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Climate and land use changes: similarity in range and abundance changes of birds in Finland and Great Britain

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Climate change and human land use are causing changes to species ranges and abundances. However, factors influencing the species-specific speed and direction of changes are not well understood. In addition, intra-specific variation in the responses has rarely been investigated and thus it is not known if the same species show similar population changes in different areas. We compared the rate of changes in range size (since the 1970s) and population abundance (since the 1980s) as well as shifts in mean weighted latitude of range (since the 1970s) and density (since the 1990s) among the same bird species in Finland and Great Britain, two countries that share similar north–south climatic gradients. Similar responses between countries could indicate that climate change is causing parallel changes in species' ranges and abundances in the countries. Furthermore, we tested whether the responses differed between habitat types, which could indicate that local habitat availability and land use may be more important than climate change. Wetland species showed parallel range size change in the wo countries, but no such connection was found in open and forested habitats. Population abundance trends were also parallel in both countries and northern species showed more negative population trends than southern species. The speed of change in species' average latitudes was positively correlated between the two countries when using occurrence data, but negatively correlated when using species density. Species that show similar changes in population sizes in Finland and Great Britain, that are likely caused by large scale population drivers, such as climate change. However, speed of latitudinal shifts in species' densities were not connected between the two countries. These potential differences are likely driven by spatial variation in land use changes and habitat availability.

1. Introduction

There is increasing evidence that climate change is shifting species ranges and abundances towards poles and mountain tops (Parmesan *et al.* 2006, Pearce-Higgins & Green 2014, Stephens *et al.* 2016). In general species tend to move slower than temperatures are changing (Devictor *et al.* 2008, Massimino *et al.* 2015b). However, species do not respond equally to changing climate and some species are moving faster than others (Välimäki *et al.* 2016, MacLean & Beissinger 2017). Understanding the reasons behind the species-specific variation is crucial when considering how species ranges and abundances may respond to future climate change. Several species traits have been associated with variation in the speed of range shift. For instance species are more responsive to climate warming by shifting their ranges more in oceans compared to terrestrial ecosystems (Lenoir *et al.* 2020), Finnish density shifts of breeding birds differed between farmland and forest species (Lehikoinen & Virkkala 2016), and non-threatened butterfly species shifted their ranges faster than threatened species (Pöyry *et al.* 2009).

In addition to inter-specific variation in range edge dynamics, very few studies have looked at intra-specific variation in changing distributions. Brommer & Møller (2010) conducted two comparative studies using European and North American bird data. In Europe, the authors compared shifts in range edge in species that occurred in Great Britain and Finland using two repeated atlases in both countries. In North America, they compared range edge changes in the State of New York (atlas data) to the changes in whole North America (road counts), and thus mixed occurrence and abundance data. In both cases the authors did not find any connection between the speed of range edge shift of the same species in two different areas. However, the study periods were relatively short (e.g. in Finland seven years between end of the first atlas period and start of the second) and only the range edge shifts were considered. Range edge changes can be more sensitive to extreme observations than when investigating the centre of gravity of species range or abundance, where the change of the overall population is considered (Kujala *et al.* 2013, Massimino *et al.* 2015b). Comparative studies where changes in species ranges have been measured using movement of the centre of gravity are rare.

Range and abundance changes of populations are not only driven by climate, but also factors such as human induced land use changes (e.g. Root *et al.* 2003, Travis 2003) and biotic interactions (Araújo & Luoto 2007, van der Putten *et al.* 2010). The relative importance of climate and land use variables on variation in species abundance may vary spatially, and climatic variables have been suggested to be more important in the north whereas land use variables have larger role in the southern latitudes (Howard *et al.* 2015). For instance, in the UK changes in farmland explain the population changes of farmland birds and climatic variables have only a minor role (Eglington & Pearce-Higgins 2012). In the UK and across much of Europe, many farmland species have declining populations (Donald *et al.* 2001, Gregory *et al.* 2005) despite agri-environmental schemes (Gamero *et al.* 2017, Tworek *et al.* 2017). In general, the leading edge of the distribution is more directly limited by climatic conditions whereas the trailing edge is more often affected by species interactions (Pearce-Higgins & Green 2015). Because of these differential processes at the edges, changes in the leading edge can be faster than changes in trailing edge (Massimino *et al.* 2015b). As a consequence, land use changes that affect community composition could potentially have more effects on the trailing edges of species ranges.

The aim of this study is to investigate whether species show consistent rates of change in range size and/or abundance in two different areas, Great Britain and Finland, which both have high quality long-term monitoring data of species' ranges and abundances. Additionally, both countries have c. 1000 km long north–south climatic gradient where the highest mountain areas are situated in the northern part of the country. Although the countries do not share exactly the same climatic space, they share many bird species and have overlapping climatic conditions. However, the land use differs drastically between countries; *c.* 78% of the land cover of Finland is forest land whereas only 8% is farmland (EEA 2015). Whereas Britain has 12% forest and 51% farmland (Morton *et al.* 2011).

Species range and population changes may be affected by large-scale factors that are common across regions, or small-scale factors that are specific to regions or habitats. First, we hypothesise that if species show similar range and population changes across the two countries, these have been influenced by large scale environmental changes. Second, if climate change has a major role in population changes of species in both areas, we expect that species' speed of the range and density shifts will be correlated between the two countries. However, if species show different range and abundance changes across the two countries, then they are more likely influenced by local land-use change, or interactions between local habitat and large-scale factors such as climate change (Heldbjerg *et al.* 2019). Third, since habitat availability influences species occurrence, the climate driven population changes may be habitat specific. Because the forest and farmland cover are substantially different between Britain and Finland, we expect that species breeding in these habitats may show different population changes. However, responses may be similar in wetland species, which live in naturally patchy habitats (Paracuellos 2006). Last, changes in populations may be associated with the climatic niches of species. We expect species with southerly distributions will increase and expand their ranges in both areas, whereas northerly species will decline and lose range. However, since northerly species may have faster shifts in their densities (Virkkala & Lehikoinen 2014), and Finland has a colder climate than Great Britain, latitude may interact with population changes.

2. Material and methods

2.1. Temperature data

To test potential differences in speed of climate change, we calculated the rate of change in temperature in Great Britain and Finland during 1980–2012, which covers the main study period. We used the observed monthly temperature anomalies in 5º × 5º grids data from Earth System Research Laboratory (Jones *et al.* 2012) and calculated the annual mean temperatures using grids, which centers were 52.5º N, 2.5º W and 57.5º N, 2.5º W for Great Britain and 62.5º N, 27.5º E and 67.5º N, 27.5º E for Finland. We modelled the rate of change in temperature with linear regression.

2.2. Range and abundance data, grid and species selection

We compared the changes across countries with two sets of parallel data sources: (i) range data including occurrence atlas mapping data, and (ii) abundance data from breeding bird surveys.

2.2.1. Range data

Three separate bird atlases have been produced in both Great Britain (1968–1972, 1988–1991, 2007–2011; Balmer *et al.* 2013, Gillings *et al.* 2015) and Finland (1974–1979, 1986–1989, 2006–2010; Valkama *et al.* 2011, Brommer *et al.* 2012). To maximize the length of the study period we used data from the first and third atlas periods in Britain. However, for Finland, we combined the data from the first and second atlas and compared this with the third atlas period. We did this because the second atlas was partly complementing the observation gaps that occurred in the first atlas, whereas the third atlas had good coverage of the whole area (Virkkala *et al.* 2014a,b). Therefore the study periods were 39 years in Great Britain (averages of the atlas periods from 1970 to 2009) and 26.5 years in Finland (from 1981.5 to 2008). Although the time periods are not identical, they are largely overlapping. Our response variable was rate of change per year, which takes into account the different time periods in the two countries.

In the atlases, volunteer bird watchers (see acknowledgements) collected evidence for each species breeding in each 10 km × 10 km grid square. The breeding evidence had three categories: i) possible breeding (e.g. species has been observed once in suitable breeding habitat), ii) probable breeding (e.g. species has been holding a territory for a long time in the same area), iii) confirmed breeding (e.g. observed nest) (Valkama *et al.* 2011, Balmer *et al.* 2013). We used all these three observation classes when calculating changes in species' ranges between two periods. The atlas data are occurrence data, which does not include information about species abundance in the grid squares.

We excluded from both countries any grid squares which are less than 25% land, as this might have affected their observation effort. This led to a reduction of coastal grids but also some Finnish grid squares along the Swedish, Norwegian and Russian borders. After these reductions we had data from 2518 and 3492 10–km grid squares from Great Britain and Finland, respectively.

We selected species that occur in at least 10 grid squares in each atlas period within each country, as with very rare species the distribution changes can be highly stochastic. Furthermore, we selected species that have a northern or southern boundary within Britain or Finland, because the distribution changes are not possible to study in species which occur across the whole country. The definition for northern and southern species was based on data from the first atlas period, where northern species were defined as those absent from the southern 10% of the country and southern species were defined as those absent from the northern 10% of the country (Valkama *et al.* 2011, Balmer *et al.* 2013). We also excluded species that have a northern boundary in one of the countries and a southern boundary in the other (e.g. Black Grouse *Tetrao tetrix*, Common Eider *Somateria mollissima* and Slavonian Grebe *Podiceps auritus*), which resulted in a total of 56 species for the atlas comparisons (Table S1).

2.2.2. Abundance data

The abundance data were from line transect counts from breeding bird surveys and territory mapping. Line transects have been conducted once per year across Finland since 1973. Finnish line transects are typically 4–6 km long, where observations are assigned to either within or outside the 50 m band around the transect line (Virkkala & Lehikoinen 2014). Abundance data for Great Britain came from two extensive volunteer surveys: the Common Bird Census (CBC) and the Breeding Bird Survey (BBS). The CBC ran from 1963 to 2000 and used a territory mapping approach to record the number of breeding birds on farmland and woodland plots annually (Marchant *et al.* 1990). The BBS has run since 1994 on a stratified random sample of 1–km squares, where squares are stratified regionally (Harris *et al.* 2020). In each square, which is visited twice between April and June inclusive, birds are recorded along two 1–km line transects. For complete methods see Massimino *et al.* (2015a), who modelled abundances of 49 common and widespread species in the UK, of which 40 species were common enough in both countries and were used in further analyses (see statistical analyses below; Table S2).

In range and abundance analyses all species were classified into one of three habitat categories based on their main habitat use during the breeding season: forest, wetland (including marine environments) or open or semiopen terrestrial ecosystems (including farmland and urban areas; Väisänen *et al.* 1998, Brown & Grice 2010, Balmer *et al.* 2013).

2.3. Statistical analyses

Our aim was to compare population changes in Great Britain and Finland using four data types: range size, mean weighted latitude based on range data (MWL), population trends, and mean weighted latitude of density (MWLD). All the analyses of the four data types followed the same procedure. Each of the four variables listed here was analysed separately and the response variable was annual change for each species in Great Britain. Covariates included in the model were: habitat type, mean latitude of the species, annual change in Finland, and interactions between the Finland variable and the other variables. Altogether this produced 10 different model combinations of fixed variables. Since closely related species may show similar responses due to the same ancestors, we also tested whether analyses were influenced by adding phylogeny in the random structure of the model. Before the model selection of the different fixed effect models, we first tested which phylogenetic random structure fit the data best. In the phylogeny comparison we used four linear mixed models each of which included the full set of fixed effects. In the three models, nested random structure of the phylogeny included i) order, family and genus, ii) family and genus and iii) genus only, and iv) a generalized linear model where no phylogenetic random structure was used (taxonomy according to IOC version 7.3, Gill & Donsker 2017; Tables S1–S2). We compared these four models using AICc (Burnhamn & Anderson 2004) (see Tables S3–S6). The best phylogenetic model structure was applied to the second modelling phase, where models with varying fixed effects were ranked based on AICc (model combinations, see Tables S7–S10). The more detailed analyses of each data type are explained below.

We used R for the statistical analyses (R version 3.4.2; R Core Team, 2018); function *lm* for the linear regression analyses, and *lmer* and *lmerTest* functions for linear mixed effect models (packages of *lme4* and *lmerTest*; Bates *et al.* 2015, Kuznetsova *et al.* 2017). We did not standardize the variables before the analyses to keep the slopes of the results more understandable. Visual inspection of residual plots did not reveal obvious deviations from homoscedasticity or normality. Furthermore, we tested whether the annual population growth rates or annual speed in range or density shifts differ between the two regions using Students *t*-test (function *t.test*).

2.3.1. Range analyses

From atlas data we calculated how much the range size changed between the survey periods. The time periods between atlases were 39 and 26.5 years in Great Britain and Finland, respectively. So the compared unit was proportional change in the number of occupied atlas grids per year. A value of 1.00 would mean that range size has remained the same. Values 1.01 and 0.99 would mean 1% annual increase and decrease in range size, respectively.

We modelled the annual rate of change in range size in Great Britain as a function of the annual rate of change in range size in Finland, habitat type (forest, wetland and open) and mean latitude of the species, and interactions between the Finnish variable and habitat preference of species as well as the Finnish variable and mean latitude (Table S7). The mean latitude was estimated by calculating first mean latitudes of species' range separately for Britain and Finland using a similar scale (from 0 to 1, southern and northern edges, respectively) and then taking the mean of these two national values for each species. Mean latitude was used as an indication of species climatic niche: species with higher values had a colder niche.

In addition, the change in range size can be strongly influenced by absolute range size and some species have very different range sizes in the two countries. Species with a small range have a larger opportunity to increase the range, compared to species whose range already covers most of the area. We therefore used the similarity of species initial range size as a weight in the analyses. For each species we calculated the proportion of each country that was within the species range during the first period. The difference in proportional occupancy across the two countries was inversely proportional to the weight of the species in the model. For example Kingfisher *Alcedo atthis* (51% and 1% of grids occupied in Great Britain and Finland, respectively) had less weight than Pochard *Aythya ferina* (20% and 18% grids occupied in Great Britain and Finland, respectively). We used the log-transformed reciprocal of the difference as a weight in range size change and mean latitude change analyses (in these examples log(1/(0.513–0.012)) = 0.7 and log(1/(0.198–0.178)) = 3.9).

In addition to range size change analyses, we calculated the change in mean weighted latitude (MWL) between the two study periods in both areas. The MWL was calculated using the equation described in Brommer *et al.* (2012). MWL weights species occurrence at a given latitude as the proportion of surveyed grid squares that contain the species. Complete absences at a given latitude gives value 0 and presence in all surveyed grid squares at a given latitude gives full weight (1). This weighing takes into account both the shape of the country (variation in number of surveyed grid squares across latitude within an atlas) and the variation in number of grid squares surveyed at each latitude between atlases. Effectively this estimates a MWL of the range within each country during each period. We calculated the average difference in the MWL per year and the unit of the shift was kilometres per year that the MWL moved northwards (negative values meaning southwards shifts).

The range shift analyses were similar to the range size change analyses using GLMM with a Gaussian error distribution. The speed of range shift in Great Britain was explained by range shift speed in Finland together with interactions with habitat type and mean latitude. Similar to range size change analyses, the difference in species-specific range sizes was included as a weight and phylogeny was tested in the random structure of the models (Tables S4 and S8).

2.3.2. Abundance analyses

The Finnish population trends in the period 1983–2012 were calculated using log-linear Poisson regression with the program TRIM (Pannekoek & Van Strien 2004) and a more detailed data description is done by Laaksonen & Lehikoinen (2013).

In Great Britain, the maximum count across the two BBS visits was modelled in a quasi-Poisson GAM with landcover covariates and a location and time-specific estimate of detectability as an offset. Population indices for the years 1983–2012 were obtained using a simple site + year generalised linear model, with Poisson distribution and log link function:

$$\log(C_{ij}) = S_i + Y_j$$

where C_{ij} is the expected number of territories (in the CBC) or expected number of birds recorded (in the BBS) at the i^{th} site in year j, and S_i and Y_j are site- and year-specific parameters (Freeman *et al.* 2007). The models were fitted using the package *speedglm* (Enea 2017) for R (R core team 2018).

Smoothed population indices were calculated by fitting a thin-plate smoothing spline to the exponentiated year parameters $\exp(Y_j)$. The number of degrees of freedom was set to the total number of years in the time series multiplied by 0.3, based on recommendations in Fewster *et al.* (2000). The change between 2012 and 1983 was calculated as the ratio of the smoothed population index in the two years.

Bootstrapping was used to assess the uncertainty around all estimates; the whole analytical process was repeated 200 times by randomly sampling sites with replacement so that 200 estimates of population change were obtained for each species. The standard deviation of this distribution of bootstrap estimates was then used as an estimate of the standard error of the change measure.

In the abundance analyses, we first investigated whether species have similar long-term population trends. We used national species-specific annual growth rates in the analyses (i.e. + 0.01 and −0.01 would mean 1% increase and decrease in population size, respectively). The species-specific population trends in Great Britain were explained by the corresponding population trends in Finland, habitat type and mean latitude and interaction between these (Table S9). Altogether we had 10 model combinations with different fixed factors similar to the range analyses. We did not weight the population abundance analyses as all investigated species were common species in both countries, but we first took the phylogeny into account similarly as in the range analyses (Table S5).

In addition to population growth rate analyses, we investigated whether the speed of shifts in species abundance was similar in the two countries. Here we measured the centre of gravity of species relative densities in a north-south direction (MWLD; Virkkala & Lehikoinen 2014). Massimino *et al.* (2015a) compared densities between the study periods 1994–1996 and 2007–2009 (the average time interval was 13 years). In Finland, Virkkala & Lehikoinen (2014) compared relative density values between the periods 1990–1999 and 2010–2012 (the average time interval was 16 years). Using both data sets we calculated the MWLD in both periods in both countries using the methodology presented by Virkkala & Lehikoinen (2014). The MWLD values were also scaled into annual changes (km / year). The modelling procedure was similar as in the population trend analyses (Tables S6 and S10).

In abundance analyses, the data included only species from two habitat categories woodland and open ecosystems, as species preferring water ecosystems were lacking. We centralized the data so that forest species had a numeric value of 0.5 and open habitat species −0.5. There are some species that occur mainly in forests in Finland, but in open habitats in Great Britain: Eurasian Cuckoo (*Cuculus canorus)*, Dunnock (*Prunella modularis)*, Winter Wren (*Troglodytes troglodytes)*, Mistle Thrush (*Turdus viscivorus)* and Song Thrush (*Turdus philomelos)* and Chaffinch *(Fringilla coelebs)*. These six species had a numeric species value 0, so that the habitat preference of these species did not influence the analyses.

3. Results

3.1. Temperature changes

Mean annual temperature increased in both Great Britain (linear regression, *b* = +0.032 ±

0.009 SE, $F = 13.25$, $P = 0.001$) and Finland ($b = +0.052 \pm 0.016$ SE, $F = 10.05$, $P = 0.003$) during 1980–2012. The rate of change did not differ significantly between these two areas ($b = -0.020 \pm 0.019$, $F = 1.17$, $P = 0.28$).

3.2. Range changes

British range size changes were significantly smaller than Finnish range size changes (Mean annual changes in Britain 1.005 ± 0.003 SE and Finland 1.026 ± 0.005 SE, paired *t*-test, $t = 4.28$, $df = 56$, $P < 0.001$). Speed in northwards change in mean weighted latitude did not differ significantly between countries (Mean annual speed: Britain 0.95 ± 0.30 SE km/year, Finland 1.42 ± 0.24 SE km/year, paired *t*-test, $t = 1.46$, $df = 56$, $P = 0.16$), although most species had a larger change in mean weighted latitude in Finland. In Great Britain, roughly equal numbers of species increased range (n = 29) and lost range (27). However, in Finland, many more species increased their range (50) compared to those that lost range (7). In both countries more species shifted their range north; 36 and 47 species (among the 56 investigated species) moved north in Great Britain and Finland, respectively.

In models explaining change in range size the best phylogeny structure included family and genus (Table S3). In the model selection of fixed effects, two models explaining range size change in Britain were within 2 ΔAICc units, but the second best more complex model was omitted due to an uninformative parameter (Arnold 2010; Table S7). The best model included range size change in Finland, habitat and their interaction. Wetland species tended to gain range or lose range in both countries (Fig. 1, Table 1), but in open and forested habitat such a connection was not found (Fig. 1, Table 1).

In models explaining the range shifts (MWL) the best phylogeny structure included genus only (Table S4). After the model selection the top ranked model included the fixed effect of MWL in Finland and habitat without their interaction (ΔAIC > 2.4, Table S8). In this model shift speed in MWL in Britain was significantly positively associated with shift speed in MWL in Finland and the British speed of MWL shifts was faster in open habitats than in wetland habitats (Table 2, Fig. 2). Changes in range size and shifts in MWL were poorly correlated in both Great Britain and Finland ($r_p = 0.10$, $P = 0.46$ and $r_p = 0.22$, $P = 0.09$, respectively).

3.2. Abundance changes

The population growth rates of species did not differ between Great Britain and Finland (mean annual rate of change in population sizes: Britain −0.002 ± 0.004 SE, Finland 0.004 ± 0.004 SE, paired *t*-test, $t = -1.13$, $df = 39$, $P = 0.265$), and there also was no significant difference in the speed of MWLD shifts between countries (mean annual speed: Britain 1.95 ± 0.61 SE km/year, Finland 0.84 ± 0.57 SE km/year, paired *t*-test, $t = -1.17$, $df = 39$, $P = 0.25$). MWLD moved northwards for 31 and 21 species and southwards for 9 and 19 species in Great Britain and Finland, respectively.

The model without phylogeny was better than the models with phylogenetic random structures when explaining the connection between population trends in UK and Finland (Table S5). Three models explaining the population growth rates were within 2 AICc units (Table S9), but the top model was the simplest among these three. We only considered this model as the others included uninformative parameters (sensu Arnold 2010). Based on the top ranked model population trends in Great Britain were significantly positively associated with population trends in Finland and negatively associated with mean latitude of species and interaction of Finnish trends and latitude (Table 3, Fig. 3a). The latter indicated that more northern species had more contrasting population trends between UK and Finland (Table 3, Fig. 3a).

The model with order, family and genus as random structure showed the smallest AICc value when explaining the connection between MWLD shifts in UK and Finland (Table S6). In the model selection of fixed effects, the top ranked model had no competing models within 2 ΔAICc units (Table S10). According to this top model, the rate of MWLD shift was negatively connected in Finland and Great Britain; species with fast shift in one country had a slower shift in the other country (Fig. 3b, $b = -0.59 \pm 0.12$, $df = 23$, $t = -5.18$, $P < 0.001$).

Table 1. Parameter estimates of the model explaining range changes in Great Britain based on the top ranked model (see Table S7 for AICc ranking of all models). RangeFin is range size change in Finnish wetland species. HabO is open or semiopen habitats (mainly urban and farmland areas) and HabF is forests; both are in comparison to wetland habitats (intercept, HabW). Significant values are in bold. The marginal and conditional R^2 values of the model were 0.293 and 0.590, respectively.

Variable	β	SE	*df*	*t*-value	*P*-value
(Intercept, HabW)	**0.677**	**0.080**	**37.7**	**8.474**	**< 0.001**
RangeFin (HabW)	**0.325**	**0.078**	**38.1**	**4.190**	**< 0.001**
HabO (compared to HabW)	0.148	0.122	47.5	1.210	0.232
HabF (compared to HabW)	**0.821**	**0.223**	**52.5**	**3.686**	**< 0.001**
RangeFin:HabO	−0.156	0.119	47.9	−1.307	0.198
RangeFin:HabF	**−0.809**	**0.218**	**52.5**	**−3.717**	**< 0.001**

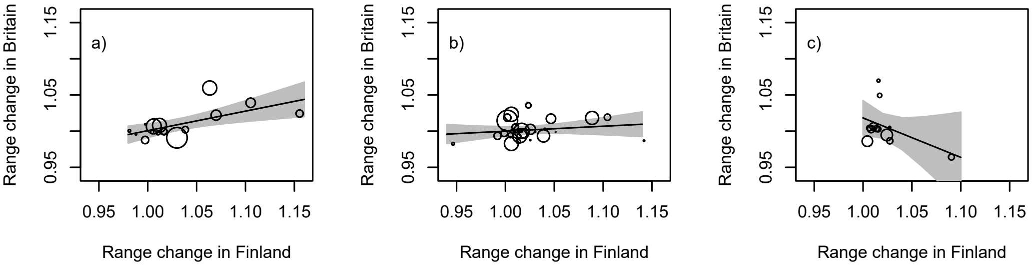

Fig. 1. Comparison of species in range size change (slope / year) in a) wetlands, b) open and c) forests habitats in Britain (y-axes) and Finland (x-axes). One dot represents one species and the size of a dot shows how similar was the initial distribution size of the species. Species with larger dots had more similar initial distribution areas and are thus more comparable than species with large difference in areas (small dots; see methods). Solid lines (dashed for Finland in panel a) show least-square regression line between variables and grey areas represents the 95% confidence limits.

The marginal and conditional R^2 values of the model were 0.135 and 0.939, respectively.

Changes in population growth rates and speed of MWLD shifts were not closely connected in Great Britain or Finland ($r_p = -0.23$, $P = 0.15$ and $r_p = 0.17$, $P = 0.29$, respectively).

4. Discussion

According to our findings, changes in range and population size of species show similar tendencies in both Britain and Finland: on average species gain or lose range and showed either increasing or decreasing population trends. Although this connection was not uniform, it suggests that one or several large scale environmental drivers are likely influencing populations in similar ways and thus our first hypothesis was supported. We also found that temperatures had increased in both areas with approximately similar speed, which indicates that impacts of climate change were approximately the same magnitude in Britain and Finland.

Concerning our second hypothesis of parallel occurrence shifts, we observed contrasting results. Shifts in central gravities of ranges showed a positive correlation between Britain and Finland, but shifts in densities were negatively correlated. Although our range and density shift analyses included partly different species, the results suggest that range shifts are more likely to be similar in different regions, whereas abundance changes within the range may display

Table 2. Parameter estimates of the model explaining rate of change in mean weighted latitude, MWL, in Great Britain based on the top ranked model (see Table S8 for AICc ranking of all models). ShiftFin is range shift change in Finland. HabO is open or semiopen habitats (mainly urban and farmland areas) and HabF is forests; both in comparison to wetland habitats (intercept, HabW). Significant variables are bolded. The marginal and conditional R^2 values of the model were 0.049 and 0.186, respectively.

Variable	β	SE	*df*	*t*-value	*P*-value
(Intercept, HabW)	−0.768	0.630	44.54	−1.22	0.229
ShiftFin	**0.297**	**0.145**	**49.81**	**2.049**	**0.046**
HabO	**2.240**	**0.690**	**50.44**	**3.247**	**0.002**
HabF	1.306	0.806	55.62	1.620	0.111

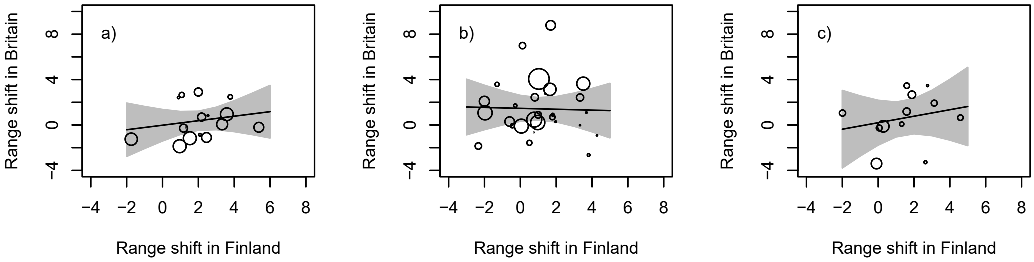

Fig. 2. Comparison of species in shifting speed of mean weighted latitude (km / year) in a) wetlands, b) open and c) forest habitats in Britain (y-axes) and Finland (x-axes). One dot represents one species and the size of a dot shows how similar was the initial distribution size of the species in the two countries. Species with larger dots had more similar initial distribution areas and are thus more comparable than species with large difference in areas (small dots; see methods). Solid line shows least-square regression line between variables and grey areas represents the 95% confidence limits.

differences. Earlier studies have found that range and abundance changes are not necessarily linked (Chamberlain & Fuller 2001, Virkkala & Lehikoinen 2014) and the link can differ between habitat types such as forest and farmland (Gaston *et al.* 1999, 2001). Thus they can tell different messages in terms of response to climate change. The majority of the shifts in MWL were northwards, indicating that climate change may have pushed species ranges polewards in both countries. These range shifts can be caused by small number of individuals colonising the northern range edge and extinctions on the southern range edge (Kujala *et al.* 2013). Density shifts on the other hand are mainly caused by overall changes in the population abundances, which can vary within species range (Virkkala & Lehikoinen 2014) and thus may be more responsive to finer scale changes in the environment than occurrences. It is also important to note that in both countries range size change and speed of shifts of MWL were poorly linked, which suggest that polewards range shifts have occurred independently of change in range size.

Our results supported the third hypothesis that the differences in range and abundance changes can be linked with habitat availability. First, similarity in range size changes was only found among wetland species, which was in line with our expectations because wetland availability is more similar in both countries. Although a small number of our study species are species of conservation concern (Annex I) of the EU Bird Directive, the general conservation measures in EU have been noted to be beneficial for many bird species (Donald *et al.* 2007, Pellissier *et al.* 2020) leading to overall population increases of waterbirds (Pavón-Jordán *et al.* 2020).

Table 3. Parameter estimates of the best model explaining population trends in Great Britain (see Table S9 for AICc ranking of all models). FinT is the population trend in Finland, and mLat is mean latitude of species. Significant variables are bolded. R^2 values of the model was 0.330.

Variable	β	SE	*z*-value	*P*-value
(Intercept)	**0.030**	**0.011**	**2.786**	**0.008**
FinT	**1.908**	**0.615**	**3.099**	**0.004**
mLat	**−0.114**	**0.034**	**−3.329**	**0.002**
FinT:mLat	**−6.474**	**2.111**	**−3.068**	**0.004**

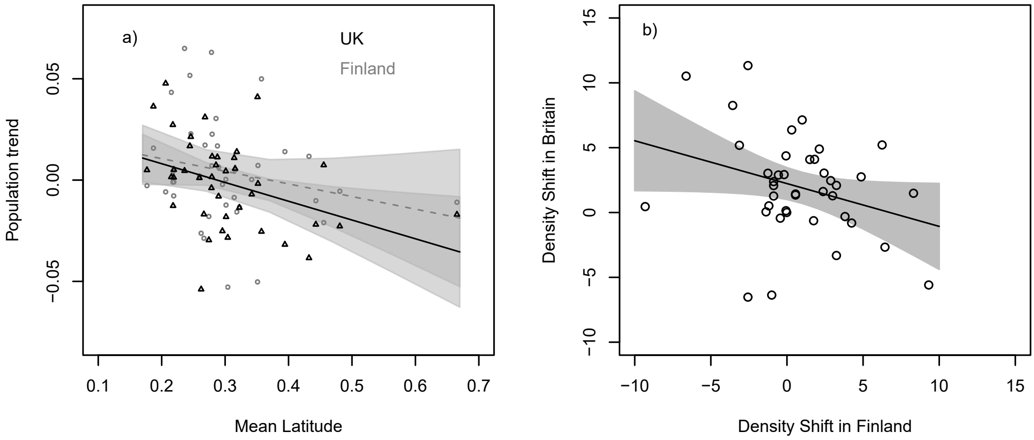

Fig. 3. (a) Population growth rates in Great Britain (black triangles) and Finland (grey circles) in relation to the average latitude of the respective populations (standardized mean latitude: low values mean southern species and high values northern species) and (b) speed of density shifts of species towards north (km / year) in Britain and Finland. Solid line shows least-square regression line between variables and grey areas represents the 95% confidence limits.

Second, speed of range shifts was faster among farmland species in Britain, compared to wetland species. It is well known that intensification of agriculture has caused severe declines of farmland species in large parts of Europe (Donald *et al.* 2001, Gregory *et al.* 2005, Jørgensen *et al.* 2016), and this has been documented also in both study countries (Eglington & Pearce-Higgins 2012, Laaksonen & Lehikoinen 2013) despite the common EU farmland policies (Gamero *et al.* 2017). Eglington & Pearce-Higgins (2012) showed that changes in farmland practices are more important drivers of farmland bird populations than climate change in the UK. In Britain, farmland intensification has been strongest in the south and east leading to shifts in range and density shifts towards north even though the densities of the northern populations have not increased (Balmer *et al.* 2013, Oliver *et al.* 2017). This suggests that fast range and abundance shifts towards north in Britain are driven largely by farmland intensification rather than climate change (Oliver *et al.* 2017).

Farmland intensification can be also one potential reason why density shifts of species show opposite directions in these two countries. In Finland, farmlands are strongly concentrated in the south, and declines of core populations in the south resulted in severe population declines and regional extinctions in the northern sink populations (Rintala & Tiainen 2007). Consequently, there are density shifts towards the south among many farmland species (Lehikoinen & Virkkala 2016), which is the opposite direction than in Britain. Direction of the density shifts in Finland differ between farmland and forest species, which suggest that habitat availability has a large role in how species abundance can spread towards poles (Lehikoinen & Virkkala 2016). However, since the contrasting trends were not only found among species preferring open areas (i.e. mainly farmlands), some other factors may be involved. For instance large scale habitat differences (Britain is dominated with farmlands whereas Finland is mainly covered by forests) and variation in impacts of forestry (e.g. Fraixedas *et al.* 2015) could contribute to the national differences. Britain and Finland have slightly different species composition in the bird communities, partially due to different habitat composition in the areas. Community composition can also affect how individual species respond e.g. through species interactions (Pearce-Higgins & Green 2015).

The mean latitude of species was only associated with the population trends of species: more northerly species had more negative population trends. This supports our last hypothesis, where increased temperatures in both regions due to climate change are linked with population declines of the cold-dwelling species (Jiguet *et al.* 2010, Tayleur *et al.* 2016, Stephens *et al.* 2016). However, the situation of British cold-dwelling species was even worse than in Finland. Results are in line with findings of Massimino *et al.* (2017), who found that species with a projected reduction in climatic suitability in Britain, already have unfavourable conservation status due to long-term population declines. Cold-dwelling species may be more limited in space in Britain, which is situated at more southern latitudes than Finland. On the other hand, northern species can also be threatened by other factors than climate such as changes in land use. For instance management of uplands in the UK could be an additional stressor for northern species (e.g. Calladine *et al.* 2013), and management of peatlands in Finland could have been contributed to the negative population trends of northern species (Fraixedas *et al.* 2017).

In conclusion, species tend to show similar tendencies in changes of population size and trends in Great Britain and Finland, that are likely caused by large scale population drivers such as intensification of agriculture and climate change. However, especially speed of shifts in species' densities towards north were poorly connected between the study areas indicating high variation in species level response in different areas. Drivers of these differences are likely spatial variation in land use changes, habitat availability and habitat quality in these areas. This highlights the need for both large and small scale studies in understanding the impacts of climate change. Multi-national analyses can clarify what factors and species-traits are driving variation in population responses of species to climate change, whilst local studies are important for planning national management actions.

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Ilmaston ja maankäytön muutokset: lintujen levinneisyyden ja runsauden muutosten samankaltaisuus Suomessa ja Iso-Britanniassa

Muutokset ilmastossa ja ihmisten maankäytössä vaikuttavat lajien levinneisyysalueisiin ja runsauksiin. Lajien välisten populaatiomuutosten nopeuteen ja suuntaan vaikuttavat tekijät tunnetaan kuitenkin puutteellisesti. Lajien välisen vaihtelun lisäksi lajin sisäistä vaihtelua ympäristömuutosten vasteissa on tutkittu harvemmin, minkä takia on edelleen epäselvää reagoiko sama laji samalla tavalla ympäristönmuutoksiin eri maantieteellisillä alueilla. Tässä työssä vertasimme muutoksia lajien pesimäaikaisissa levinneisyysalueiden koossa (1970-luvulta lähtien) ja runsauksissa (1980-luvulta lähtien) sekä lajien levinneisyys- (1970-luvulta lähtien) ja tiheyssiirtymien (1990-luvulta lähtien) nopeudessa samoilla lintulajeilla Suomessa ja Iso-Britanniassa. Nämä maat ovat samankokoisia ja niillä on samanlainen

pohjois-etelä-ilmastogradientti ja lämpötilat ovat nousseet molemmissa maissa samalla nopeudella. Samanlaiset vasteet eri maissa voisivat viitata siihen, että globaali ilmastonmuutos aiheuttaa yhteneviä muutoksia lajien levinneisyysalueissa ja runsauksissa. Lisäksi testasimme, eroavatko vasteet eri elinympäristöjä käyttävien lajien välillä, mikä voisi viitata siihen, että maankäytön muutokset ovat tärkeämpiä kuin ilmastonmuutos lajien populaatiomuutoksia selitettäessä. Vesistöissä elävien lajien levinneisyysaluemuutokset olivat samansuuntaiset Suomessa ja Iso-Britanniassa, mutta vastaavaa yhteyttä ei havaittu metsien ja avomaiden lajeilla. Pesimäkantojen runsausmuutokset olivat samansuuntaisia ja pohjoisten lajien kannat taantuivat molemmissa maissa. Lajien levinneisyyssiirtymien nopeudet kohti pohjoista olivat yhteneviä Suomessa ja Iso-Britanniassa, mutta vastaavat siirtymänopeudet lajien pesimärunsauksissa korreloivat negatiivisesti.

Lajien samankaltaiset populaatiomuutokset Suomessa ja Iso-Britanniassa viittaavat, että muutosten taustalla on laaja-alaiset ympäristömuutokset kuten ilmastonmuutos. Toisaalta, etenkin lajien runsauksien päinvastaiset nopeussiirtymät kohti pohjoista viittaavat, että paikallisilla vaihteluilla ja muutoksilla maankäytössä, kuten maa- ja metsätaloudessa, on keskeinen vaikutus lajien runsauksiin. Tämän takia sekä kansainväliset laaja-alaiset että paikalliset tutkimukset ovat tärkeitä selvittämään mm. ilmastonmuutoksen lajistovaikutuksia. Kansainväliset tutkimukset voivat auttaa paremmin ymmärtämään, mitkä tekijät vaikuttavat miten lajit reagoivat ilmastonmuutokseen, kun taas paikalliset tutkimukset ovat tärkeitä kansallisten maankäyttösuunnitelmien ja hoitotoimien kohdentamisessa.

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Online supplementary material

The supplementary material includes lists of species and species level information used in the range and abundance change analyses (Tables S1–2) as well as model section tables covering Akaike Information Criterio values of ranked models (Tables S3–9).