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Species' ecological traits correlate with predicted climatically-induced shifts of European breeding ranges in birds

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Abstract: Climatically induced shifts of species' geographic ranges can provide important information about the potential future assembly of ecological communities. Surprisingly, interspecific variability in the magnitude and direction of these range shifts in birds has been the subject of few scientific studies, and a more detailed examination of species' ecological traits related to this variability is needed. Using maps in the Climatic Atlas of European Breeding Birds (Huntley et al. 2007) we calculated the potential shifts of European breeding ranges in 298 bird species, and explored their relationships with breeding habitat, dietary niche, migration strategy, life history and geographic position of the current breeding range. Breeding habitat type showed the strongest relationship with the potential range shifts, with forest and wetland species showing the largest magnitude of shift. At the same time, ecological specialists showed a larger magnitude of shifts than generalists. In addition, we found that species with current ranges situated near continental borders and species with lower migratory capacity are more limited in their potential to shift due to climate change. Our analyses thus indicate which ecological groups of birds will be most likely forced to move their ranges under predicted climate change. This knowledge can help to adopt proper conservation actions. These actions will be particularly important in the case of specialist species, which have been shown to be the most sensitive to climate change impacts.

Introduction

Some recent studies have shown that climate plays a key role in the population changes of many bird species (Crick 2004, La Sorte and Thompson 2007, Jiguet et al. 2010). Climate influences bird populations both directly, for instance, an increase of precipitation in spring may cause higher mortality of nestlings (Fairhurst and Bechard 2005), and indirectly, through particular components of the trophic chain (Sanz et al. 2003, Both et al. 2006, 2010).

Since population processes are closely linked to range dynamics, climatically induced population changes might result in the geographic range shifts of bird species (Araujo and New 2006, Pautasso 2012). There is an increasing body of evidence that these already occur in nature, as many species have moved their range boundaries poleward (e.g. Thomas and Lennon 1999, Hitch and Leberg 2007, Brommer 2008). That climate can play a key role in driving species' range dynamics has been confirmed by a study showing a close correspondence between past bird ranges modelled using bioclimatic variables capturing conditions of the Last Glacial Maximum and locations of sites with fossil record of the same bird species (Smith et al. 2013), as well as by bioclimatic modelling of current distributions of bird species (Jiménez-Valverde et al. 2011, Rapacciulo et al. 2012). Several recent studies have found that species' ecological traits explain a significant proportion of the interspecific variability of these climatically induced range shifts observed over the last decades (Pöyry et al. 2009, Angert et al. 2011, Chessman 2012, Kharouba et al. 2013). Those specific traits associated with the largest range shifts observed in birds are a small geographic range size and broad ecological niche (Angert et al. 2011).

As climate change is expected to proceed with accelerating rate in the 21st century (IPCC 2007), it is expected that range shifts will be much larger in the future (Huntley et al. 2008, Barbet-Massin et al. 2012). Future range shifts under conditions of ongoing climate change have been estimated using climate envelope models (Araujo et al. 2009). Climate envelope is defined by the climatic conditions in the geographic range of a given species and can be expressed by using various measures such as thermal range, thermal optimum, mean precipitation or latitudinal midpoint (Jiguet et al. 2007). The climate envelope models are thus based on the relationships between current species distribution and climatic conditions in species geographic ranges (Huntley et al. 2007). Using these relationships and projected climatic scenarios for a focal time period in the future, we can model potential species ranges expected under given climatic conditions. The difference in geographic position between the current and modelled future species ranges is called the potential range shift. Because climatic envelopes markedly differ among species (Chessman 2012) and, moreover, patterns of climate change vary across space, potential shifts show strong variability among species (Huntley et al. 2006, 2008). This variability can have important biological and conservation implications. For instance, Gregory et al. (2009) have shown that European bird species whose ranges are predicted to contract the most during the 21st century currently show the steepest population declines. A similar exercise was performed by Goodenough and Hart (2013) using the same dataset, but relating the changes in range size, range margins and overlap to a larger set of species' traits. Similarly to studies focusing on the changes in bird distribution observed over the past few decades (Angert et al. 2011), they found that the predicted changes in range size were related to species' habitat use, current range size and endemism (Goodenough and Hart 2013).

The aim of this study is to further explore the variability in climatically induced potential range shifts of European birds from a perspective of species' ecological characteristics. We do not focus on changes in range size, range margins or overlap, since this work has already been performed in some recent studies (Gregory et al. 2009, Goodenough and Hart 2013). Instead, we focus on the magnitude and direction of potential shifts of range centres. These variables provide information on distance by which the range of a given species has moved as a whole. There is thus a straightforward link to the intensity of the potential pressure of future climate change on a given species (Huntley et al. 2007). At the same time, the magnitude and direction of potential shifts has to date remained unexplored from the perspective of interspecific variability. Specifically, we ask which traits are typical for species shifting their ranges further, in contrast to species with smaller range shifts. Even though we may be unable to resist the impacts of climate change, if we reveal which ecological groups of species are predicted to be under the highest pressure (here expressed as the potential range shift), we can better focus on means of effective mitigation (Pearce-Higgins et al. 2011). For example, water birds seem to be significantly shifting their ranges as a result of climate change, therefore clear focus should be on the protection of wetlands in order to avoid a double threat – climate change accompanied by the disappearance of breeding habitats. The interaction between climatic processes and land use change has been recently recognized as one of the most important threats for biodiversity (Butchart et al. 2010). Several studies showed that land use change is a dominant driver in trends of species' abundance and distribution even under the conditions of recent climatic changes (Reif et al. 2010, Eglington and Pearce-Higgins 2012, Beale et al. 2013). However, the climate change can seriously increase the risk species' extinction when the habitats are deteriorated by human exploitation (Matyka-Pringle et al. 2012). For example, in Sahel hunting pressure in wetlands is highest and has the most negative impact on water bird populations in years with the lowest rainfall (Zwarts et al. 2010).

Here we focus on traits that have been found in previous studies to be importantly related to changes in European bird distributions and abundances (Lemoine et al. 2007, Jiguet et al. 2010, Koleček and Reif 2011): breeding habitat preference, dietary niche, migration strategy and life history. Since current changes in bird distribution and abundance are linked to species' potential range shifts (Gregory et al. 2009), we expect that these traits could also be significantly related to variability in the magnitude of potential range shifts. Specifically, we formulate the following predictions. First, species breeding in forest habitats will show larger shifts than open habitat species because forests are confined to colder areas that are undergoing a higher rate of warming (Barnagaud et al. 2012). Second, species breeding near humans will show smaller shifts than other species because their distribution is less limited by climate (Møller et al. 2012). Third, species with narrow ecological niches (either habitat or dietary) will show larger shifts, as their distributions are more determined by climatic factors than the distribution of ecological generalists (Hernandez et al. 2006). Together with ecological traits, we test for the limiting effects of the current latitudinal and longitudinal geographic range position on potential range shifts in the future. In association with this, we predict that species breeding closer to continental borders will show a smaller magnitude of shifts than other species (La Sorte and Jetz 2010).

Material and methods

Potential range shifts

We assessed potential shifts in the breeding ranges of European birds by using maps in A Climatic Atlas of European Breeding Birds (Huntley et al. 2007). These maps were constructed using bioclimatic modelling of current breeding bird distribution in Europe (Hagemeijer and Blair 1997). The species' breeding ranges were expressed as presences and absences in a 50-km square Universal Transverse Mercator (UTM) grid over the continent, excluding most of Russia. Huntley et al. (2007) first modelled the present climatic ranges of every species as a function of observed breeding distributions in Europe and the values of three bioclimatic variables in the UTM squares by a locally weighted regression. They applied the following bioclimatic variables: coldest-month mean temperature, annual temperature sum above 5°C and the annual ratio of actual to potential evapotranspiration; all expressed as means for the time period 1961-1990. In the next step, Huntley et al. (2007) predicted future climatic ranges of bird species given the relationships revealed in the first step and climatic projections for the period 2070 – 2099. The climatic projections were based on the HadCM3 model (Hadley Centre Coupled Model, version 3) from the IPCC (2001). See Huntley et al. (2007) for more details on the generation of species' breeding climate range maps.

We digitalized the maps of current climatic breeding ranges and predicted future climatic breeding ranges of 298 bird species recorded as breeding in Europe from Huntley et al. (2007) into ArcGIS 9.2 (Esri 2006). Huntley et al. (2007) provide data on 363 species but we excluded 65 marine and/or extremely rare species whose potential range shifts were not estimated reliably according to Huntley et al. (2007). We calculated the mean centre of the respective climatic ranges for every species (i.e. mean latitude and mean longitude). We then calculated the potential range shift as the distance between the mean centres of the current and predicted future climatic breeding range in each species (Appendix). These distances were taken as the response variable for further analyses. We also estimated the direction of the shift as an azimuth expressed in degrees.

We sorted the species into three distinct groups according to the direction of the potential shift: (i) species shifting their range northward with a degree range from 337.5 to 22.5, where 0 degrees is north (157 species), (ii) species shifting their range north-eastward with a degree range from 22.5 to 90, where east is 90 degrees (52 species), and (iii) species shifting their range north-westward with a degree range from 270 to 337.5, where 270 degrees is west (89 species); see Appendix. These groups were used in further analysis.

Defining explanatory variables

We defined the following seven trait variables to explain the interspecific variability in potential range shifts. All trait variables were extracted from Cramp (2006), an extensive database assembling trait information for the entire European avifauna. Here we briefly describe their calculation [see Koleček and Reif (2011) for more details]. Habitat niche was based on the classification of each species into one or more habitat classes according to Böhning-Gasese and Oberrath (2003): closed forest (1), open forest (2), forest edge (3), woodland, orchard, garden (4), scrubland (5), open country with solitary trees or shrubs (6), and open country without solitary trees or shrubs (7). For each species the mean value of its habitat classes defines its (i) habitat niche position, while the difference between the largest and smallest values defines its (ii) habitat niche breadth. (iii) Species position along the humidity gradient was based on the classification of each species into categories according to Böhning-Gasese and Oberrath (2003): non-humid (1), wetland (2) or water (3). (iv) Dietary niche breadth was based on the classification of species by Böhning-Gaese et al. (2000) as obligatory herbivorous or obligatory insectivorous/carnivorous (1), herbivorous and insectivorous/carnivorous (2), or omnivorous (3). (v) Relation to built-up areas was assessed using information on the habitat use of particular species, sorting bird species as either non-urban (0) or urban (1). (vi) Migration strategy classified species as residents (1), short-distance migrants (2), or long-distance migrants (3). (vii) Life history ordinated species along a slow-fast life history axis. This axis was calculated using principal component analysis on a correlation matrix of six species' life-history traits: body mass, egg mass, number of broods per year, laying date (Julian date of the beginning of laying in the first breeding), clutch size and length of incubation, expressed as mean values from published data (Cramp 1977–1994), and represents the first principal component accounting for 55.6 % of the variability in life history traits across bird species (Hořák et al. unpublished data).

Moreover, we used two explanatory variables quantifying the geographic position of species' ranges because this position can limit the potential range shift. For this purpose, we used the (i) latitude and (ii) longitude of the mean centres of current species' climatic ranges based on maps in Huntley et al. (2007).

Statistical analysis

First, we explored possible differences in the magnitude of potential range shift among groups of species defined by the shift direction using analysis of variance (ANOVA) and the Tukey HSD post hoc test.

Then, we focused on predictors of the potential range shift. We first related the explanatory variables to the potential range shifts for all species together to find a general pattern. In the next step, we performed the analysis for each of the three groups defined by the shift direction separately. By these separate analyses we wanted to take the differences between latitudinal and longitudinal climatic gradients into account. The latitudinal gradient is characterized by decreasing temperature from south to north, while degree of continentality in climate increases from west to east (Hoffman 1983). Therefore, we suggest that a potential range shift of the magnitude of 1000 km in northern direction has to some extent different biological interpretation from, for example, the eastward shift of the same magnitude. At the same time, the shift directions also differed in possible effects of limitation by continental borders: the limitation should be more evident in northward and westward direction than in eastward direction.

We ran linear models to test whether the magnitude of potential shift (response variable) is related to the above mentioned ecological characteristics and the latitudinal and longitudinal position of each species' range (explanatory variables). The variable longitudinal position was not included into the models for those species with northward directional shifts because we do not expect longitudinal limitation in these species. We first defined a full model which included all explanatory variables, and this model was subsequently simplified by using the "step" function in R 2.12.0 (R Development Core Team 2010). This function performs automatic backward elimination of variables from a model based on Akaike Information Criterion (AIC). The elimination stopped when dropping a variable would decrease the model fit as indicated by AIC. These models we call "final models". The accuracy of the estimates of predicted future climatic ranges modelled by Huntley et al. (2007) differed among species. Therefore, we used species-specific squared areas under curve (AUC) from Huntley et al. (2007) as model weights in our analyses to give more importance to species with more accurate estimates of potential range shifts.

Finally, closely related species can show similar climatically-induced range shifts (Buckley and Kingsolver 2012). Therefore, we tested the potential impact of a common evolutionary history in the examined species on the observed relations by quantifying the degree of phylogenetic autocorrelation at the species, genus, family and order levels, respectively, in the residuals of the respective final models using Moran's I in the R package "ape" (Paradis 2009). Non-significant autocorrelation would indicate no influence of species taxonomy on the observed relationships.

Table 1. The effects of habitat niche position (on a gradient from closed forest to open landscape), habitat niche breadth, habitat humidity, dietary niche breadth, relation to built-up areas, migration strategy, life history (gradient from slow to fast life histories) and latitudinal and longitudinal range position on predicted shifts of European breeding ranges for (a) all 298 bird species, (b) 157 species shifting their range northward, (c) 52 species shifting their range north-eastward and (d) for 89 species shifting their range north-westward, tested by linear models. Significant results are printed in bold.

a) All species

variable	estimate	standard error	t	p-value
Habitat niche position	**-27.61**	**7.30**	**-3.55**	**< 0.001**
Habitat niche breadth	**-15.73**	**7.98**	**-1.97**	**0.049**
Habitat humidity	**64.05**	**17.69**	**3.62**	**< 0.001**
Relation to built-up areas	-74.14	47.32	-1.57	0.118
Migration strategy	**31.50**	**15.22**	**2.07**	**0.039**
Latitudinal range position	**-1.57**	**0.78**	**-2.01**	0.045

b) Northward shifting species

variable	estimate	standard error	t	p-value
Habitat niche position	**-27.79**	**10.02**	**-2.77**	**0.006**
Habitat niche breadth	**-27.87**	**10.55**	**-2.64**	**0.009**
Habitat humidity	46.06	24.44	1.88	0.061
Dietary niche breadth	**-64.79**	**29.51**	**-2.20**	**0.030**
Relation to built-up areas	-93.88	65.14	-1.44	0.152
Migration strategy	31.10	20.76	1.54	0.125
Latitudinal range position	-1.08	0.78	-1.40	0.165

c) North-eastward shifting species

variable	estimate	standard error	t	p-value
Habitat niche position	-24.20	13.75	-1.76	0.085
Habitat humidity	**80.93**	**31.74**	2.55	0.014

d) North-westward shifting species

variable	estimate	standard error	t	p-value
Habitat humidity	39.41	20.64	1.91	0.060
Relation to built-up areas	-95.32	58.91	-1.62	0.109
Latitudinal range position	**-7.40**	**2.01**	**-3.67**	**< 0.001**
Longitudinal range position	5.69	3.12	1.83	0.071

Results

The groups defined by their potential range shift direction significantly differed in the mean magnitudes of their shifts (ANOVA: F = 5.81, $p < 0.001$; Tukey HSD test: $p < 0.001$ for all pairwise comparisons). The largest mean shift was found for the group shifting northward (491.5 km ± SD 195.3 km), then for the group shifting north-eastward (383.5 km ± 174.7 km), and the smallest shift was found for the group shifting north-westward (246.3 km ± 167.0 km).

For all species together, habitat niche position, habitat niche breadth, habitat humidity gradient, migration strategy and latitudinal range position explained significant part of variability in potential range shifts according to the final model (Table 1a). Species breeding in more forested habitats showed larger magnitude of shifts than species breeding in more open habitats (Table 1a). Habitat specialists showed larger magnitude of shifts than habitat specialists (Table 1a). Larger magnitude of shifts was also expressed by wetland species and species migrating on longer distances (Table 1a). Finally, species with more northern latitudinal range position showed smaller magnitude of shifts than the species with ranges in lower latitudes (Table 1a).

In northward shifting species the final model resulted in three variables with significant effects on the magnitude of potential range shifts: habitat niche position, habitat niche

Table 2. The amount of phylogenetic autocorrelation at the species, genus, family and order levels, respectively, quantified by Moran's I in residuals of the final models shown in Table 1.

Taxonomic level	All species		Northward shifting species		North-eastward shifting species		North-westward shifting species	
	Moran's I	p-value	Moran's I	p-value	Moran's I	p-value	Moran's I	p-value
Species	0.09	0.667	0.01	0.970	0.06	0.767	0.15	0.779
Genus	0.10	0.156	0.02	0.828	0.07	0.807	0.01	0.900
Family	-0.06	0.149	-0.07	0.292	0.19	0.246	-0.05	0.691
Order	0.03	0.233	0.00	0.855	0.10	0.252	-0.01	0.988

breadth and dietary niche breadth (Table 1b). The effects of these variables show that forest species express a larger magnitude of potential range shifts than open habitat species, and both habitat and dietary generalists showed smaller shifts than specialists (Table 1b).

For north-eastward shifting species, the final model found that an association with humid habitats was the only trait explaining a significant proportion of the variability in potential range shifts. Specifically, species with tighter associations with this habitat showed larger potential shifts (Table 1c).

In north-westward shifting species, the magnitude of their potential range shift was related to habitat humidity, with the species breeding in wetter habitats shifting more than species of drier habitats, and to latitudinal range position, where more northerly distributed species showed smaller shifts (Table 1d). However, whereas the effect of latitude was significant, the effect of habitat humidity was marginally insignificant ($p = 0.06$).

Residuals of all final models did not reveal any significant phylogenetic autocorrelation at any taxonomic level (Table 2).

Discussion

Our examination of climatically induced potential shifts in the breeding ranges of 298 bird species breeding in Europe revealed several important patterns. First, species shifting their potential ranges north-westward showed smaller shifts than species shifting their ranges north or north-eastward. Second, species' habitat requirements were strong predictors of the interspecific variability in the magnitude of potential range shifts within the groups of species defined by shift direction. Third, species with narrow habitat or dietary niches showed larger magnitudes of potential range shifts than ecological generalists. Fourth, the current latitudinal range position acts as a strong limiting factor in the species' potential range shifts.

The first and last patterns stress the importance of continental borders on a species' ability to track changing climate. Clearly, species breeding in northern latitudes and western longitudes have less space to shift their ranges than species breeding in southern and eastern regions. These limitations are important from a conservation perspective, because the lack of space available for shifts will result in a contraction of a species' range and thus a higher extinction risk (Gregory et al. 2009). Although this threat is more serious in the case of the altitudinal ranges of montane species that can simply lose their habitat due to a warming climate (La Sorte and Jetz 2010), a similar effect can affect species breeding in the highest latitudes. Moreover, climate change is predicted to proceed at the highest rate in the northernmost latitudes (Jetz et al. 2007), and this factor can further strengthen the limitation effect of continental borders.

The effect of space limitation could also produce a potential bias in our results since species with ranges in the western part of the continent have less land mass available for potential range shift than the species breeding in the eastern part. As a consequence, the bioclimatic models can estimate smaller potential range shifts for the former species just due to the lack of sites with suitable climatic conditions. However, we do not think this bias is substantial because vast majority of species used for the analysis occupy wide range of longitudinal bands and is thus not confined to the western part of the continent (note that we excluded the species with extremely small ranges from data prior to the analysis because of high uncertainty in the potential range shift estimates, see Huntley et al. 2007). Moreover, taking longitudinal position into account did not show its significant effect on potential range shift in our model. Despite of a strong limiting effect of latitudinal range position and significantly smaller magnitude of range shift in westward shifting species (see above), we do not suggest that the longitudinal position of species' range *per se* hampers the revealed relationships between ecological traits and potential range shifts described below.

Our results indicate that the magnitude of potential range shifts is strongly related to species' habitat niche. This concurs with the findings of Goodenough and Hart (2013), who also analysed maps of climatic ranges of European birds in Huntley et al. (2007) but focused on changes in range size, range margins and overlap, and not on shifts of range centres. The dominance of habitat-related ecological traits among the significant explanatory variables is not surprising given the recently described correlation between habitat and the climatic niches of European birds (Barnagaud et al. 2012). For species shifting their ranges north-eastward or north-westward, we found the largest shifts in species dependent on humid habitats. This pattern can be explained by the predicted increase in rainfall due to climate change in northern parts of the continent in contrast to a decrease in rainfall in southern parts (IPCC 2007). As a result, the ranges of species associated with humid habitats are predicted to move further north and, at the same time, the future distribution of those species might be affected by a shortage of humid habitats in southern parts of the continent. The predicted relationship between shift magnitude and humid habitat specialization may be, however, obscured by human impacts. As has recently been reported, many water and wetland birds observed in various European countries are undergoing a range expansion (Van Turnhout et al. 2007, Lemoine et al. 2007, Koleček et al. 2010). These species have possibly wider climatic ranges than they currently occupy because their distribution may have been strongly limited in recent history by human pressures such as hunting (Van Turnhout et al. 2007). After the recent establishment of legal protections in Europe, these species have started to colonize additional suitable sites (Donald et al. 2007). Climatic models do not reflect human activities (such as hunting pressure, habitat modification etc.), and therefore future predictions inform us rather about changes in geographical ranges under conditions which favour the wider distribution of birds living in wet habitats.

Concerning those species with northward shifts, a larger magnitude of potential shifts was found in habitat specialists and forest species than in habitat generalists and open-habitat species, respectively. These patterns confirm our initial expectations. Forest species breed in colder areas than open habitat species (Barnagaud et al. 2012), and these areas will shift further according to climatic projections due to a higher magnitude of warming in northern latitudes (IPCC 2007, Buckley and Kingsolver 2012). It is possible that forest species would be generally more sensitive to future climatic changes than species breeding in open habitats, because similar patterns to those in our results have also been observed in birds of California (Jongsomjit et al. 2013). There, the largest changes in breeding distribution caused by climatic factors were predicted for forest species, while climate contributed only slightly to the distribution changes of grassland and desert species (Jongsomjit et al. 2013). It is interesting that species of coniferous forests were predicted to contract their ranges, whereas species of broad-leaved woodland were predicted to enlarge their ranges (Jongsomjit et al. 2013). Unfortunately, we did not classify the habitat use of forest species in such detail, but it would be interesting to perform such an analysis for European birds as well.

The effect of habitat specialization observed in our results suggests that ecologically specialized species will be under higher pressure to move northward under the conditions of future climate change. In contrast, the geographical ranges of ecological generalists will be less affected. This result is alarming, as specialized species seem to be sensitive to both human-induced habitat alteration and range shifts due to predicted climate change (Jiguet et al. 2007). Consequently, their populations might be under substantial threat in the future.

We found a correlation between potential range shifts and species' migration strategy: species migrating on longer distances showed larger magnitude of shifts. This pattern cannot be explained by better dispersal ability of long-distance migrants (Barbet-Massin et al. 2012) because this trait was not considered in the models estimating the potential range shifts (Huntley et al. 2007). Instead, we suggest that the larger shift of long-distance migrants can be connected with latitudinal distribution of bird species with different migration strategies across Europe. With increasing latitude, both number and proportion of long-distance migratory species in bird communities decrease, i.e. these species are mostly confined to lower or mid-latitudes (Lemoine and Böhning-Gaese 2003) and have thus more space to shift their range in response to climate change than the short-distance migrants and residents, which form majority in bird species in northern regions (Lemoine and Böhning-Gaese 2003). However, the significant effect of migration strategy was found only in the model analysing all species together and the separate analyses for the species groups defined by shift direction did not maintain this effect. This suggests that the relationship of migration strategy to species' climatic niche is probably weaker than the effect of habitat niche variables which were significant in both kinds of models.

The predictions of future ranges modelled by Huntley et al. (2007) solely using climatic scenarios and assuming no effects of dispersal limitation, biotic interactions or land use, have recently been challenged by studies pointing out the importance of these factors constraining the species' geographic ranges (Rapacciulo et al. 2012, Pigot and Tobias 2013). Although there have been attempts to incorporate these factors into predictions of species' future geographic ranges (Barbet-Massin et al. 2012), we used the maps from Huntley et al. (2007) because these were appropriate for purposes of our study. Our aim was not to predict the exact locations of species' ranges in the future for purposes of, for instance, assessment of their coverage by current protected areas (Hole et al. 2009, Virkkala et al. 2010). Instead, we aimed to link the intensity of the pressure posed by climate change, as expressed by the potential range shift of a given species, to species' ecological traits. For this purpose, the range shifts based solely on climatic models were sufficient.

Our study provides more detailed insights into the observations of Huntley et al. (2006, 2008), whose predictive models suggest radical spatial reorganization of European bird communities in the second half of the 21st century as a consequence of global warming. We have shown that the variability in potential shifts of European climatic breeding ranges of bird species are closely linked with species' ecology, most notably their habitat preferences and ecological niche breadth. The importance of this link has been confirmed by other studies focusing on patterns in the future changes of species ranges (Goodenough and Hart 2013, Jongsomjit et al. 2013), and indicates which ecological groups of birds will be forced to most move their ranges under predicted climate change. As different ecological groups of birds definitely have different abilities to cope with predicted changes, this knowledge is important for adopting proper conservation strategies (Buckley and Kingsolver 2012). It is important to note that these inferences do not deal with other potential changes not linked to climate, e.g. habitat alteration caused by changes in human land use. These non-climatic factors can effectively inhibit the species from tracking their climatic optima (Reif et al. 2010, Devictor et al. 2012), resulting in an interaction between the habitat and climate change effects (Mantyka-Pringle et al. 2012). Therefore, we suggest that those species whose ecological characteristics correlate with the largest magnitude of potential range shifts caused by climate, i.e. forest species, wetland species and ecological specialists, should be the central focus of ecologists and conservationists. The conservation strategies should include securing population in their current ranges by, for example, enforcement of existing protected areas, thus providing enough individuals to disperse (Thomas et al. 2012, Beale et al. 2013). At the same time, it is worth to start the process of establishment of new protected areas to conserve the habitats (e.g. wetlands) in regions where such species can possibly move their range and along the dispersal routes (Hole et al. 2009).

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Appendix

Data used for the analysis of the relationships between potential range shifts and ecological traits of European birds. The file may be downloaded from www.akademiai.com