across habitats in the winter, but also influence migratory patterns and range shifts of species.

## KEYWORDS

citizen science, farmlands, global warming, habitat selection, snow cover, winter ecology

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## 1 | INTRODUCTION

A fundamental insight from ecology is that the distribution and abundance of populations, species and communities vary spatially because of adaptation to micro- and macro-habitats (MacArthur, 1965). However, climate change is now generating rapid increases in temperature and spatiotemporal changes in precipitation (Thuiller, 2007). These changes in local conditions mean species must either move to avoid unfavourable habitats, or stay and adapt (Chen et al., 2011). Understanding how unfavourable environmental conditions shape habitat preferences is therefore of increasing importance. For example, snow is a key factor that affects the survival, abundance, distribution and community of organisms (Callaghan et al., 2011), yet snowfall in the Arctic region is predicted to decline in the coming decades (Bintanja & Andry, 2017) and could have broad ecological consequences. For example, wolves tend to hunt adult elk only when snow is deep, but also hunt their calves when snow depth reduces (Huggard, 1993). Accumulation of snow over the years also affects the fecundity of white tailed deer and moose, with the cumulative depth in the last three winters being inversely proportional to vulnerability of calves (Mech et al., 1987). Decreases in snow cover duration could accelerate local species extinction of vascular plants, lichen and moss in the Arctic regions (Niittynen et al., 2018). Changes in snow depth also have potential downstream consequences in other seasons; for example, snowmelt is an important predictor of the advancements in clutch initiation dates of birds (Liebezeit et al., 2014).

Despite the large extent of predicted changes to snow cover, however, its effect on habitat preferences of animals has been overlooked compared to other environmental variables (Niittynen et al., 2018) [e.g. temperature (Pigeon et al., 2016; Street et al., 2015), anthropogenic noise (Kleist et al., 2017) and green cover (Moorcroft et al., 2002)]. This gap is exacerbated by the fact that collecting snow cover data at a scale relevant to animal populations is a challenge in the remote locations of higher latitudes (Boelman et al., 2019). This is especially the case for long-term changes in snow cover and its effects on habitat preferences of species. There is often a lag between cause and subsequent change in ecological systems (Magnuson, 1990). This makes it crucial to have data collected over a sufficiently long period to understand the patterns emerging in natural systems. However, the number of long-term studies of changes in animals' habitat preferences due to environmental conditions still remains small (Uboni et al., 2015). To our knowledge only two papers explore the effect of snow on habitat preferences over a period longer than a decade (Adam et al., 2015). Adam et al. (2015) showed the importance of cold weather refuge sites to water birds and Wegge and Rolstad (2011) showed that while minimum temperatures (rather than snow) were an important indicator of fecundity, habitat selection in black grouse *Lyrurus tetrix* and capercaillie *Tetrao urogallus* was very flexible and not dependent on environmental variables. The effects of response to long-term changes in environmental variables are important to understand as animals play various roles in the ecosystem like that of seed disperser, pollinator, predator, prey or scavenger. Hence, their habitat preferences,

movements and interactions may shape the homogeneity of future ecosystems (Rija et al., 2014).

Alternate habitat selection by animals in response to changing environmental conditions can be understood better by looking at species-specific traits. Larger animals can disperse further than smaller animals (MacLean & Beissinger, 2017) and can hence move to alternate habitats more easily. In fragmented habitats, larger frugivorous birds are seen to move across habitats more frequently as compared to smaller birds of other feeding guilds (Neuschulz et al., 2013), while in urban habitats hole-nesting omnivorous bird species fare better than other feeding guilds (Jokimäki et al., 2016). Migration behaviour can also affect habitat use by animals, for example, migratory mule deer have access to higher quality habitat than non-migratory individuals (Nicholson et al., 1997). Whereas in birds, habitat specialists are seen to migrate shorter distance than habitat generalists (Reif et al., 2016). However, our current understanding of how species-specific traits can help predict shifts of animals to other habitats remains limited (MacLean & Beissinger, 2017). Understanding what species-specific traits can explain trends in habitat selection in response to climatic variables would help predict the composition of future winter communities in the Arctic regions.

Birds are highly mobile (Podulka et al., 2004) and can move over large distances and overcome physical barriers like large bodies of water or mountains with more ease than other taxa (Podulka et al., 2004). This makes them ideal study subjects for looking at the effects of changing environmental conditions and land use changes caused by humans. In this study, we use 32 years of winter bird monitoring data including almost 3 million individual birds to explore habitat preferences in response to snow depth across Finland. Extending from 59°N to 70°N, Finland falls within the boreal and sub-arctic region and is predicted to experience a decrease in snowfall in the coming decades (Rasmus et al., 2004).

Here we test the hypothesis that changes in winter conditions (temperature, snow depth) alter the abundances of bird species across three habitats: built-up areas, farmlands and forests. We first investigate if there are temporal changes in abundance across years in these habitats, then we test for correlations between abundance changes versus snow depth or temperature. We predict that (a) abundances of birds will increase over the study period as snow depths decrease and winter temperatures increase and (b) built-up habitats will have higher abundances than other habitats during periods of high snow depths and low temperatures due to the presence of more supplementary feeding (Tryjanowski, Sparks, et al., 2015) as well as a warmer microclimate (Manley, 1958). Finally, we explore whether species traits (body mass, migration strategy and feeding guild) can explain variation in habitat selection to investigate which species are most likely to be affected by future declines in snow depths. We make three non-mutually exclusive predictions that species will be more responsive to changes in snow if they are: (i) larger and hence able to move to alternate habitats more easily, (ii) ground feeding as their food availability will be the first to be limited by snow cover or (iii) partial and short-distance migrants, which are likely to be more mobile than residents.

## 2 | MATERIALS AND METHODS

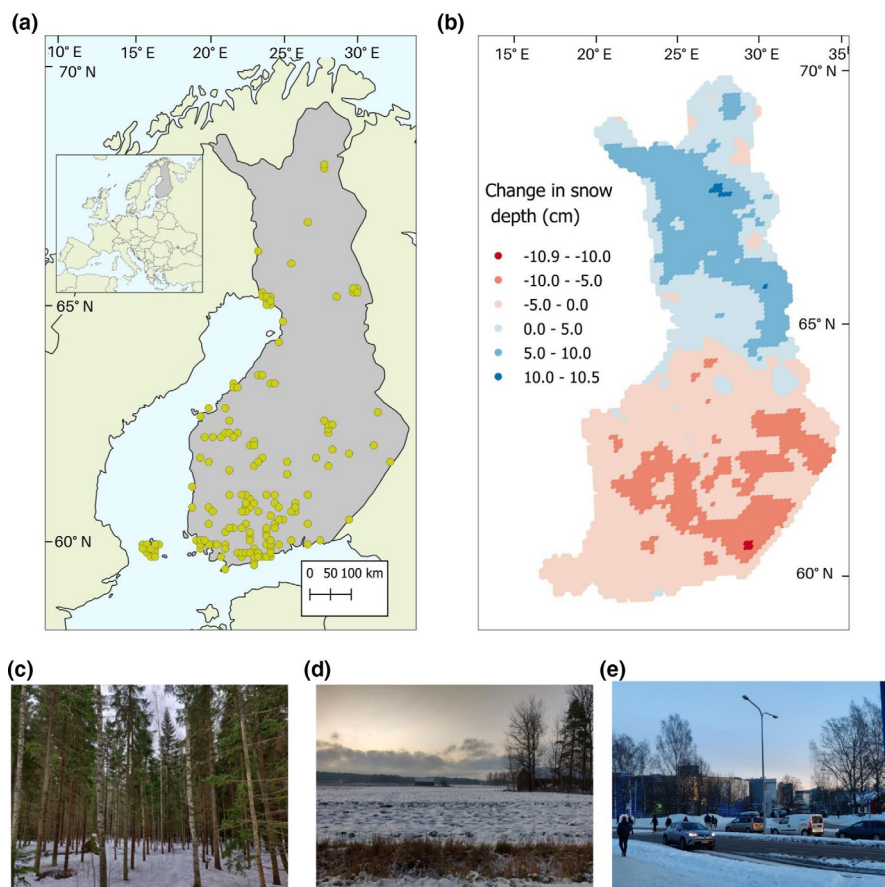
### 2.1 | Bird monitoring

Censuses of bird distributions in Finland have been conducted regularly since 1956 by volunteers recording the number of birds belonging to different species seen or heard along a transect (Koskimies & Väisänen, 1991). Transects are repeated three times per year by either walking or skiing the route (Koskimies & Väisänen, 1991). The volunteer initiating a particular transect is responsible for surveying it also in the coming years; in case responsibility is handed over, this is usually done under the supervision of the original census taker. Volunteers are encouraged to conduct the census when the weather conditions are most optimal during each census period. The mid-winter census period (25 December to 7 January) receives the best survey effort of the three census periods (Lehikoinen et al., 2013). This period also has the most variation in snow cover across the country so here we only use data from mid-winter censuses. This part of the year has the shortest day lengths in Finland. Hence, birds are active throughout the day to make the best use of the few light hours for foraging. Snow and the lack of leaves on trees, along with the high activity of the birds ensures that census takers can detect birds with ease. Additionally, due to the cold weather birds are less likely to move across large distances. Therefore, we are not aware of any particular reason why birds' detectability would change in different habitats with snow across different years. Hence, we have

assumed that the detectability of birds within the three habitats is high, even though it might vary among them.

From 1987, volunteers were asked to also record biotopes on their census routes and in which biotopes they observed birds. Hence, in this study we used 32 years of data (from 1987 to 2018). The location of bird sightings was classified as one of eight biotopes: (i) garbage dumping ground or fur farm, (ii) urban settlement, (iii) rural settlement, (iv) arable land and pasture, (v) forest, (vi) clear-cut area or stand of saplings, (vii) reed-bed or shore scrub and (viii) 'other', which included, for example, birds in wetlands or on active migration. We excluded the category 'other' from our analyses, because birds in various and heterogeneous habitats were recorded in it. We grouped the remaining biotopes into habitat categories based on the degree of human presence as follows: (1) Built-up habitat: dumping ground or fur farm, urban settlement and rural settlement (Figure 1e); (2) farmland habitat: including pasture and arable land (Figure 1d); and (3) forest habitat: forest, clear-cut areas or stands of sapling, and reed-bed or shore scrub (Figure 1c). Volunteers were encouraged to include multiple biotopes in the routes they census, so that the route would represent the habitats in the same proportion as they appeared in the surrounding area. Due to changes in land use along the route, the distances covered in each habitat varied between years and this has been registered by the census takers.

In total, 162 bird species were censused across the study period. Many of these species were poorly represented across years (76 species had fewer than 100 observations over the study period and of these 39



**FIGURE 1** This figure summarizes the locations, habitats and the climatic conditions that have been included in the study. Each point on the map in panel (a) represents the starting point of a survey transect. Panel (b) details the mean difference in snow conditions during the survey period between 1987–1992 and 2013–2018. Panels (c), (d) and (e) represent the typical forest, farmland and built-up areas respectively

species had fewer than 10 observations). Hence, for the analyses we included the 50 most abundant species after summing their records in forest, farmland and built-up areas (see Appendix S1; Table S1). We also excluded very strict habitat specialist species (e.g. *Tetrao urogallus* which is a forest specialist) as we were interested in changes in habitat selection. The 50 selected species accounted for 99.9% of recorded bird individuals. Furthermore, to track changes in habitat selection across years, we only included routes surveyed more than 25 times since 1987. This resulted in 196 routes (Figure 1a). The absence of birds along a route or in a particular habitat was as important to our research questions as their presence. Therefore, a zero value was introduced for each species that was not seen during a census in a particular habitat on a particular route.

## 2.2 | Snow and temperature data

Census volunteers used the following categories to record snow on the day they conducted a transect: (a) No snow, (b) snow in some places, (c) less than 5 cm of snow, (d) 5–10 cm, (e) 11–20 cm, (f) 21–50 cm, (g) 51–100 cm and (h) more than 1 m. The volunteers also recorded the temperature during the transect. For the study, we have used snow depth and temperature data from the Finnish Meteorological Institute (FMI, 2020). The data are collected in a 10 by 10 km grid by the FMI; we used the grid cell closest to the survey route to assign values of the environmental variables. As birds are likely to respond to temperatures earlier than the day of the survey itself, we also took into account temperature on the route 14 days before the survey. We found that the snow depth ( $r = 0.83$ ) and temperature ( $r = 0.93$ ) data collected by the volunteers on the day of the survey were correlated with the data collected by FMI.

## 2.3 | Bird guilds, migration strategy and body mass

To determine whether morphological or behavioural traits influenced response to snow depth in the three habitats, we compiled information on body mass, migration strategy and feeding guild for each species (Table S1). Body mass was taken from Piha and Lehtikoinen (2015) and Piha et al. (2018) which are two reports that compile morphological measurements of Finnish birds recorded by bird ringers from 1979. For migration strategy, we defined categories using the movement data from Finnish ring recoveries (Saurola et al., 2013): short-distance migrant ( $N = 12$ ), partial migrant ( $N = 20$ ) and resident ( $N = 18$ ). 'Short-distance migrant' species do not overwinter in their breeding grounds and included, for example, species that bred in northern Finland but spent winter in southern Finland. 'Partial migrants' sometimes overwintered in their breeding grounds while 'resident' species did not migrate at all. The feeding guilds (based on Cramp, 1977): tree feeding ( $N = 21$  species), ground feeding (including water surface,  $N = 20$ ) and both tree and ground feeding ( $N = 9$ ) were based on the winter feeding habits of the species. For example, blackbird *Turdus merula* feeding on insects on the ground but also on berries was classified into the 'both' feeding guild. While bohemian waxwing *Bombycilla garrulous* largely feeding on berries,

was classified into the 'tree' feeding guild. The bird species that were excluded from the analyses did not differ from the included species in body mass ( $\chi^2 = 121.38$ ,  $df = 131$ ,  $p = 0.715$ ). However, there were differences in the migration strategy ( $\chi^2 = 40.666$ ,  $df = 3$ ,  $p < 0.01$ ) and feeding guild ( $\chi^2 = 29.714$ ,  $df = 3$ ,  $p < 0.01$ ) of the included and excluded species. Many of the short-distance migrant species were excluded from the analyses compared to residents. This is intuitive as many of the excluded species are scarce irregular wintering visitors, which overwinter typically in the southern latitudes. Hence, more short-distance migrants are excluded compared to, for example, more abundant residents and partial migrants overwintering in the northern latitudes. Additionally, many of the excluded 'ground feeding' species are dependent on water, like ducks (Table S1), and so do not use habitats of interest in our study.

## 2.4 | Statistical analysis

We carried out all analyses in R (version 3.2.5) (R Core Team, 2019).

### 2.4.1 | Changes in bird abundances over the years in different habitats

We investigated changes in bird abundances over the 32-year period using zero-inflated generalized linear mixed model with Poisson error distribution using the glmmTMB package (Brooks et al., 2017). The count of birds of each species in a habitat on a route was the response variable. The year of census, habitat and their interaction were included as explanatory variables. Species and route ID were added as random effects, together with the random slopes and intercept of the interaction of year and habitat added for each species, allowing species-specific variation in trends in each habitat. The distance covered along each route (log transformed due to the error structure of the model) in each of the three habitats was used as an offset in the model to account for the species–area relationship (Arrhenius, 1921). This analysis consisted of two parts, a conditional model with the actual counts of birds in a habitat on a route and a Bernoulli model that analyses the presence or absence of birds in a habitat on a route.

### 2.4.2 | Change in habitat preference with snow and temperature

We used the glmmTMB package (Brooks et al., 2017) and constructed a zero-inflated generalized linear mixed model with a negative binomial error distribution to investigate the effect of snow depth, the presence or absence of snow, temperature on day of the survey and temperature 2 weeks before the survey on habitat selection by birds. We constructed eight models for each of these four environmental variables (as they were highly correlated, snow and temperature,  $r = -0.44$ ) and the minimally adequate model was selected using the Akaike information criterion (AIC). Details of all the models can be found in Table



S2. The general structure of the models is as follows: The number of individuals of each species counted within a habitat on a transect as the response variable, the mean snow depth (or snow as a binary variable/temperature during the survey/temperature 14 days before the survey) and the interaction of habitat type and snow depth (or temperature on the survey or temperature 14 days before the survey) as covariates. The mean snow depth or temperature for each route was also added as a covariate. We included route ID, species and year as random effects in the model. Additionally, we allowed for random slopes and intercepts for the interaction of habitat and environmental variables for each species, due to this species can respond differently to environmental variables and habitats. As in the earlier model, the log-transformed distance covered in each habitat was used as an offset. For ease of regression analysis, we centred the year of the census as well. As before, the analysis had two parts: a conditional model and a Bernoulli model.

### 2.4.3 | Traits of birds and their effect on habitat selection

We used the 'nlme' package (Pinheiro et al., 2021) to extract the random slopes (Table S3) from the minimally adequate model of habitat selection by birds with change in snow depth. We used these random slopes to analyse whether the body mass, migration strategy or feeding guild of the bird species explained their selection of habitat. As we had a wide range in the size of birds, body mass was taken on the log scale to avoid heavy outliers biasing the trend. Additionally, as closely related bird species might have similar responses to environmental conditions, we added the phylogenetic relationships of the bird species in the model. One hundred phylogenetic trees of the 50 bird species were downloaded from 'www.birdtree.org' in the form of a phylogenetic correlation matrix and included in the model with the 'ppls' function of the 'caper' package (Orme et al., 2018). We used three separate generalized least square regression models for the slopes extracted from the interaction of snow depth in each of the three habitats against the three traits of bird species as covariates. As the migration strategy and feeding guilds were correlated, there were added in separate models. The best models were then selected using AIC values. In the case of competing models, we have disregarded the models with uninformative predictors (Arnold, 2010).

## 3 | RESULTS

A total of 5863 censuses were undertaken along 196 routes over the 32-year period, generating a total of 2,937,528 birds recorded from 754,400 observations. Among the 50 selected species, the most abundant species was *Parus major* and the least abundant was *Linaria cannabina* (Table S1). The average transect length was 9 km (SD = 3.45). Snow depth varied widely by longitude and latitude: snow loss was observed in the southern part of the country whereas snow depth increased in the north (Figure 1b).

### 3.1 | Changes in bird abundances over the years in different habitats

We find statistically significant contrasting trends in bird abundances in the three habitats (Table S4). Year was a significant predictor of change in abundances ( $Z = 24.0$ ,  $p < 0.001$ ; Table S4) referring to an increasing trend in the forest bird abundances (intercept of the habitat categories). Bird abundances increased significantly faster in farmland habitats compared to forest habitats ( $Z = 30.1$ ,  $p < 0.001$ ; Table S4). In contrast, in built-up habitats, there was a statistically significant negative trend observed in bird abundances compared to forest habitats ( $Z = -57.6$ ,  $p < 0.001$ ; Table S4). The Bernoulli part of the model, showed that the occurrences of birds had not changed over the sample period in forests ( $Z = 0.15$ ,  $p = 0.884$ ; Table S4). The occurrence of birds in built-up habitats was significantly higher than in forests over the study period ( $Z = -8.98$ ,  $p < 0.001$ ; Table S4). The increase in abundance of birds in farmland habitats is similar in magnitude to the decrease in the abundance of birds in built-up habitats.

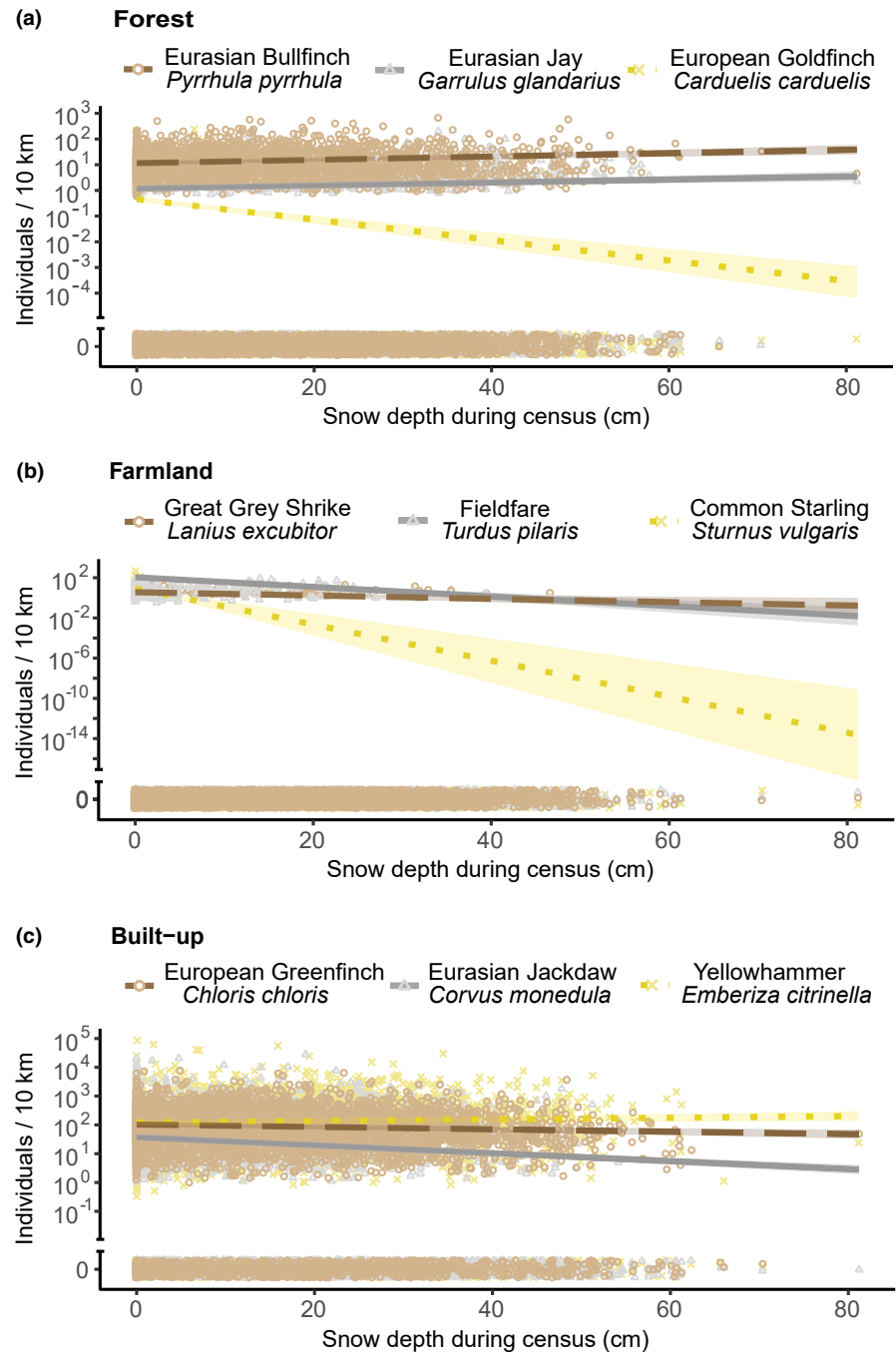
### 3.2 | Bird habitat selection and change with snow depth

Snow depth was a better predictor of habitat selection for over wintering birds than temperature (Table S2). We find that as snow depth on the survey date and the mean snow depth at route level increase, bird abundances decrease (Table S5). There was a significantly higher abundance of birds in built-up areas ( $Z = 5.212$ ,  $p < 0.001$ ; Table S5) than in forests. Similar trend was observed in farmlands ( $Z = 2.117$ ,  $p = 0.034$ ; Table S5). In forests, with the interaction of snow depth bird abundances decreased ( $Z = -2.896$ ,  $p = 0.003$ ; Table S5), however, it had a significant positive effect on the occurrence of birds ( $Z = 15.06$ ,  $p < 0.001$ ; Table S5). Furthermore, the interaction of snow depth and habitat revealed that bird abundances in farmland habitats decreased significantly with increasing snow depth compared to the situation in forests ( $Z = -2.994$ ,  $p = 0.002$ ; Table S5). In contrast, bird abundances in built-up habitats increased as compared to forest habitats ( $Z = 1.813$ ,  $p = 0.069$ ; Table S5). The Bernoulli part of the model produced opposite results, with the occurrences of birds in farmland habitats increasing with an increase in snow depth ( $Z = 4.163$ ,  $p < 0.001$ ; Table S5). In addition to the effect of the interaction of snow depth and year, the species-specific slopes displayed considerable amounts of variation (Table S3; Figure 2).

### 3.3 | Role of different traits in habitat selection

Migration strategy was the best predictor of the change in abundances of birds in all three habitats (Table S6, Figure 3). In forests and farmlands, the abundances short-distance migrants decreased faster than those of partial migrants as snow depths increased

**FIGURE 2** Model estimates of abundances of three example bird species in response to snow depth in each of the three habitat: Figure shows three example bird species with various responses to snow on the day of census in forest (a), farmland (b) and built-up (c) habitat. The species are chosen based on their random slopes in the given habitat and they represent the species with a mean slope (grey) and one standard deviation above (brown) and below (yellow) the mean. The lines show the estimated effects of snow cover in a route with an average number of individuals seen on an average year of abundance and with a median value of the average route-specific snow depths across the years (13 cm). Shaded bands represent the 95% confidence intervals of the estimated effects. Triangles represent all the data points of the species with mean random slope in that habitat, crosses the species with a slope of one standard deviation lower and circles the species with one standard deviation higher than the species with the mean random slope

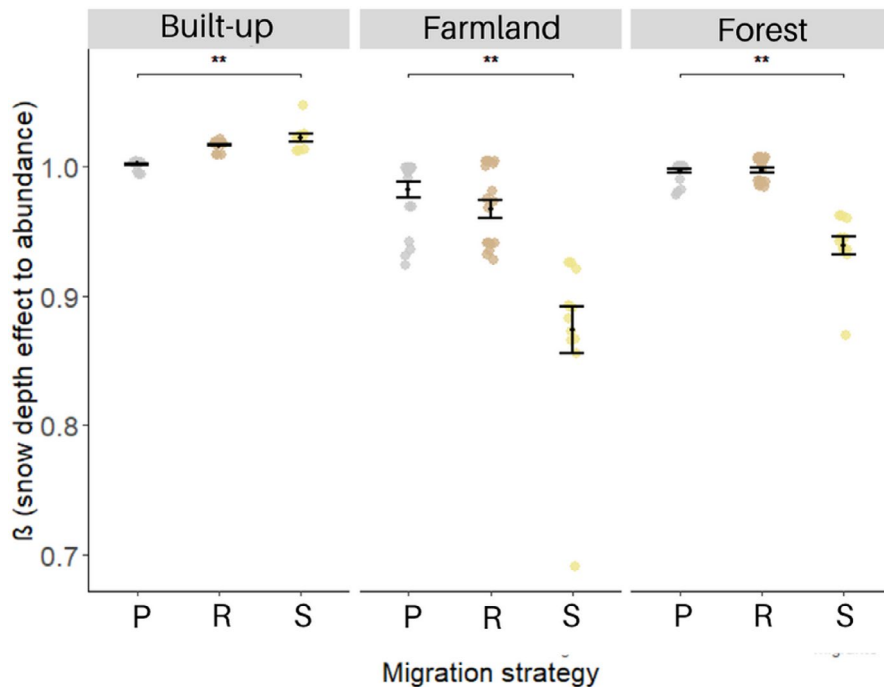


( $t = -2.908$ ,  $p = 0.005$  and  $t = -3.026$ ,  $p = 0.004$  respectively; Table S6a,c). In built-up habitats, as snow depths increased, abundances of short-distance migrants also increased ( $t = 2.5276$ ,  $p = 0.015$ ) and residents showed a positive trends approaching statistical significance as compared to partial migrants (Table S6d). In farmlands, the ground feeding strategy and log of body mass of birds showed a negative trend with increase in snow cover (Table S6b,c).

## 4 | DISCUSSION

Species are redistributing all over the world due to climate and land use change (Guo et al., 2018; Pecl et al., 2017) and our study

highlights the importance of changes in snow depth as one of the drivers of such species redistributions. Boreal and arctic species are adapted to the presence of snow (Niittynen, 2020), and here we show how long-term decreases in snow depth at northern latitudes could affect habitat selection of overwintering birds in these regions. We find that snow depths rather than temperature likely affect the habitat preferences shown by overwintering birds. Our results indicate that in the past three decades there has been an increase in the abundance of overwintering birds in Finland overall, and in farmlands in particular. Birds in farmlands are more responsive to snow depths as compared to forest and built-up habitats and hence the increase in their abundances is likely to be driven by the simultaneous decrease in snow depth (Irannezhad



**FIGURE 3** Response to snow according to migration strategy: Migration strategy was the only species-specific trait that explained changes in abundances in the different habitats. Abundances of short-distance migrants (S;  $N = 12$ ) decreased significantly in farmlands and forests in relation to an increase in snow cover as compared or residents (R;  $N = 18$ ) or partial migrants (P,  $N = 20$ ). In built-up areas, abundances of short-distance migrants increased significantly as compared to those of partial migrants

et al., 2017 and this study). Among the species-specific traits, migration strategy was the best predictor of the response of birds to changing snow depths. As migration strategy explains more variation than feeding guilds and body mass this could indicate that the ability of a species to move is an important factor to cope with changing environmental variables.

Increase in winter bird abundances has been observed in other studies conducted on birds in the northern latitudes (Askeyev et al., 2018; Lehikoinen et al., 2016) and water birds (Fraixedas et al., 2015). This increase is more pronounced in populations in colder parts of the winter distribution (Lehikoinen et al., 2016). Our study echoes results of these earlier studies, with the increase in abundance of overwintering birds over the 32-year study period likely being driven by an increase in abundances in farmland habitats. Contrary to our expectations, there is a significant decrease observed in bird abundances over the study period in built-up habitats. This could be because of intensified urbanisation of certain parts of Finland over the study period (Heikkilä, 2003) and a simultaneous negative trend in the provisioning of food for birds in urban areas during the winter (Deshpande et al., *in prep*).

When the long-term trends in bird abundances are looked at with the long-term changes in snow depths the pattern is clearer. Our results confirm the speculations of earlier studies that the absence of snow on farmlands could increase the abundance of overwintering birds (Golawski & Kasprzykowski, 2010). Over the study period, an 85% decrease has been observed in the snow depths recorded in the month of March, which usually consists of the maximum snow depths recorded yearly in Finland (Luomaranta et al., 2019). This would explain the consequent increase in the abundance of birds in farmland habitats. The strongest responses were found, for example, in Whooper Swan (*Cygnus cygnus*), Common Gulls (*Larus canus*) and Herring Gulls (*Larus argentatus*) and Eurasian Starling (*Sturnus*

*vulgaris*) (Table S3). With a decrease in snow depth, it is easier for birds including these four species to reach food on the ground (Field et al., 2007). Hence, birds depending on insects and grains in farms would not need to move away from farmlands in winters when snow depths are low. In the United Kingdom, it has been shown that even a small amount of winter crops will attract large abundances of farmland bird species associated with the particular crop species (Hancock & Wilson, 2003; Henderson et al., 2004). The predicted decrease in snowfall due to climate change could make winter crops more available for birds in northern latitudes and thus could have a marked effect on winter bird assemblages. We also find that in the Bernoulli part of the model, as snow increases birds disperse more and do not aggregate in large numbers in farmlands. This further indicates the role of aggregated food sources on the presence of birds in farmlands. These changes in farmland bird communities need to be studied carefully as manmade disturbances like agricultural intensification have already caused decline in farmland bird abundances in many parts of the world (Chamberlain et al., 2000). For instance, the above-mentioned Starling has experienced a long-term decline in Finland due to changes in farming practices (Rintala & Tiainen, 2007). However, the wintering number of Whooper Swans and Common and Herring Gulls has increased in recent decades in Finland (Fraixedas et al., 2015).

Even though snow depths are decreasing over the study period in Finland (Luomaranta et al., 2019), our results indicate that in the event of high snow depths, bird abundances increase in the built-up areas. This result is of importance as it indicates that built-up areas could provide an alternate habitat in the event of unfavourable weather conditions. With changing climates and warmer winters, a poleward range shift has been observed for many species (Luomaranta et al., 2019). However, extreme weather events are also predicted to increase with climate change (Coumou & Rahmstorf, 2012). Hence,



the species moving poleward that cannot adapt to the extreme weather events might face an ecological trap. The effect of extreme weather events on species is not as well understood as species response to gradually changing climates (Parmesan et al., 2000). Our results indicate that built-up areas, which have a higher amount of food provisioning (Tryjanowski, Skórka, et al., 2015) and a warmer microclimate (Manley, 1958), could provide an important alternative habitat for bird species as they shift their ranges poleward.

Migration strategy was the best predictor of species responses to snow in all habitats, indicating that more mobile short-distance migrants likely drive the main changes in abundances in the three habitats. This result is in line with climate change expectations and recent observations, which suggest that short-distance migrant species expand their wintering range to higher latitudes by decreasing their migration distances (Hovick et al., 2016). Earlier work, for example, on water birds, which also use farmland areas for foraging including swans and gulls, shows that cold spells can push species wintering ranges south-westwards (Fraixedas et al., 2015; Pavón-Jordán et al., 2020). As snowfall decreases in the future, it is possible that short-distance migrants in farmland and forest habitats would also start to behave like partial migrants as ample feeding resources become available. On the other hand, some species are very sedentary and do not move much during winter such as some forest grouse and tit species and many species fall between sedentary and short-distance migrants (Saurola et al., 2013; Valkama et al., 2014). Both residents and short-distance migrants decrease in built-up areas with a decrease in snow depths. This could be due to other less disturbed habitats being available to birds. This result further indicates that built-up areas can provide a good alternative habitat in the case of extreme weather events.

## 5 | CONCLUSIONS

In this study, we found that snow is an important driver of winter bird redistributions and changes in bird assemblages in Finland. We observe an increase in the abundance of overwintering birds from 1987 to 2018, which is largely driven by an increase in abundances of birds in farmland and forest habitats. On closer inspection, migration strategy, body mass and feeding guilds to varying extents explain the trends of bird abundances in the three different habitats. These results indicate that the scarcity of snow due to climate change in the future can aid the poleward movements of species differently in different habitats. Here we show that snow cover plays an important role in the changes of abundances among habitats in bird species. This is not to say that its role is more important than that of temperature, but more that these two variables could be working in different ways and warrant further investigation.

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## CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

## DATA AVAILABILITY STATEMENT

The data used here are available for download on GBIF.org under 'Finnish Winter Bird Census' <https://doi.org/10.15468/vmdzin>.

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**BIOSKETCH**

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