Species richness of migratory birds is influenced by global climate change
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ABSTRACT

Aim Global climate change is increasingly influencing ecosystems. Long-term effects on the species richness and composition of ecological communities have been predicted using modelling approaches but, so far, hardly demonstrated in the field. Here, we test whether changes in the composition of bird communities have been influenced by recent climate change.

Location Europe.

Methods We focus on the proportion of migratory and resident bird species because these groups are expected to respond differently to climatic change. We used the spatial relationship between climatic factors and bird communities in Europe to predict changes in 21 European bird communities under recent climate change.

Results Observed changes corresponded significantly to predicted changes and could not be explained by the effects of spatial autocorrelation. Alternative factors such as changes in land use were tested in a first approximation as well but no effects were found.

Main conclusions This study demonstrates that global climate change has already influenced the species richness and composition of European bird communities.

Keywords Bird community composition, long-distance migrants, Europe, future predictions, GCM, model validation.

INTRODUCTION

Global warming is increasingly influencing the phenology, reproductive success, abundance range size and range position of plant and animal species, resulting in observable changes from the level of individuals to whole communities (Peñuelas & Filella, 2001; McLaughlin et al., 2002; Walther et al., 2002; Parmesan & Yohe, 2003; Root et al., 2003). Many plant species, for example, have extended their growing season (Menzel & Fabian, 1999) and some hibernating species have shortened their winter sleep (Humphries et al., 2004). Birds start breeding earlier (Forchhammer et al., 1998; Dunn, 2004), and migratory birds arrive earlier on their breeding grounds and leave later in autumn (Lehikoinen et al., 2004). Changes in climate have also resulted in range shifts of a number of species (Thomas & Lennon, 1999; Van der Veken et al., 2004; Walther, 2004).

To evaluate the impact of climate change on the species richness and on the structure of ecological communities most studies have used modelling approaches. These modelling approaches have predicted, for example, that forest composition, including species richness, should be strongly affected by climate change (Scheller & Mladenoff, 2005). Several forest plant species in France, Belgium and the Netherlands can be expected to move several hundreds of kilometres northward and thereby change present-day community structures (Van der Veken et al., 2004). For 26 European forest herbs, expected consequences in terms of lost and gained range size and shifts in distribution were estimated (Skov & Svenning, 2004), and loss of diversity for Mediterranean butterfly assemblages over the coming years can be predicted under the most plausible scenarios of climate change (Stefanescu et al., 2004).

However, only a few studies have actually demonstrated empirically that climate change has already caused observable changes within species communities. Global warming should especially influence the species richness and structure of ecological communities. Climatic changes seemed to have altered, for example, the communities of specialized phytophagous beetles (Andrew & Hughes, 2004) and bat populations of northern
the spatial variation in the composition of bird communities and future changes in bird community composition. 

Birds are a very well-studied group of organisms and can probably respond rapidly to environmental changes. They have a very active metabolism and are therefore highly sensitive to climatic changes. Furthermore, they are very mobile and can react immediately to environmental changes. As a result, birds seem to be qualified as pioneer indicators for changes related to global warming and many bird species have already responded to climatic changes (Møller et al., 2004). Nevertheless, only little evidence exists showing that climate change results in systematic changes in the species richness and in the structure of bird communities (Böhning-Gaese & Lemoine, 2004).

The proportion of migratory and resident birds in a temperate bird community is expected to be influenced by seasonal variation in temperature (Herrera, 1978). The population density of resident birds might be limited by low resource levels related to low temperature in winter. High levels of resources in spring can then be shared between residents and incoming migrants. Changes in winter and spring temperature may change the proportion of migratory birds within the communities (O’Connor, 1990; Lemoine & Böhning-Gaese, 2003; Böhning-Gaese & Lemoine, 2004). These changes can manifest themselves as evolutionary effects with changing proportions of migratory individuals within a species, or as ecological effects with changing proportions of migratory species within bird communities. In the present study, we focus on the ecological effects of global climate change and shifts in the composition of bird communities.

Global warming will probably be reflected in increasing winter and spring temperatures (McCarthy et al., 2001). As one consequence of those temperature changes for bird communities we expect changes in the proportion of long- and short-distance migratory bird species. Therefore, we analysed temporal changes in temperature and in the composition of bird communities in Europe over the last few decades. One intrinsic problem when analysing temporal changes in bird communities is to verify that global climate change was actually the causal factor behind these changes. To evaluate the impact of climatic changes on bird communities it is necessary to analyse temporal changes in bird community composition in areas where isochronic climatic changes were observed. Those temporal changes in bird communities can then be compared with changes in bird communities, which we would expect under the observed climate change. The expected changes in bird community composition can be calculated by using the spatial variation in bird communities and climatic conditions in Europe (Lemoine & Böhning-Gaese, 2003). Given that observed changes in bird community structure are similar to expected changes, the spatial relationship between bird communities and climatic factors can then also be used to make predictions for future changes in bird community composition.

In an earlier study, Lemoine & Böhning-Gaese (2003) analysed the spatial variation in the composition of bird communities and climatic factors in Europe. They developed spatial regression models and quantified the relationship between the proportion of migratory and resident bird species and climatic conditions. Lemoine & Böhning-Gaese (2003) used the mean temperature of the coldest month (TCM), mean spring temperature (TSPR, average of April, May and June) and spring precipitation (PSPR, average of April, May and June) as measures of climatic conditions in winter and during the breeding period. The proportion of long-distance migrants increased with decreasing winter temperature and increasing spring temperature (Lemoine & Böhning-Gaese, 2003). These spatial regression models can now be used to calculate expected changes in bird community composition under observed changes in winter and spring temperature and precipitation.

An additional problem when analysing temporal changes in bird communities is spatial autocorrelation of adjacent sites. Bird communities in neighbouring sites might show more similar changes than in more distant sites because for most bird species their ranges extend over more than one site. Climatic conditions in adjacent sites are also more similar than in more distant sites and can therefore be spatially autocorrelated. Finally, changes in bird community composition can also be caused by alternative factors besides global climate change. Migrants and residents have preferences for different habitat types (Mönkkönen et al., 1992; Böhning-Gaese & Oberrath, 2003). Therefore, changes in species richness of migratory and resident bird species might have been caused by changes in land cover in Europe or by changes in the intensity of agricultural land use. Thus, it is necessary to test these alternative hypotheses.

In the present study, we analysed temporal changes in breeding bird communities in Europe over the last few decades using bird atlas data for 21 sites. Our objectives were, first, to calculate changes in the proportion of migratory and resident bird species on the breeding grounds and to compare these observed changes with changes we would expect from the spatial relationship between bird community composition and climate (Lemoine & Böhning-Gaese, 2003). Secondly, we tested whether temporal changes in bird communities could be explained by spatial autocorrelation effects or by alternative factors such as changes in forest area and fertilizer consumption. In the case that observed and expected changes in bird community composition showed good congruence and spatial autocorrelation or alternative factors were of minor importance, we could then use the spatial relationship between bird community composition and climate to make predictions for future changes in bird community composition using a general circulation model for future climate change.

METHODS

Bird data

To analyse the temporal changes in the breeding bird communities, we compared observed changes and changes we would expect from the spatial relationship between bird community composition and climate (Lemoine & Böhning-Gaese, 2003) for
21 sites in Europe (Fig. 1). The objectives for selecting the bird data and sites were, first, the availability of species lists collected at a spatial scale of 100 × 100 km squares, because the spatial regression models of Lemoine & Böhning-Gaese (2003) were developed at that scale. The second objective was the availability of species lists for two separate time periods. These objectives could be met by using bird atlas data from areas where two separate censuses had been conducted. Of the available sites in Europe that met these conditions we chose 21 sites with the additional objectives, first, to cover as much of Europe as possible and secondly, to space the sites as uniformly over Europe as possible (Fig. 1).

For the 21 sites, the dates of the first census period varied from 1968 to 1972 for Great Britain and Ireland to 1985 for one site in Germany (Table 1). The average date of the first census period (averaging the first and last year of the census period over all sites) was 1972–76. For the second census, we considered the most recent atlas in all study sites. The second census was conducted on average during 1988–92, with at least 7 years and an average of 12 years between the last year of the first period and the first year of the second census period (Table 1). Temperatures are known to have increased since about 1980 (Jones et al., 1999). Thus, for each of the 21 study sites, at least the second census has been conducted in a time period of global warming. A potential lack of climate change between the two census periods at some of the sites should not bias the results, because in these cases we expected no change in community composition for the observed changes as well as for the expected changes.

Unfortunately, the quality of the European bird atlas data and the methods of data collection were inconsistent among the different European countries and usually also between the two census periods within one site. Inconsistent data quality should have a strong influence on measures of absolute species numbers, but should affect the recording of long-distance migratory, short-distance migratory and resident bird species equally. We therefore calculated the proportion of long-distance migratory, short-distance migratory and resident bird species and used these values for further analyses. For each site and census period we compiled a species list for a 100 × 100 km square and calculated the proportion of long-distance migratory, short-distance migratory and resident bird species. We excluded all species that use marine, coastal, freshwater and wetland habitats because they have distinctly different ecological needs. Therefore, they might be influenced by climatic change in a different way. The migratory behaviour of a species was defined as a fixed trait according to the biogeographical distribution of the breeding and wintering range (Lemoine & Böhning-Gaese, 2003). We defined long-distance migrants as birds regularly wintering south of the breeding range with the centre of the wintering range south of the Sahara or east of the Pakistan/India border; short-distance migrants as species regularly wintering south of the breeding range with the centre of the wintering range north of the Sahara or west of the Pakistan/India border; and residents as species not regularly leaving the breeding ground in winter (Lemoine & Böhning-Gaese, 2003). For each of the 21 sites we calculated the change in the proportion of long-distance migrants, short-distance migrants and resident bird species between the two census periods.

Table 1 Country, bird census periods and references of the 21 sites in Europe selected for the present study

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<tr>
<th>Site</th>
<th>Country</th>
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With this approach we do not consider intra-specific variation in migratory behaviour. Correspondingly, when analysing temporal changes in bird communities we measure only changes in the composition of bird communities caused by the exchange of species with different migratory behaviour (ecological sorting) and not changes in the migratory behaviour within species (evolution). However, data about temporal changes in migratory behaviour of all species at all 21 sites between the two census periods are not available. Therefore, we had to focus upon changes in community composition.

Climate data

For each site and census period we compiled climatic data for TCM, TSPR and PSPR (Lemoine & Böhning-Gaese, 2003) from the Tyndall Centre for climate change research (Mitchell et al., 2004). We used the mean TCM as a measure of resources available for resident birds in winter, and mean TSPR and PSPR to characterize the climatic conditions during the breeding period. Spring temperature and precipitation is thought to be a good measure of resource availability in the breeding period (e.g. Perrin & Boyer, 2000). When compiling the climatic data, we also included the climatic values for the year before the census period started because the population size of migrants in one year appears to be influenced by the winter conditions of the previous year (O’Connor, 1990). For example, the data for the Atlas of Breeding Birds in Britain and Ireland (Sharrock, 1977) were collected from 1968 to 1972. As climatic data we then used the mean of 1967–72.

Comparison of observed and expected changes in bird communities

For each site we calculated the observed changes in the proportion of long-distance migrants, short-distance migrants and resident bird species between the two census periods (see Bird data). To test if observed and expected changes in bird community composition showed good congruence, we calculated expected changes for the proportion of long-distance migrants, short-distance migrants and resident bird species at the same sites. Expected changes were calculated from the spatial relationship between bird community composition and climatic conditions (Lemoine & Böhning-Gaese, 2003) and the observed changes in TCM, TSPR and PSPR at the 21 sites between the two census periods.

The spatial relationship between bird communities and climatic conditions was derived from spatial regression models that quantified the proportion of long-distance migratory, short-distance migratory and resident bird species in 595 squares in Europe as a function of TCM, TSPR and PSPR from the long-term average of 1961–90, both at the scale of 100 × 100 km squares (Lemoine & Böhning-Gaese, 2003). The proportion of long- and short-distance migratory species were well described by TCM, TSPR and PSPR ($R^2_{\text{long}} = 68.7\%$, $R^2_{\text{short}} = 59.8\%$). For the proportion of resident species, the relationship with the climatic variables was weak ($R^2_{\text{resid}} = 26.3\%$; Lemoine & Böhning-Gaese, 2003). To calculate the expected changes in the proportion of long-distance migrants, short-distance migrants and resident bird species we inserted the values for TCM, TSPR and PSPR for each of the 21 sites and each census period into the formulas of the spatial regression models (Lemoine & Böhning-Gaese, 2003). We then calculated the change in the expected proportion of long-distance migrants, short-distance migrants and resident bird species between the two census periods. These expected changes are changes in the bird community composition we would expect if only climatic factors influenced the bird communities.

The observed changes between the two census periods were compared with the expected changes in bird community composition for each of the 21 sites in Europe. After testing for normality, we analysed the relationship between the observed and expected changes using Spearman’s rank correlations. Only a significant positive correlation between the observed and expected changes demonstrates that the temporal changes in bird community composition can be quantitatively predicted by the spatial regression models of Lemoine & Böhning-Gaese (2003).

Autocorrelation effects and alternative factors

To control for the possible effects of spatial autocorrelation we repeated the analyses using Mantel tests and included the spatial distance of the 21 sites as a covariable (Oberrath & Böhning-Gaese, 2001). With this method, for each pair of grid cells their dissimilarity in the dependent variable is compared with their spatial distance and with their dissimilarity in the other independent variables. As dependent variable we used the observed changes in the proportion of long-distance migrants (short-distance migrants and resident bird species, respectively) and as independent variables the spatial distance between the 21 sites and the expected changes in the proportion of long-distance migrants (short-distance migrants and resident bird species, respectively).

Finally, we tested whether changes in the proportion of long-distance migrants, short-distance migrants and resident species between the two census periods might have been caused by changes in land cover or by changes in the intensity of agricultural land use in Europe. As indicators for changes in land cover and intensity of agricultural land use we used forest area and fertilizer consumption. Forest area was calculated as percentage of land area, and fertilizer consumption as the sum of nitrogenous, potash and phosphate consumption. Both data sets were available only at the spatial scale of the country, but at the temporal scale of years (FAOSTAT data, 2004). Thus, we calculated for each site and census period the mean value for forest area and fertilizer consumption. We then calculated the changes in forest area and fertilizer consumption for each site between the two census periods. To analyse the influence of forest area and fertilizer consumption on the observed changes in the proportion of long-distance migrants, short-distance migrants and resident bird species we used Spearman’s rank correlations similar to the comparison of the observed and expected changes in bird community composition. When testing the potential effects of changes in land cover or fertilizer consumption it would have
been better to have used data from the same 100 × 100 km squares on which birds were counted. However, data are only available at the scale of the country. Thus, the tests of these alternative factors should be treated as a first approximation.

Future predictions

In the case that observed and expected changes in bird community composition showed good congruence and that spatial autocorrelation or changes in forest cover and fertilizer consumption were of minor importance, we used the spatial regression models (Lemoine & Böhning-Gaese, 2003) to make predictions for future changes in bird community composition under future climate change. Future surface temperatures and precipitation in Europe were taken from Mitchell et al. (2004). This study uses the Hadley General Circulation Model (GCM) HadCM3 (Gordon et al., 2000) and a high-resolution data set of surface climate (New et al., 2002) to predict monthly climate for Europe in a spatial resolution of 10′ × 10′ grids. The original data cover 31,143 land grid boxes in a European window (11 W–32 E longitude, 34 N–72 N latitude). For our study, we merged climate information to 1° × 1° grids.

From the scenarios calculated in Mitchell et al. (2004), three were chosen to predict future changes in bird community composition: HadCM3 A1FI, A2 and B1. The three Special Report on Emission Scenarios (SRES) scenarios differ in future greenhouse gas emissions and consequently predict different future climatic conditions. A1FI assumes rapid economic growth and convergence among regions driven by a fossil-fuel intensive source of energy. It therefore leads to the greatest increases in temperature. Scenario B1 yields more moderate climate changes, because it assumes global solutions to economic, social and environmental sustainability. The theme underlying A2 is self-reliance and preservation of local identities leading to a slower economic growth than in A1FI and thus predicting intermediate future climate changes, lying between the two other scenarios.

For each scenario we calculated the average of TCM, TSPR and PSPR for the time period 1961–90 and 2051–80 and inserted the values into the spatial regression models (Lemoine & Böhning-Gaese, 2003). We then calculated the changes in the proportion of long- and short-distance migrants for the time period 2051–80 in Europe as predicted under future climate change. For resident species, predictions were not reliable because neither the spatial regression models nor the temporal changes in species richness (Fig. 2c) showed a strong relationship between the proportion of resident species and climatic factors.

RESULTS

First, we calculated the mean changes in bird community composition and in climatic conditions between the two census periods at the 21 sites in Europe. The mean proportion of long-distance migratory species increased only slightly and nonsignificantly (paired t-test: t = 1.09, P = 0.29, n = 21, Table 2),
the proportion of short-distance migratory species decreased significantly (paired t-test: \( t = -2.29, P = 0.033, n = 21, \) Table 2) and the proportion of resident bird species showed hardly any change (paired t-test: \( t = 0.48, P = 0.64, n = 21, \) Table 2). For the climatic conditions we found that TSPR increased significantly by 0.47 °C between the two census periods (paired t-test: \( t = 5.66, P < 0.0001, n = 21, \) and TCM and PSPR decreased nonsignificantly (paired t-test: \( t = -1.39, P = 0.18 \) and \( t = -0.12, P = 0.91, \) respectively).

Analysing the relationship between observed and expected changes in bird community composition, we found significant correlations for the proportion of migratory bird species but not for residents (Spearman’s rank correlation: long-distance migrants: \( \rho = 0.45, P = 0.038, \) Fig. 2a; short-distance migrants: \( \rho = 0.46, P = 0.037, \) Fig. 2b; residents: \( \rho = 0.23, P = 0.32, \) Fig. 2c; \( n = 21 \)). Observed changes in the proportion of long-distance migratory species were significantly more negative than expected (Wilcoxon’s signed rank test: d.f. = 20, \( S = -66.5, P = 0.017, \) Fig. 2a), observed changes in the proportion of short-distance migratory species were significantly more positive than expected (\( S = -79.5, P = 0.003, \) Fig. 2b) and observed changes for resident bird species were marginally more positive than expected with the spatial regression models (\( S = -49.5, P = 0.085, \) Fig. 2c).

The possible effects of spatial autocorrelation between the 21 sites did not influence the results (multiple regression Mantel test: effect of spatial distance: long-distance migrants: \( t = 2.76, P = 0.16, \) short-distance migrants: \( t = 0.80, P = 0.33, \) residents: \( t = -0.26, P = 0.19, n = 210, 10,000 permutations \). Changes in bird community composition were correlated neither with changes in forest area nor in fertilizer consumption between the two census periods (Spearman’s rank correlation: forest area: long-distance migrants: \( \rho = -0.20, P = 0.41, \) short-distance migrants: \( \rho = -0.40, P = 0.094, \) residents: \( \rho = -0.06, P = 0.82; \) fertilizer consumption: long-distance migrants: \( \rho = 0.04, P = 0.86, \) short-distance migrants: \( \rho = 0.04, P = 0.85, \) residents: \( \rho = -0.11, P = 0.65, n = 21, \) respectively). Changes in the proportion of long-distance and short-distance migratory species could be predicted by the spatial relationship between bird community composition and climatic conditions. No influence of spatial autocorrelation effects or of forest cover and fertilizer consumption could be detected. Thus, the spatial regression models can be used to make predictions for changes in bird community composition in the future.

The General Circulation Model HadCM3 estimated an increase in mean TCM in Europe between 1961–90 and 2051–80 by 4.3 °C (A1FI), 3.4 °C (A2) or 2.8 °C (B1). TSPR is expected to rise by 3.9 °C (A1FI), 3.0 °C (A2) or 2.3 °C (B1). PSPR is expected to decrease by 11.6 mm (A1FI), 4.2 mm (A2) or 3.8 mm (B1), with strong regional differences. Inserting the estimated values for TCM, TSPR and PSPR into the spatial regression models (Lemoine & Böhning-Gaese, 2003), we calculated the predicted changes in the proportion of long- and short-distance migratory species between 1961–90 and 2051–80 (Fig. 3).

For the proportion of long-distance migratory species, the three scenarios predicted weak increases in most parts of Europe. Stronger increases were predicted for southern Europe, especially parts of Portugal and Spain (Fig. 3a). For the short-distance migrants, the results suggested declining proportions in the whole of Europe, especially pronounced in western and northern Scandinavia and Spain (Fig. 3b). In both long-distance and short-distance migratory birds, scenario B1 predicted the mildest changes, while scenario A2 and especially scenario A1FI predicted more pronounced changes.
DISCUSSION

Our analyses indicated that observed changes in the proportion of long-distance migratory species in 21 sites in Europe between 1972–76 and 1988–92 were less pronounced than one would expect from the literature. Contrary to other studies, in which more negative trends for long-distance migrants than for short-distance migrants or residents were found at the EU and Pan-European level (BirdLife International, 2004), our results showed a slight increase in the proportion of long-distance migratory species and a significant decrease in the proportion of short-distance migratory species. These changes can be explained by the isochronic changes in temperature and precipitation in the 21 sites. Spring temperature increased significantly, while the temperature of the coldest month and spring precipitation did not change. Lemoine & Böhning-Gaese (2003) found that the proportion of long-distance migrants increased and the proportion of short-distance migrants decreased with increasing spring temperature in a spatial analysis across Europe. Thus, given the fact that only spring temperature increased in the sites we happened to select in our study, increases in the proportion of long-distance migratory species and decreases in the proportion of short-distance migratory species are to be expected.

However, in spite of these small changes in bird community composition, observed changes in species richness of migratory birds corresponded significantly to the expected changes if climate change alone had influenced the birds. The correlation of observed and expected changes in bird community composition was statistically significant, although sample size was small \((n = 21)\) and expected values were calculated with a rather large error. The spatial regression models on which the expected values were based were able to explain only 68.7% of the variance in the proportion of long-distance migratory species and 59.8% of the variance in the proportion of short-distance migratory species by climatic factors (Lemoine & Böhning-Gaese, 2003). We found good congruence of observed and expected changes for the

Figure 3  Predicted changes in the proportion of (a) long-distance migratory and (b) short-distance migratory species in bird communities for the time period 2051–80 in relation to 1961–90 as percentages for three different SRES scenarios (A1FI, A2 and B1). Resolution of grids is \(1° \times 1°\). The data shown are for all grids covering more than 50% land area.
proportion of long- and short-distance migrants. In contrast, we did not find any significant correlation between observed and expected changes in the proportion of resident bird species. This might be explained by a poor relationship between species richness of resident birds and climatic factors. Correspondingly, the spatial regression models explained only 26.3% of the variance in the proportion of resident bird species by climatic factors (Lemoine & Böhning-Gaese, 2003).

Observed changes were significantly more negative than predicted in the proportion of long-distance migratory species (Fig. 2a) and significantly more positive than predicted in short-distance migratory species (Fig. 2b). These results indicate that factors apart from climate influenced the changes in the proportion of migratory birds. Therefore, we also analysed alternative factors such as changes in forest area and fertilizer consumption on the breeding grounds. However, we did not find any significant influence of these factors on the changes in bird community composition. Unfortunately, the data for forest area and fertilizer consumption were not very detailed. We could only use data at the scale of the country, and not for the specific sites where the bird data had been collected. This might underestimate the effect of changes in forest area and fertilizer consumption, because both factors may differ within a country. Therefore, a more detailed investigation of alternative factors might potentially lead to different results. Nevertheless, this is one of the first studies on climate change that has analysed alternative factors. To our knowledge, only Thomas & Lennon (1999) controlled for alternative factors when analysing climate-related changes in the breeding distributions of British birds.

Alternatively, the fact that observed changes in the proportion of long-distance migratory species were significantly lower than expected and that observed changes in the proportion of short-distance migratory species were significantly higher than expected might be caused by factors acting on the wintering grounds. For example, long-distance migrants might face, in addition to the change in climatic factors on the breeding grounds, deteriorating conditions on the wintering grounds in tropical Africa or Asia. It would be interesting to test for such alternative factors. However, a prerequisite for testing these factors is to know where the different migratory species at the 21 sites spend their winter. Although an impressive collection of ringing data exists, to conduct such a study we would need ringing data for each species from each of the 21 study sites. Presently, such knowledge is unavailable. Thus, factors on the wintering grounds cannot easily be tested. Moreover, it is not known which factors might influence migratory birds on their wintering grounds. In addition to climatic factors, changes in food resources, interspecific competition, predation pressure or parasitism might be important.

Short-distance migrants, in contrast, mainly overwinter in the Mediterranean region. Thus, in contrast to long-distance migrants, they might benefit from increases in winter temperature in Europe. Furthermore, the migratory behaviour of short-distance migrants might be controlled more by environmental factors such as temperature, while the migratory behaviour of long-distance migrants seems to be more genetically controlled. Thus, short-distance migrants can probably adapt faster to climatic changes and arrive earlier on their breeding grounds than long-distance migrants (Møller et al., 2004). In the case that short-distance migrants and resident bird species are able to adapt to warmer spring conditions faster and start breeding earlier (Møller et al., 2004), for incoming long-distance migrants, therefore, fewer nest sites are available and competition pressure will probably increase.

In addition to the ecological effects of global climate change on the composition of bird communities analysed in this study, we expect evolutionary changes in the migratory behaviour of these birds. Migratory birds can change their migratory behaviour rapidly in only a few generations (Berthold et al., 1992; Pulido & Berthold, 2003). In recent years, changes in many aspects of migration behaviour have been observed and attributed to climate change: changes in timing of the movements to the breeding and wintering areas, changes in migratory directions (as a consequence of the establishment of new wintering areas), decreasing migration distances and increasing numbers of residents (Fiedler, 2003; Pulido & Berthold, 2004; Bearhop et al., 2005). Thus, the phenomenon of migration is influenced on the one hand by changes in the number and proportion of migratory species, i.e. by ecological sorting, and on the other hand by evolutionary changes in the behaviour of these birds.

In our study we made the assumption that migratory behaviour was a fixed trait within a bird species and was the same over the whole range of the species within Europe. We did not include intraspecific variation in the migratory behaviour of migrants nor evolutionary changes of migratory behaviour into the analyses. Might these assumptions bias our results? Assuming that the migratory behaviour of the species also evolves, we would expect that migratory restlessness should decrease. Thus, migrants will become less migratory. As a consequence we would expect fewer changes in the proportion of migratory species in bird communities as the species that are present are able to adapt. If these evolutionary changes are more important than ecological sorting we expect, as an extreme result, no change in the proportion of migratory bird species in these communities. Under these circumstances we would also expect no correlation between observed changes in bird community composition and expected changes calculated from the spatial regression models. Thus, by comparing observed and expected changes in bird community composition we take a statistically conservative approach. The fact that we do find a significant correlation between observed and expected changes in the proportion of migratory bird species (Fig. 2) demonstrates that evolutionary changes in migratory behaviour are not overwhelmingly important and do not ‘destroy’ the significant relationship.

Our predictions of future changes in migratory species within the European bird communities suggest increasing proportions of long-distance migratory species and declining proportions of short-distance migratory species. According to our models, changes will be especially pronounced in south-western Europe and Scandinavia. It would be interesting to evaluate if these changes in the proportion of migratory species can be related to changes in the absolute numbers of species. Unfortunately, earlier analyses including the absolute number of species did not
reach a satisfactory congruence between expected and observed changes in bird community composition. Therefore, it was not reasonable to predict changes in the number of migratory and resident bird species for the future.

This study demonstrates that climate change has already changed the composition of European bird communities. The changes in bird community composition could be predicted quantitatively from spatial variation in bird communities and climatic factors across Europe. Furthermore, changes could not be explained by the alternative factors tested. Changes in species richness of migratory birds over the past 40 years have been small, with much more dramatic changes expected in the future (Fig. 3). It is important to note, however, that environmental changes on the wintering grounds are not included in our analyses and might lead to more negative trends than anticipated.

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REFERENCES


N. Lemoine et al.

... auf 768 km² Stadtbäche zwischen 1997 und 2000. Arbeitskreis
an der Staatlichen Vogelschutzvarte Hamburg, Hamburg.
climate change. Advances in Ecological Research, vol. 35. Elsevier
Palaeartic and Nearctic bird migration; comparisons and
overview of life-history and ecology of migrant passerines.
Ibis, 134 (Suppl. 1), 7–13.
resolution data set of surface climate over global land areas.
Climate Research, 21, 1–25.
Fischer Verlag, Jena.
O’Connor, R.J. (1990) Some ecological aspects of migrants
and residents. Bird migration: physiology and ecophysiology (ed.
Test to cope with autocorrelation in comparative analyses.
of climate change impacts across natural systems. Nature, 421,
37–42.
Science, 294, 793–794.
Perrin, M.R. & Boyer, D.C. (2000) Seasonal changes in the popu-
lation dynamics of hairy-footed gerbils in the Namib Desert.
of migratory behaviour. Avian migration (ed. by P. Berthold,
E. Gwinner and E. Sonnenschein), pp. 53–77. Springer-Verlag,
Berlin.
climate change. Birds and climate change (ed. by A.P.
in Ecological Research, vol. 35. Elsevier Academic Press,
London.
Brutvögel Deutschlands. Rheinischer Landwirtschaftsverlag,
Bonn.
Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C.
Scheller, R.M. & Mladenoff, D.J. (2005) A spatially interactive
simulation of climate change, harvesting, wind, and tree species
migration and projected changes to forest composition and
biomass in northern Wisconsin, USA. Global Change Biology,
Schmid, H., Ludet, R., Naef-Daenzer, B., Graf, R. & Zhinden, N.
(1998) Schweizer Brutvogelatlas Verbreitung der Brutvögel in
der Schweiz und im Fürstentum Liechtenstein 1993–96. Verlag
Schweizerische Vogelwarte Sempach, Sempach.
Sharrock, J.T.R. (1977) Atlas of breeding birds in Britain and
change on the distribution of forest herbs in Europe. Ecography,
birds in the Czech Republic 1985–89. Academia, Praha.
Stastny, K., Randik, A. & Hudec, K. (1987) Breeding bird atlas of
species richness in the north-west Mediterranean Basin:
the role of natural and human-induced factors. Journal of
Biogeography, 31, 905–915.
Sachse. Lößnitz Druck GmbH, Radebeul.
De Lange van Leer bv, Deventer.
Thomas, C.D. & Lennon, J.J. (1999) Birds extend their ranges
Pesimälinnusto. Otava, Helsinki.
gradient explain changes in plant community composition
of the forest understorey: an extrapolation after climate
Plant Ecology, Evolution and Systematics, 6, 169–185.
Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C.,
Ornithologique de France, Paris.
nicheurs de France 1985–89. Société Ornithologique de France,
Paris.

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