



Impact of climate change on migratory birds: community reassembly versus adaptation

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ABSTRACT

Aim Species can respond to global climate change by range shifts or by phenotypic adaptation. At the community level, range shifts lead to a turnover of species, i.e. community reassembly. In contrast, phenotypic adaptation allows species to persist *in situ*, conserving community composition. So far, community reassembly and adaptation have mostly been studied separately. In nature, however, both processes take place simultaneously. In migratory birds, climate change has been shown to result in both exchange of species and adaptation of migratory behaviour. The aim of our study is to predict the impact of global climate change on migratory bird communities and to assess the extent to which reassembly and adaptation may contribute to alterations.

Location Europe.

Methods We analysed the relationship between current climate and the proportion of migratory species across bird assemblages in Europe. The magnitude of community reassembly was measured using spatial variation in the proportion of potentially migratory species. Adaptation was inferred from spatial variation in the proportion of potentially migratory species that actually migrate at a specific site. These spatial relationships were used to make temporal predictions of changes in migratory species under global climate change.

Results According to our models, increasing winter temperature is expected to lead to declines in the proportion of migratory species, whereas increasing spring temperature and decreasing spring precipitation may lead to increases. Changes in winter and spring temperature are expected to cause mainly adaptation in migratory activity, while changes in spring precipitation may result in both changes in the proportion of potentially migratory species and adaptation of migratory activity.

Main conclusions Under current climate change forecasts, changes in the proportion of migratory species will be modest and the communities of migratory birds in Europe are projected to be altered through adaptation of migratory activity rather than through exchange of species.

Keywords

Bird migration, European bird community, evolutionary response, global warming, migratory activity, species turnover.

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INTRODUCTION

Climate change and habitat loss are the two greatest threats to biodiversity in the present century (Sala *et al.*, 2000; Carpenter *et al.*, 2005; Jetz *et al.*, 2007). Global climate change has already been shown to affect a wide spectrum of organisms, from plants to invertebrates and vertebrates, in their morphology, physiology, phenology, life history, abundance and distribution

(Hughes, 2000; Root *et al.*, 2003; Parmesan, 2006). In principle, species can respond to climate change by two different processes. Species can move, i.e. they can shift their ranges. This process, which is most probably taking place between generations rather than within, can lead to colonization of new sites and local extirpation. Most extremely, it can lead to the global extinction of a species. Alternatively, species can respond by phenotypic adaptation, either as a result of true evolutionary change or

as a result of phenotypic plasticity (Holt, 1990; Bradshaw & Holzapfel, 2006). In this study we use the term adaptation for any process of adjustment to climate change, including both true evolutionary change and phenotypic plasticity, which are not mutually exclusive.

At the level of ecological communities, the two processes have different effects on community composition. Colonization and local and global extinctions of species lead to a turnover of species in a community or community reassembly. As reassembly causes new species to arrive in a community and others to be lost, it alters community composition and might lead to changes in species richness and dominance relationships (Barry *et al.*, 1995). If changes are profound, species interactions might be disrupted (Niemela *et al.*, 2001, Nussey *et al.*, 2005). Thus, Groom *et al.* (2006) consider this process to be the most worrisome biotic impact of global climate change. In contrast, phenotypic adaptation to local conditions allows a species to persist *in situ*. As a consequence, the species remains in the local species assemblage and community composition is expected to be conserved. Thus, further effects on other organisms in the assemblage might be less profound than in the case of community reassembly.

So far, researchers have made separate studies of the impact of climate change on community reassembly and on the adaptation of species. For example, ecologists have amply documented range shifts in plants, invertebrates and vertebrates (Parmesan, 2006). Separately, evolutionary biologists have provided evidence of the first evolutionary adaptations to global climate change (Bradshaw & Holzapfel, 2006). In nature, however, both processes take place simultaneously. If climate changes, communities may gain or lose species, but species within the community also adapt to local conditions. To predict the consequences of climate change for ecological communities, it is therefore important to assess the extent to which the two processes may affect species and communities.

Birds are among the few groups of organisms in which both community reassembly and adaptation of species to climate change have been documented. Climate change has resulted in birds shifting their ranges and colonizing new localities (Thomas & Lennon, 1999; Böhning-Gaese & Lemoine, 2004). Consequently, climate change has altered the species richness and composition of avian communities (Lemoine *et al.*, 2003, 2007a,b). Most studies reporting adaptive responses to climate change have not documented true evolutionary (i.e. genetic) change but provide evidence for phenotypic adaptation with evolutionary change being a likely explanation (Jonzen *et al.*, 2007). Adaptations to climate change have been suggested for body mass (Yom-Tov, 2001) and for the amount, timing and direction of migratory activity of a number of migratory birds (Bezzel & Jetz, 1995; Fiedler, 2003; Jonzen *et al.*, 2006; but see Both, 2007). Finally, changes in the degree and direction of migratory activity of blackcaps (*Sylvia atricapilla*) can be interpreted as adaptations to climate change (although earlier studies suggested a response to winter feeding in Britain and Ireland; Berthold *et al.*, 1992; Bearhop *et al.*, 2005; Bradshaw & Holzapfel, 2006).

Because climate change results in both changes in the number of migratory species and adaptation of migratory behaviour, migratory bird communities are a suitable model system to compare the impacts of these two processes. The proportion of migratory species in a local community is a measure that usefully characterizes the climate-dependent migratory propensity and activity of a local community. Under community reassembly it may decline due to local extinction of a migratory species or immigration of a non-migratory species. Under phenotypic adaptation it may decline if migratory species evolve to become resident.

Community reassembly of migratory species in European bird communities has been demonstrated by Lemoine *et al.* (2007b). They showed that recent changes in the proportion of long-distance and short-distance migratory species in 21 European bird communities corresponded to climatic changes in the respective sites. In contrast, evolutionary changes in the amount of migratory activity of bird species have been documented for individual species at single sites (Pulido & Berthold, 2004; Bearhop *et al.*, 2005) but not at the level of whole communities. While the effect of climate change on the number and proportion of migratory species in a bird community is known, the effect on the migratory activity of these species is not understood.

Here we develop climatic models of migratory propensity and migratory activity of European birds and use them to predict future proportions of migrants under climate change. We define migratory propensity as the proportion of potentially migratory species, i.e. species that are migratory in at least part of their range. We use current spatial variation in migratory propensity to investigate the potential for climate-induced community reassembly to alter migratory bird communities. We define migratory activity as the proportion of *potentially* migratory species that *actually* migrate at a specific site. We use current spatial variation in migratory activity to assess the potential for species to adapt migratory behaviour in response to climate change. We proceed to evaluate the relative predominance of community reassembly and adaptation in response to climate change. Specifically, we provide a first evaluation of how predicted future climate may affect spatial patterns in migratory bird communities.

METHODS

Study area and bird data

The study area included Europe from Gibraltar to northern Norway (12° W–50° E; 35° N–72° N) excluding Iceland. The area was divided into 5232 grid cells of 0.5° × 0.5° latitude and longitude, considering only cells with a land area of more than 50%. This procedure excludes cells with very little land area and thus extreme numbers and proportions of migratory species. The remaining variation of land area in the grid cells is minimal and affects the number of migratory and resident species in similar ways with negligible effect on their relative proportions. Bird data were taken from Snow *et al.* (1998), which gives breeding and wintering ranges of all European breeding bird species.

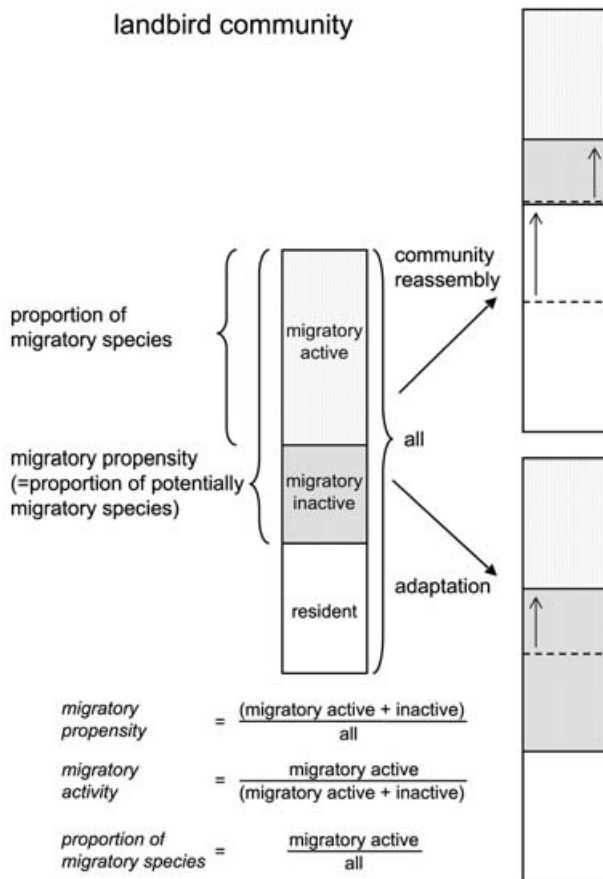


Figure 1 Conceptual approach illustrated for an example land bird community. For every grid cell the community was divided into potentially migratory species (all species that leave at least part of their European breeding range in winter, light and dark grey) and non-migratory, resident species (white). Of the potentially migratory species, in a specific community some are migratory active (light grey) and some are inactive (dark grey). We call the proportion of potentially migratory species in a bird community the *migratory propensity* of this community. The proportion of migratory active species of all potentially migratory species is called the *migratory activity*. The proportion of migratory active species of all species is referred to as the *proportion of migratory species*. Note that columns represent proportions, whereas in the formulae species numbers are used. *Community reassembly* occurs when the migratory propensity (i.e. the proportion of potentially migratory species in a bird community) changes. Arrows within columns indicate the direction of change from the former proportion (dashed line) to the new proportion (solid line). *Adaptation* occurs when migratory activity changes. Both processes affect the proportion of migratory species in a community with proportion of migratory species = migratory propensity × migratory activity. In order to simplify the figure we only illustrated the unidirectional case of decreasing proportions of migratory species as would be expected in a warming situation. Please keep in mind that these processes are bidirectional and changes can happen in either direction.

Range maps were available in digital format from the publisher and geo-registered to a known projection in GIS. We included only breeding land birds (324 species, defined as species that live

in and obtain their resources from terrestrial habitats) in our analysis, because species that use marine, coastal or freshwater habitats have distinctly different ecological needs and might react differently to climate change.

Community reassembly and adaptation

Community reassembly is characterized by gains and losses in migratory species and thus by changes in the migratory propensity of a bird community. We define migratory propensity as the proportion of potentially migratory species in a bird community, i.e. the proportion of species that are migratory in at least parts of their range. To measure migratory propensity we divided for each grid cell assemblage the number of potentially migratory species (regardless of their actual migratory activity in the grid cell) by the total number of species in that grid cell (migratory propensity = number of potentially migratory species/total number of species; Fig. 1). We use current spatial variation in migratory propensity to assess the magnitude of community reassembly under future climate change.

Adaptation of migratory activity is characterized by a migratory species developing residency or a resident species developing migratory activity in a specific site. We define migratory activity of a bird community as the proportion of *potentially* migratory species that *actually* migrate at a specific site. We quantified the migratory activity of the bird community in a specific grid cell by dividing the number of potentially migratory species that are migratory active (those that were found in that cell only in the breeding season) by all potentially migratory species in that cell (migratory activity = migratory active potentially migratory species/all potentially migratory species; Fig. 1). We use current spatial variation in migratory activity to estimate the magnitude of adaptation in response to climate change.

The proportion of migratory species in a grid cell is given as migratory active potentially migratory species divided by the total number of species (Fig. 1). Note that this proportion of migratory species is determined both by migratory propensity and migratory activity of the bird community with proportion of migratory species = migratory propensity × migratory activity. For example, a bird community with 100 species in a grid cell might have 25 migratory species (proportion of migratory species = 0.25) because it has 25 potentially migratory species all of which are migratory in the respective grid cell (migratory propensity = 0.25, migratory activity = 1.00; proportion of migratory species = 0.25 × 1.00 = 0.25), or because all 100 species are potentially migratory species with 25 of these being migratory active in the respective grid cell (migratory propensity = 1.00, migratory activity = 0.25; proportion of migratory species = 1.00 × 0.25 = 0.25), or because 50 species are potential migratory species with 25 of these showing migratory activity (migratory propensity = 0.50, migratory activity = 0.50; proportion of migratory species = 0.50 × 0.50 = 0.25). Please note that we use ‘migratory species’ and ‘proportion of migratory species’ to refer to the proportion of *all* species that leave a grid cell in winter; ‘potentially migratory species’ refers to species that are migrants somewhere in Europe, ‘migratory propensity’

refers to the proportion of potentially migratory species in a bird community and 'migratory activity' indicates the proportion of *potentially* migratory species that leave a grid cell in winter.

We derived the classification of the species in a grid cell by using the breeding and wintering ranges of the species and not the migratory behaviour of the local individuals. This procedure leaves partial migration (when a fraction of the population leaves the grid cell) or simultaneous shifts of populations (e.g. when the individuals in the grid cell leave this grid cell but are replaced by wintering individuals from a more northern population) unconsidered (Newton & Dale, 1996). Our approach reflects whether a specific grid cell is able to support a particular species only in the breeding season or throughout the year.

Climate data

To calculate regression models that describe the spatial relationship between the migratory bird community and climatic factors we used average temperature and precipitation data from 1961–90 compiled for the same $0.5^\circ \times 0.5^\circ$ grid cells (New *et al.*, 2002). We used the temperature of the coldest month (T_{CM}) to characterize conditions on the wintering grounds in Europe, and temperature in spring (T_{SPR} , average temperature in April, May and June) and precipitation in spring (P_{SPR} , sum of precipitation in April, May, and June) to characterize conditions during the breeding period. These measures were chosen because a number of studies demonstrated that the prevalence of migration in a bird community depends on the severity of winter conditions and the availability of resources in spring (Herrera, 1978; Hurlbert & Haskell, 2003). Attempts to replace T_{SPR} and P_{SPR} by net primary production (NPP) in spring resulted in much lower R^2 values of the models. Quadratic terms of the variables were not included in the models because they increased the proportion of explained variation only very slightly.

Statistical analysis and future predictions

To study the effect of climate on migratory species, on community reassembly and on adaptation, we ran ordinary least squares (OLS) linear regression models across 5232 grid cells in Europe. We used the number and proportion of migratory species, migratory propensity and migratory activity as response variables and the three climatic factors as predictor variables. We used number and proportion of migratory species to be able to compare effects on the absolute and relative numbers of species. The residuals of all models were approximately normally distributed. The resulting regression coefficients provide a measure of the sensitivity of these numbers and proportions to spatial variation in temperature and precipitation. Using a space-for-time approach, we used these coefficients to estimate the changes in migratory bird communities that are expected given changes in temperature or precipitation.

We tested the residuals of the regression models for potential spatial autocorrelation using Moran's I (Legendre, 1993). Residuals showed strong positive spatial autocorrelation up to a distance of

1370–1925 km (for results see Appendix S1 in Supplementary Materials). Therefore, we repeated the climate regressions using simultaneous autoregression (SAR) models as implemented in the SAM software (Rangel *et al.*, 2006). For the analysis we used geographical distances, an α of 3, and equal number of pairs in the distance classes. The SAR models effectively removed the spatial autocorrelation (Appendix S1). We used both the estimates resulting from the OLS models and the estimates from the SAR models to quantify the influence of community reassembly and adaptation on migratory species.

Finally, we used the regression models (with and without taking spatial autocorrelation into account) to predict changes in migratory species under future climate change. We used future temperatures and precipitation predicted using the Hadley general circulation model (GCM) HadCM3 (Gordon *et al.* 2000) and the Special Report on Emissions Scenarios (SRES) scenario A2 as given by Mitchell *et al.* (2004). Scenario A2 assumes moderate economic growth due to a preservation of local identities and regions, causing temperatures to increase at a moderate rate compared with other, more extreme, scenarios. Climate data were available in a $1^\circ \times 1^\circ$ grid for a European window spanning from 11° W to 32° E and from 34° N to 72° N. Future changes in migratory bird communities were predicted by calculating changes in the number and proportion of migratory species, migratory propensity and migratory activity using the coefficients of the regression models and T_{CM} , T_{SPR} and P_{SPR} of the time periods 1961–90 versus 2051–80.

Spatial autocorrelation in response data is likely to violate the assumption of non-independence of model residuals in regression analysis and may cause inflation in type I errors. Spatial models such as SAR can account for spatial autocorrelation in model residuals, but yield parameter estimates that are dependent on the type of modelling approach used. The magnitude and causes of this cross-model variability in model coefficients is still not well understood (Diniz-Filho *et al.*, 2003; Kissling & Carl, 2007; C.F. Dormann *et al.*, unpublished), but we note that SAR models are thought to yield relatively reliable parameter estimates (Kissling & Carl, 2007). Finally, the constancy of the spatial autocorrelation structure of species distributions over time is questionable, which severely limits the use of coefficients from spatial models to predict future patterns. Therefore we quantify community reassembly and adaptation and predict changes in migratory birds under future climate change using the parameter estimates of both OLS and SAR models.

RESULTS

Spatial pattern

The number and proportion of migratory species increased towards eastern Europe (Fig. 2a, b). Migratory propensity ranged between 56 and 92% and had its maximum mainly in south-eastern Europe (Fig. 2c). Migratory activity increased towards the north-east and reached > 90% over large areas in Scandinavia and north-eastern Europe (Fig. 2d).

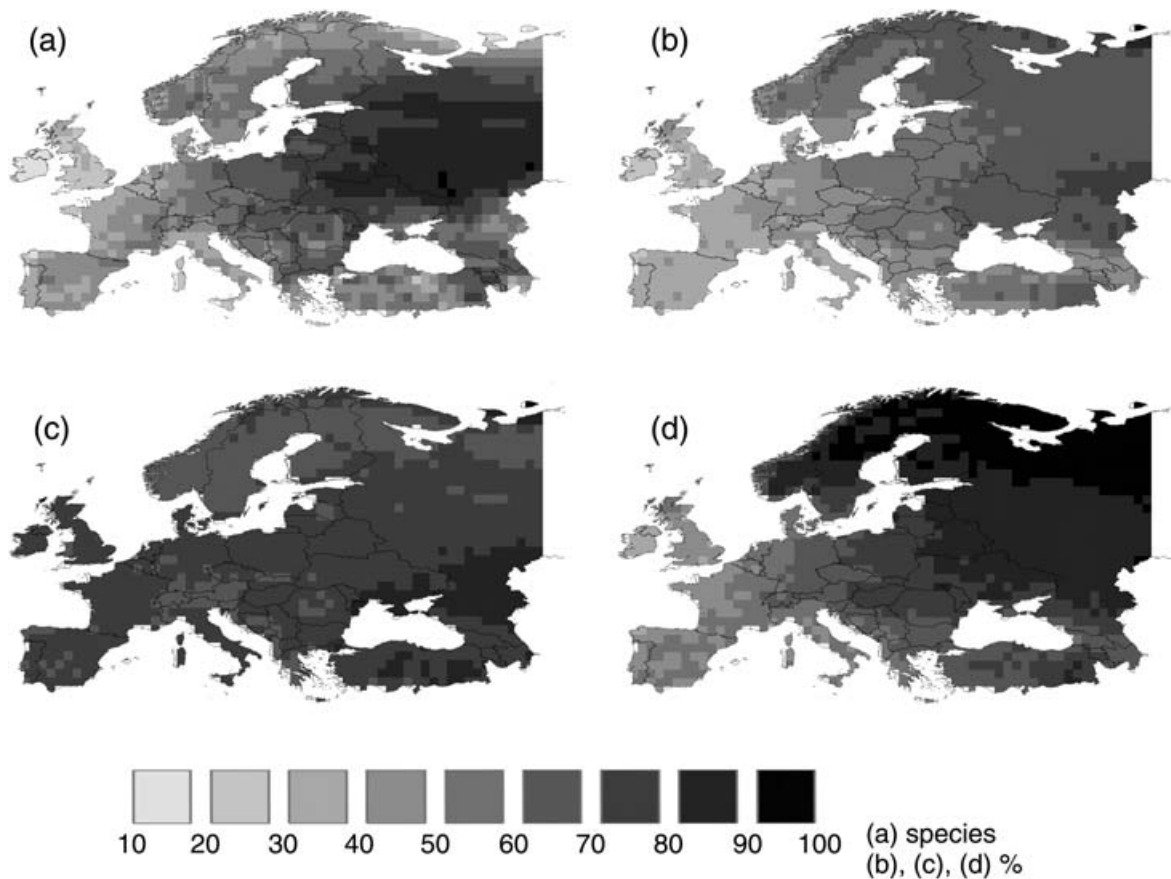


Figure 2 Spatial pattern of migratory bird communities in Europe: (a) number of migratory species; (b) proportion of migratory species; (c) migratory propensity; (d) migratory activity. The legend gives species numbers and percentages below the grey scale. For details see Methods.

Using OLS regressions, the number and proportion of migratory species decreased with increasing temperature of the coldest month and increased with increasing spring temperature (Fig. 3a, Table 1). Thus, migratory species benefited from cold winters and warm springs. The decrease of migratory species with increasing winter temperature was mainly caused by a decrease in migratory activity (Fig. 3a–c, left column, Table 1). Thus, under warm winter conditions, potentially migratory species showed little migratory activity. The increase in migratory species with increasing spring temperature was caused by both increases in migratory propensity and migratory activity (Fig. 3a–c, central column, Table 1). Thus, high spring temperatures were correlated with high migratory propensity and high migratory activity. With regard to precipitation, the proportion of migratory species decreased with increasing spring precipitation, mostly because migratory activity declined with increasing precipitation (Fig. 3a–c, right column, Table 1).

When spatial autocorrelation of the data was taken into account, all but two parameter estimates were very similar to the estimates from the OLS regressions (Table 1). As an exception, the SAR models showed a smaller influence of T_{SPR} on migratory propensity and an increased influence of T_{SPR} on migratory activity. Thus, following the SAR models, the increase in migratory species with increasing spring temperature was

caused mainly by an increase in migratory activity and to a lesser extent by an increase in migratory propensity of the community.

Future predictions

Applying a space-for-time approach, we used the regression coefficients from the spatial relationships between migratory species and climatic factors to predict changes in bird communities under climate change. Here we use expected changes in migratory propensity to measure community reassembly and expected changes in migratory activity to measure adaptation in migratory species. Using the regression coefficients from the OLS regressions, a 1 °C increase in T_{CM} was expected to cause a decline of 2.81 migratory species (Table 1). This corresponds to a –1.90% decline in the proportion of migratory species, caused by a strong adaptation (–2.31% in migratory activity) and a weaker community reassembly effect (–0.25% in migratory propensity). In contrast, a 1 °C increase in T_{SPR} was predicted to cause an increase of 3.45 migratory species. The 1.50% increase in the proportion of migratory species was driven by reassembly and adaptation effects of a similar magnitude (0.96% and 0.94%, respectively). An increase in precipitation of 1 mm was expected to cause an increase of 0.09 migratory species and a decrease of

Table 1 Multiple regression models describing the spatial relationship between migratory bird species and climatic variables in Europe. Top: OLS (ordinary least squares) models, bottom: SAR (simultaneous autoregression) models. Response variables: number of migratory species; proportion of migratory species; migratory propensity (proportion of potentially migratory species, i.e. species that are migratory at least in parts of their range); migratory activity (proportion of migratory active potentially migratory species). Predictor variables: T_{CM} , temperature of the coldest month; T_{SPR} , spring temperature; P_{SPR} , spring precipitation; for more details see Methods. $n = 5232$.

| Response variable | Process | Predictor variables | | | | | | Intercept | t | R^2 |
|---------------------------------|------------|---------------------|--------|-----------|------|-----------|-------------------|-----------|-------|-------|
| | | T_{CM} | t | T_{SPR} | t | P_{SPR} | t | | | |
| OLS | | | | | | | | | | |
| Number of migratory species | Both | -2.81 | -88.0 | 3.45 | 68.4 | 0.09 | 28.8 | -9.06 | -9.4 | 0.60 |
| Proportion of migratory species | Both | -1.90 | -145.4 | 1.50 | 73.0 | -0.04 | -28.1 | 33.44 | 84.7 | 0.85 |
| Migratory propensity | Reassembly | -0.25 | -21.7 | 0.96 | 53.9 | -0.01 | -9.8 | 62.82 | 183.4 | 0.41 |
| Migratory activity | Adaptation | -2.31 | -147.0 | 0.94 | 38.0 | -0.04 | -26.3 | 58.37 | 122.6 | 0.87 |
| SAR | | | | | | | | | | |
| Number of migratory species | Both | -1.30 | -7.2 | 1.35 | 5.4 | 0.02 | 1.8 ¹ | 20.89 | 5.4 | 0.98 |
| Proportion of migratory species | Both | -1.78 | -16.3 | 1.47 | 9.7 | -0.01 | -2.3 ² | 33.32 | 14.4 | 0.99 |
| Migratory propensity | Reassembly | -0.20 | -3.6 | 0.30 | 4.0 | -0.01 | -3.9 | 71.98 | 60.6 | 0.95 |
| Migratory activity | Adaptation | -2.18 | -37.9 | 1.70 | 21.3 | -0.01 | -2.4 ³ | 46.63 | 38.4 | 0.98 |

P for all t -values < 0.001 with the exception of ¹ $P = 0.069$, ² $P = 0.024$, ³ $P = 0.015$.
 R^2 for SAR models include variation explained by spatial structure.

-0.04% in the proportion of migratory species, caused by a reassembly (-0.01%) and an adaptation effect (-0.04%).

As stated above, the SAR models yielded similar results for the effect of T_{CM} . For T_{SPR} the SAR models predicted that the 1.47% increase in the proportion of migratory species is driven mainly by adaptation (1.70%) while community reassembly is less important (0.30%). Finally, the effect of precipitation in the SAR models was reduced to a -0.01% decrease in the proportion of migratory species per millimetre of additional precipitation, caused by reassembly and adaptation effects of similar strength (-0.01%).

For the study area, emission scenario A2 predicted an average increase of temperature of the coldest month of 3.4 °C [$\pm 1.4^\circ$ (standard deviation, here and later), range 1.1–8.2°], an increase of spring temperature of 3.0 °C ($\pm 0.6^\circ$, range 1.0–4.7°) and a decrease in spring precipitation of -4 mm (± 29 mm, range -98 to +58 mm). Given the standard deviation and range of changes in spring precipitation, the changes in migratory species caused by increasing or decreasing precipitation were expected to be on average lower but of the same order of magnitude as changes caused by increases in temperatures.

Under emission scenario A2, the number and proportion of migratory species was expected to change moderately with both reassembly and adaptation of species (Fig. 4). In general, the predictions resulting from the SAR models resulted in a similar but less pronounced pattern than those from the OLS models. Concerning numbers of migratory species, the models predicted some areas of increase (mainly the Iberian Peninsula and central Europe) while in other areas numbers were expected to decline (Fig. 4a). The proportions of migratory species were predicted to increase in southern and western Europe and to decline in northern Europe (Fig. 4b). The migratory propensity of the bird community was expected to increase through exchange of species

in the whole study area, but especially in southern Europe (Fig. 4c). Finally, adaptation was expected to result in declining migratory activity in most parts of the study area (Fig. 4c). This decline became stronger towards the north-east of Europe.

DISCUSSION

Our analyses suggest that increasing winter temperature is likely to lead to declines in the proportion of migratory species in European bird communities whereas increasing spring temperature and decreasing precipitation will lead to increases. SAR models imply that changes in winter and spring temperature will mainly cause adaptation in migratory activity, while changes in spring precipitation are expected to result in both reassembly of potentially migratory species and adaptation of migratory activity. If climate changes as predicted under the emission scenario A2, the communities of migratory species in Europe will be altered through adaptation of migratory activity rather than through exchange of species.

The spatial relationship between migratory propensity (i.e. the proportion of potentially migratory species), migratory activity and climatic factors found in this study can be well explained by processes documented at the level of bird populations. The regression analyses showed that increasing winter temperature was correlated with a smaller proportion of potentially migratory species and lower migratory activity. The smaller proportion of migratory species may be caused by higher survival of non-migratory, resident species in mild winters and a resulting increase in their population densities (Newton, 1998; Forsman *et al.*, 2002). High population densities of non-migratory species can lead to declines in the population density of migratory species through competition for food, breeding territories and nest-sites (O'Connor, 1990). In addition, as a consequence of

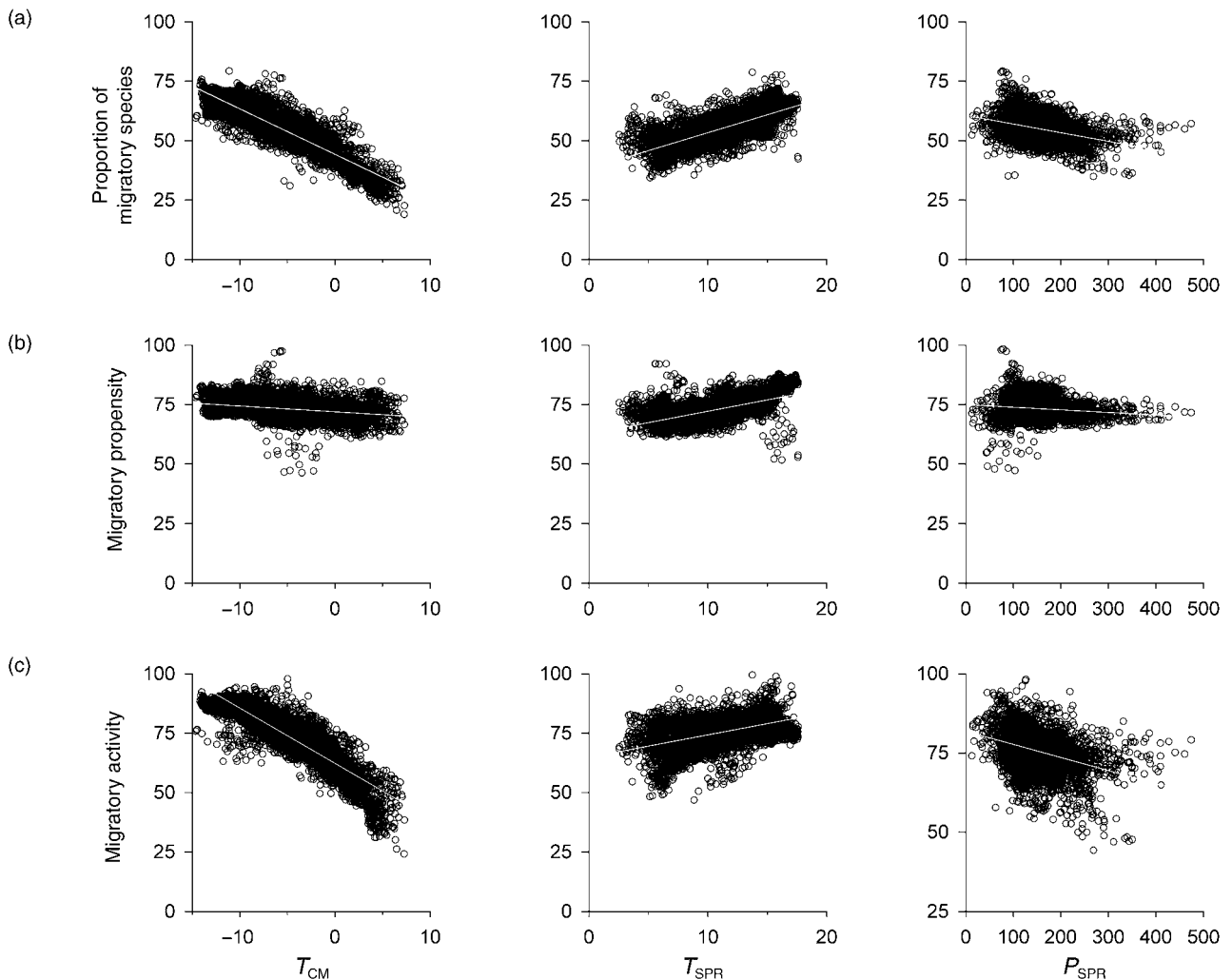


Figure 3 Migratory bird communities in relation to three climatic factors across Europe: (a) proportion of migratory species; (b) migratory propensity; (c) migratory activity. Note that the proportion of migratory species = migratory propensity \times migratory activity. T_{CM} , temperature of the coldest month; T_{SPR} , spring temperature; P_{SPR} , spring precipitation. Leverage (i.e. partial residuals) plots that control for the respective other climatic variables in the same line. For the number of migratory species see Table 1.

higher population densities and warmer winters, non-migratory species might disperse and colonize new sites, thus increasing competition pressure on migratory species in these sites (Root, 1988).

The lower migratory activity of potentially migratory species in sites with high winter temperature can be explained by evolution of this trait. In most populations of migratory species, a small number of individuals show very weak or no migratory activity. If these individuals survive better because winters are mild, more will reproduce and their number in the population will increase (Adriaensen & Dhondt, 1990; Berthold, 1998). Additionally, assortative mating of individuals with similar migratory activity (Bearhopp *et al.*, 2005) might enhance this increase, eventually resulting in the species evolving from a migratory into a non-migratory population in the respective site.

In contrast, increasing spring temperature was correlated with a higher proportion of potentially migratory species and higher

migratory activity. An increase in spring temperature with no change in winter temperature is expected to allow for higher resource availability in spring but no change of resource availability in winter (Hawkins *et al.*, 2003). This increase in resource availability in spring is expected to benefit only migratory species, i.e. species that leave the site in winter. Migratory species can increase in population density and extend the breeding ranges to new sites, formerly too cold and too resource-limited for colonization.

Similarly, increased resource availability in spring with no change in winter might also lead to an increase in migratory activity in thus far resident species. Usually, resident individuals have higher reproductive success because they can occupy better breeding territories, breed earlier and have a longer breeding season than migratory individuals (Berthold, 1984; Adriaensen & Dhondt, 1990). When resource availability in spring increases, and these resources cannot be used by resident individuals

because winter temperature and survival stay the same, these resources can be used by migratory individuals that left the site in winter. Again, this might result in higher reproductive success of migratory individuals and the species evolving locally from a non-migratory into a migratory population.

Finally, the spatial analyses across Europe demonstrated a negative effect of spring precipitation on the proportion of potentially migratory species and on migratory activity. Additional precipitation may increase resource availability only if resources are limited by water availability (Hawkins *et al.*, 2003). Correlations between amount of rainfall, survival and population density are mainly known from arid areas, whereas in most of Europe high spring temperature seems to be more important than spring precipitation (Newton, 1998). Increasing spring precipitation may have rather negative effects on breeding birds, for example because of decreasing resource availability (e.g. fewer flying insects; Koskimies, 1950) and increasing nest mortality (e.g. after heavy rainfall; Ricklefs, 1969). Increasing spring precipitation might affect resident species and individuals less severely, because they start breeding earlier than migrants, and may benefit from additional time for repeated breeding attempts (Price & Liou, 1989).

The expected changes in migratory bird communities in the future (Fig. 4) differed markedly between regions, depending on the locally predicted climate regime. This was caused by the fact that increases in winter and spring temperature had opposite effects on migratory species and that predicted changes in spring precipitation were heterogeneous across Europe. In our predictions for the future, increasing proportions of migratory species in the bird communities of southern and south-western Europe, and decreasing proportions especially in northern Europe, were the combined result of exchange of potentially migratory species in the south and pronounced adaptation of migratory activity in the north. Increasing proportions of potentially migratory species in the south and decreasing migratory activity of migratory species in the north, where migratory activity is currently high (Fig. 2b), is expected to lead to a more even distribution in the proportion of migratory species across Europe. Our predictions suggest no general threat to the number and proportion of migratory species or the phenomenon of bird migration in Europe.

In contrast to our results, modelling approaches studying the impact of climate change upon geographical distributions of individual bird species predict considerable declines in bird species richness in southern Europe and large impacts especially on migratory birds (Huntley *et al.*, 2006). These discrepancies result from methodological differences between the species–climate envelope approach used in Huntley *et al.* (2006) and our community-based analysis. First, as we wanted to compare the processes of adaptation and reassembly, we did not analyse species numbers but species proportions. The predicted increase in the proportion of potentially migratory species in southern Europe (Fig. 4c) was mainly caused by a decrease in species richness of resident species, while the number of potentially migratory species hardly changed. Secondly, Huntley *et al.* (2006) use a ‘closed system’ approach, i.e. species future ranges are modelled

only if their range is currently within Europe. Thus, species can be lost from the study area when their future ranges become very small or disappear, but new species cannot immigrate, e.g. from northern Africa or Asia. This approach almost inevitably leads to an overestimation of declines in species richness in areas close to the borders of the study area, i.e. in southern Europe, although the impact of immigrants from Africa on the general pattern of declining species richness in Europe may be small (Huntley *et al.*, 2006). In the present study we used an ‘open system’ approach, regressing community attributes on climatic factors and assuming that ‘open positions’ in a community will quickly be filled by other species. Thirdly, species–climate envelope modelling approaches ignore the possibility that species can adapt to changing climatic conditions (Pearson & Dawson, 2003; Hampe, 2004). The strong adaptation effect we detected in our study therefore challenges the results of these studies.

When predicting the future composition of migratory bird communities under climate change, using the spatial relationship between the proportion of migratory species and climatic factors, we assume that bird communities are in equilibrium with climatic conditions. Thus, we assume that increases and decreases in the population density of species, and dispersal among grid cells, are fast enough to keep communities in equilibrium with climate. Population densities of birds are known to vary rapidly between years, especially in the case of low winter temperature (see Newton, 1998, for various references). Further, birds have comparatively high dispersal distances. The mean natal dispersal of European bird species is 22.8 km for migrants and 15.6 km for residents (the range for all species is 0.7–44.5 km; Paradis *et al.*, 1998). Thus, in a mostly contiguous area of limited size such as Europe, dispersal is probably not limiting. This is especially true because, to keep communities in a grid cell in equilibrium with climatic conditions, dispersal is not necessary across the whole continent but only among neighbouring grid cells. We therefore assume that bird communities are to a large extent in equilibrium with climatic conditions, especially when averaging 30-year periods (i.e. 1961–90 and 2051–80). Support for this approach comes from a study that showed that regression models derived from the spatial relationship between proportions of migratory species and climatic factors across Europe predicted a significant amount of variation in temporal changes in these species (Lemoine *et al.*, 2007b).

A further assumption of our analyses is that adaptation of migratory activity occurs as fast as exchange of migratory species. Adaptation of migratory activity can result from phenotypic plasticity, i.e. the ability of an organism to express different phenotypes depending on the environment, or from evolutionary change (Przybylo *et al.*, 2000; Pulido *et al.*, 2001). Adaptation through phenotypic plasticity is expected to show no time lag because birds react instantaneously to changing environmental conditions (Hüppop & Hüppop, 2003). In contrast, evolutionary change of migratory activity might take longer or might even be impossible. Species may have different rates of adaptive response (e.g. short- and long-distance

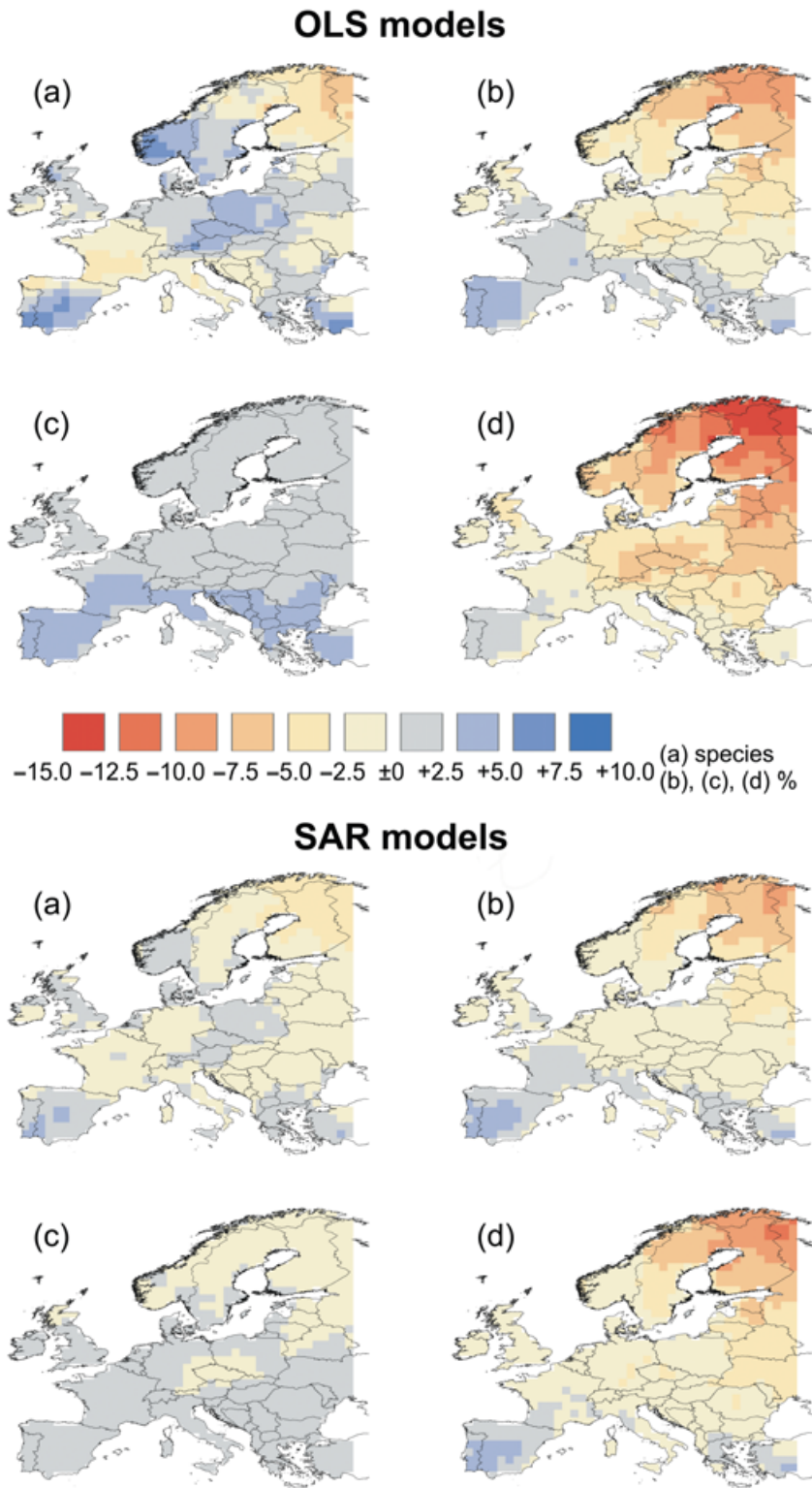


Figure 4 Predicted changes in migratory bird communities in Europe under future climate change calculated from ordinary least squares (OLS) models and from simultaneous autoregression (SAR) models. Differences in numbers and proportions were calculated using emission scenario A2 and climate data for 1961–90 and 2051–80. Changes in the (a) number of migratory species; (b) proportion of migratory species; (c) migratory propensity; and (d) migratory activity.

migrants) or might even show evolutionary inertia. There is evidence for constraints on the adaptability of migratory behaviour, especially of long-distance migrants (Potti, 1998; Both & Visser, 2001). Moreover, even in a species with a very high evolutionary potential, such as the blackcap, selection must be very strong to obtain a substantial change in migratory activity in

a few generations (Berthold & Pulido, 1994). As a consequence of strong selection, populations may decline, limiting further adaptive response.

Nevertheless, studies on the heritability of migratory behaviour in birds have shown that traits such as direction, timing or amount of migratory activity can evolve quickly (Berthold *et al.*,

1992, Pulido & Berthold, 2004). In the blackcap, laboratory studies demonstrated the presence of high genetic variation in the amount of migratory activity. Under strong selection this variation could result in rapid genetic changes in migration distance and turn a migratory into a resident population and vice versa in only a few generations (Berthold & Pulido, 1994). Several other studies have demonstrated that long-distance migrants have also adapted rapidly to recent climate change (Fiedler, 2003; Pulido & Berthold, 2004; Jonzen *et al.*, 2006). These findings suggest that adaptation, both through phenotypic plasticity and evolution, has the potential to change migratory bird communities as fast as community reassembly and that both processes, adaptation and reassembly, are likely to affect bird communities on similar temporal scales.

In addition, it is important to point out that our models consider only breeding bird communities and climatic factors in Europe. Future changes in migratory bird communities will also depend strongly on the response of migratory species to changing climatic conditions along the migratory routes and on the wintering grounds. Decreasing productivity in Africa caused by increasing temperatures (Hulme *et al.*, 2001) might lead to lower winter survival, delayed departure and reduced reproduction of long-distance migrants, resulting in much stronger declines of migrants than predicted from the present study (Gordo *et al.*, 2005). Furthermore, future changes in migratory bird communities will depend strongly on future changes in human land use, again on the breeding grounds, along the migratory pathways and especially on the wintering grounds. Finally, it is important to note that the present study was conducted at the scale of bird communities. Thus, in our study we make predictions for the number and proportion of migratory bird species and not for individual species.

We demonstrated that both processes – community reassembly and adaptation of behaviour – are expected to change bird communities. Furthermore, the proportion of migratory species in bird communities was affected much more by adaptation of migratory behaviour than by reassembly of species. So far, most studies on the response of organisms to climate change have reported ecological effects such as range shifts (Parmesan, 2006), whereas only a little evidence for evolutionary adaptation has been found (Bradshaw & Holzapfel, 2006). The small number of studies documenting evolutionary adaptations is probably because of the difficulties of proving such adaptations in the field. This might lead to an underestimation of adaptive responses to climate change. As adaptation is causing a species to persist in a local community, it is a process that mitigates the consequences of climate change. Thus, present studies might have underestimated the ability of species to adapt to changing climatic conditions.

To conclude, our models suggest that global climate change will affect the proportion of migratory species in European bird communities. Although the effect is expected to differ markedly between European regions, the overall effect size appears to be modest, with most changes occurring through adaptation of migratory activity and, to a lesser degree, reassembly of migratory species. Our model predictions suggest that predicted climate

change is unlikely to have a severe impact upon migratory species in Europe as a whole. However, given the community approach taken and the set of additional factors affecting migratory birds not considered in this analysis (see above), single migratory species may well be at peril even within Europe. Furthermore, adaptation of migratory behaviour may allow species to adapt to changing climate. However, migratory activity in birds is a well studied and rapidly evolving trait. Other species and other traits may evolve more slowly, because of lower genetic variability, genetic correlations or the much longer generation times of species other than birds. It remains to be investigated whether in these cases evolution will be fast enough to prevent exchange of species, species extinctions and much more profound community reassembly.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Results of spatial structure analysis and simultaneous autoregression models.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1466-8238.2007.00341.x>

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