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Linking habitat specialization with species' traits in European birds

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Ecological specialization provides information about adaptations of species to their environment. However, identification of traits representing the relevant dimensions of ecological space remains challenging. Here we endeavoured to explain how complex habitat specializations relate to various ecological traits of European birds. We employed phylogenetic generalized least squares and information theoretic approach statistically controlling for differences in geographic range size among species. Habitat specialists had narrower diet niche, wider climatic niche, higher wing length/tail length ratio and migrated on shorter distances than habitat generalists. Our results support an expected positive link between habitat and diet niche breadth estimates, however a negative relationship between habitat and climate niche breadths is surprising. It implies that habitat specialists occur mostly in spatially restricted environments with high climatic variability such as mountain areas. This, however, complicates our understanding of predicted impacts of climatic changes on avian geographical distributions. Our results further corroborate that habitat specialization reflects occupation of morphological space, when specialists depend more on manoeuvrability of the flight and are thus more closely associated to open habitats than habitat generalists. Finally, our results indicate that long distance movements might hamper narrow habitat preferences. In conclusion, we have shown that species' distributions across habitats are informative about their positions along other axes of ecological space and can explain states of particular functional traits, however, our results also reveal that the links between different niche estimates cannot be always straightforwardly predicted.

Ecological traits provide information about adaptations of species to the environment as well as their roles in the ecosystem (Webb et al. 2010). Therefore, based on them we can estimate niche position and width of a particular species which is informative about the level of ecological specialization (Futuyma and Moreno 1988, Gregory and Gaston 2000). Moreover, knowledge of species specific specializations can be instrumental in prediction of extinction risk or community simplification and thus has application in nature conservation (Colles et al. 2009). For instance, biotic homogenization was described as on-going change in community composition acting at the European scale and resulting from the replacement of habitat specialists by habitat generalists (Le Viol et al. 2012).

Ecological niche, however, is thought to be multidimensional (Hutchinson 1957) and identification of traits which represent the biologically most relevant dimensions of niche space remains a challenge for ecologists (Webb et al. 2010). From a descriptive point of view, traits can be classified into different groups which represent different aspects of species' lives such as habitat preferences, diet specializations or reproductive strategies. In this respect, Devictor et al. (2010) have emphasized the discrimination between Grinellian and Eltonian specialization. While Grinellian specialization refers to species' performance across a range of ecological conditions (Grinnell 1917), Eltonian specialization focuses on species' impact and ecological function (Elton 1927). To date, only a few studies aimed to link these two dimensions to each other (Devictor et al. 2010). For example, it remains unknown whether Grinellian niche quantified as the frequency of species' occurrence in different habitats is related to Eltonian niche defined by species' morphology and resource use. As a result, specializations are frequently calculated using one aspect of species' ecology only and correlations among adaptations to different parts of ecological space are implicitly assumed (Gaston et al. 1997, Julliard et al. 2006).

Although it is obvious that the ecological traits are intercorrelated, this assumption remains poorly tested in context of habitat specialization. For purposes of testing such relationships, birds provide a suitable model due to their high diversity of life histories and ecological adaptations, and, perhaps more importantly, existence of high quality data on habitat occupancy as well as on various traits.

Some of the relationships between niche components are expected, although thorough empirical evidence for their direction and magnitude is still lacking. From an evolutionary perspective, habitat specialization should have links to avian morphology. Wing and leg morphology should be related to avian mobility in general (Norberg 1979) but also to habitat utilization (Zeffer et al. 2003). We can thus expect that more mobile species utilize more habitats. Body mass determines species' energetic requirements constraining its diet structure, breeding density and range size (Brandl et al. 1994, Jetz et al. 2004). Larger-bodied species have large home ranges to satisfy their high energetic requirements (Jetz et al. 2004) and thus they do not probably discriminate among fine-scale habitat classes as the smaller-bodied species do. Therefore, we can expect a negative relationship between habitat specialization and body mass.

It is possible that diet and habitat specialization also share a common basis (Brändle et al. 2002) when diet specialists should be also habitat specialists, but no evidence was found for such a relationship in birds of the former East Germany (Brändle et al. 2002). Habitat preference of birds thus can be viewed as a highly complex trait that largely combines information about many aspects of avian life (Pigot and Tobias 2013). However, it remains unclear to which extent specialization on a habitat axis corresponds to specializations on other niche axes.

Species' habitat specialization further reflects large scale space use in birds. Firstly, it contributes to forming species geographic ranges and, the other way round, geographic range size should predict how many habitats the species can encounter within its area of occupancy (Gaston et al. 1997). At the same time, distribution of habitats at large spatial scales is determined by climatic conditions prevailing on particular sites (Hawkins et al. 2003). Therefore, both range size and climatic niche breadth should be, at least to some extent, negatively related to species' habitat specializations (Barnagaud et al. 2012, Slatyer et al. 2013). Secondly, many avian species show migratory behaviour dividing their lives between breeding and wintering areas and it has been suggested that habitat specialization might be a factor influencing its evolution (Levey and Stiles 1992, Cresswell 2014). Specifically, broad habitat niche was important trait characterizing ancestors of the present-day long-distance migratory species (Levey and Stiles 1992). Therefore, negative relationship between habitat specialization and migration distance could be expected (Cresswell 2014).

In this study, we focused on European birds as reliable information exists about the traits of species inhabiting the continent. We tried to decompose complex habitat specialization information into more specific avian adaptations by correlating it to traits related to different ecological space axes. Specifically, we employed literature data about diet specialization, climatic niche, range size, migratory strategy and morphological traits, excerpted from Cramp (1977–1994), Hagemeijer and Blair (1997) and Haylock et al. (2008), to explain variation in habitat specialization. Based on the theoretical reasoning described above, we formulated following hypotheses focused on the relationships between habitat specialization and particular species' traits. 1) Habitat and diet specialization are positively linked because species being able to exploit more types of food resources should have broader habitat niches. 2) Habitat specialization is negatively related to range size and climatic niche breadth because species with larger ranges encounter more habitats and climatic zones than species with smaller ranges. 3) Habitat specialization is negatively related to migration distance because long distance movements evolved in species which can utilize various habitat types. 4) Habitat specialization is negatively related to body mass because species with smaller body masses discriminate habitats at much finer spatial resolution than larger-bodied species. 5) Habitat specialization is negatively related to wing length/tail length ratio. Species with relatively longer wings are better able to fly among habitats and should be thus habitat generalists. 6) Habitat specialization is positively related to tarsus length/body length ratio. Species with relatively longer legs are ground dwelling, which limits their ability to utilize different habitats.

Since distribution of habitats in European landscape is strongly affected by long-term human manipulation (Blondel and Aronson 1999), species' habitat specialization might be linked to population trends and reflected in realized habitat niche. For this reason, we tested whether the expected relationships between species habitat specialization and their traits hold for declining species, too.

Material and methods

Species selection

For most species' traits we used data from Bird of Western Palaearctic interactive (BWPi), a comprehensive electronic handbook based on Cramp (1977–1994) describing ecology of all European bird species in considerable detail. From this data source, we excerpted information on all species breeding in Europe (n = 499 species) excluding wetland species (n = 187), marine species (n = 34), exotic species (n = 18) and extremely rare species (n = 28). (Note that some species were excluded according to several criteria). Their omission was motivated by the need to keep the focal variables comparable among species. In the case of wetland and marine species, their habitat specialization was most likely formed by markedly different selection pressures than in the case of terrestrial species (Gill 2006) and it would be thus inappropriate to include these species groups together into a common analysis. In the case of exotic species, their habitat use is probably strongly affected by the current stage and history of their introduction into the new range (Duncan et al. 2003) and it is thus not comparable to the native species breeding in the same area. The extremely rare species were defined as those occupying less than 20 grid cells in the EBCC Atlas of European breeding birds (Hagemeijer and Blair 1997). Such species overlap Europe by only small part of their ranges (Hagemeijer and Blair 1997) and thus the conditions in their area of occupancy in Europe do not provide reliable information about their ecological niche.

We performed all analyses separately for two data sets (Supplementary material Appendix 1 Table A1): all focal species (n = 252) and passerines (n = 156). Passerine species are the most species-rich and phylogenetically homogenous avian order (Barker et al. 2004) and are often used as representative of all birds in comparative analyses (Laube et al. 2013). However, they also cover narrower spectra of ecological adaptations including both habitat utilization and morphological traits (e.g. they lack zygodactyl foot or prolongation of tarsus, or neck). We thus aimed to test whether the relationships observed for all bird species in our dataset hold true in the passerine subset too.

Species' traits

To quantify species' *habitat specialization*, we discriminated 15 breeding habitats (deciduous forest, coniferous forest, woodland, shrub, savannah, tundra, grassland, mountain meadow, reed, swamps, semi-desert, freshwater, marine, rocks, human settlements) that were also used in BWPi. For each habitat we recognized whether or not it is occupied by a given species based on the information in the text of BWPi. We classified as 'presence' (quantified as 1) when a species occupied a given habitat and as 'absence' (quantified as 0) when a habitat was not occupied by that species. Thus for each species we obtained a vector of presences-absences across the 15 habitats. From these presence–absence data we calculated species habitat specialization index as a coefficient of variation of a given species' occurrence across the 15 habitats (Julliard et al. 2006). Specialists have thus high values of this specialization index, while generalists have low values. Various studies exploring species' habitat selection used this index as a suitable indicator of species' habitat niche breadth (Devictor et al. 2008, Barnagaud et al. 2012) and it shows also a good agreement with expert judgement (Reif et al. 2010).

Diet specialization was expressed in a similar way like the habitat specialization. We recognized presence–absence of eight food types (foliage, fruit, grain, insects, other invertebrates, terrestrial vertebrates, water vertebrates, carrion) in diet of each bird species during their breeding period based on information in BWPi. From these data we calculated the index of diet specialization as a coefficient of variation of species' use of particular food types.

Climatic niche breadth was estimated by overlaying maps of species breeding ranges in Hagemeijer and Blair (1997) and climatic data. Breeding ranges were depicted as presence–absence of every species in 50 × 50 km squares in UTM grid. We excluded the European part of Russia due to large proportion of squares with missing data. Climatic data were extracted for the same UTM grid cells as bird occurrence data from Haylock et al. (2008). For each species, we calculated the mean temperature during the peak breeding season (April–June) in each grid cell occupied. The climatic niche breadth was then quantified as a difference between the mean temperature in 5% hottest and 5% coldest mapping squares occupied by the species (Jiguet et al. 2007).

Breeding area of occupancy in Europe was simply the number of mapping squares in Hagemeijer and Blair (1997) occupied by a given species. The variable was log transformed for further analysis.

Species' *migration distance* we assessed using information from BWPi sorting species into four categories along an ordinal scale: 1) resident over whole European range, 2) European population partly resident, partly migratory, 3) migratory within Europe and North Africa, 4) migrant to sub-Saharan Africa or Indian subcontinent.

Finally, we defined three morphological variables based on mean values in BWPi: body mass, wing length/tail length ratio and tarsus length/body length ratio. Wing length/tail length ratio expresses species' ability to fly through dense vegetation: the higher the ratio, the higher the preference for more open habitats (cf. Norberg 1995). Tarsus length/body length ratio expresses species' affinity to ground: the higher the ratio, the more ground dwelling is the species (Kaboli et al. 2007). Body mass was log transformed for further analysis.

As stated above, in the case of habitat specialization, diet specialization, climatic niche breadth and the area of occupancy in Europe we restricted the information to the breeding period of the focal species. This restriction was due to much higher quality of data originating from the breeding period than from other parts of bird's annual cycle (see BWPi or Hagemeijer and Blair 1997). This data limitation is particularly strong in long-distance migrants because the information about their ecological needs and distribution in wintering quarters is seemingly poor. However, we suggest this restriction is biologically relevant because bird populations face high energy demands during the period of reproduction (Newton 1998) and are under strong selection pressures in that time (Gill 2006).

Statistical analysis

Relationships between traits are expected to be constrained by the phylogenetic relatedness between species. We therefore related the habitat specialization to particular traits using phylogenetic generalized least squares (PGLS) performed in the R-package 'ape' (Paradis et al. 2004). Phylogenetic data were obtained from Jetz et al. (2012) which is currently the most comprehensive source of phylogenetic information in birds providing also branch lengths.

We assessed all possible combinations of explanatory variables in PGLS models using Akaike information criterion corrected for small sample sizes (AIC_c) run under the R-package 'MuMIn' (Bartoń 2009). The separate analysis was performed for all-species and passerines-only datasets. The parameter estimates and confidence intervals were produced using averaging across all models (Burnham and Anderson 2002). The explanatory variables whose model-averaged confidence limits do not overlap zero can be viewed as important predictors of habitat specialization. To visualize their effects, we plotted the relationship between habitat specialization and each of the important predictors accounting for the effects of all other explanatory variables. The plots were prepared only for the all-species dataset.

In all models we included by default the area of occupancy to factor out a trivial effect of limited distribution on habitat specialization. The more limited distribution results into narrower habitat niche partly due to sampling effects irrespective to species' ecology (Burgman 1989, Slatyer et al. 2013). Therefore, the relationships between habitat specialization and the other traits can be viewed as not affected by the range size effects.

We also tested the univariate relationships between habitat specialization and particular ecological traits (i.e. performing separate model for each trait) to see whether the relations change when the effects of other traits are not controlled for.

Finally, we tested whether the relationships between species habitat specialization and their traits depend on species' long-term population trend, namely population decline. For this purpose, we excerpted population trends for the time period 1990–2000 from BirdLife International (2004) discriminating declining species (n = 85; species undergoing small, moderate and large decline, respectively, according to the classification of BirdLife International 2004) and other species (n = 167; species with all other trend categories according to the classification of BirdLife International, 2004). Then we took the traits recognized as important by the model averaging described above, and composed a PGLS model containing the two-way interactions with the trend (the categorical variable with two levels: 'decline' and 'other') and respective traits. A significant interaction suggests that a relationship between the habitat specialization and a given trait differs according to the species' population trend.

All continuous variables were standardized to zero mean and unit variance prior the analyses to obtain comparable parameter estimates.

To test the sensitivity of the patterns revealed in statistical analysis to our habitat classification, we also calculated the habitat specialization using 10 and 8 habitat categories, respectively, revealed by merging the original 15 habitat classes (Supplementary material Appendix 1 Table A2).

Results

All bird species

Model-averaged estimates obtained using the PGLS models assessing performance of all possible combinations of predictors showed that the habitat specialization of European birds is most strongly connected to the breeding area of occupancy in Europe (Table 1a). The larger the area of occupancy, the lower was the level of species habitat specialization (Fig. 1a). The second most important, and more biologically informative, predictor of the degree of species habitat specialization was the wing length/tail length ratio (Table 1a) with longer wings to tail resulting in higher habitat specialization (Fig. 1d).

Three other traits with confidence intervals non-overlapping zero were almost equally important: diet specialization, climatic niche breadth and migration distance (Table 1a). Habitat specialists are thus also dietary specialists (Fig. 1b), but have wider climatic niches (Fig. 1c) and migrate to shorter distances than habitat generalists (Fig. 1e).

For both body mass and tarsus length/body length ratio we did not find any relationships to habitat specialization (Table 1a).

Applying the habitat specialization calculated with reduced number of habitat categories, the relationships remained qualitatively unchanged after reducing the number of habitat classes from 15 to 10 (Supplementary material Appendix 1 Table A3a). When only eight habitat classes to the calculation of habitat specialization were applied, the effect of migration distance became unimportant and the effect of wing length/tail length ratio was marginally insignificant (Supplementary material Appendix 1 Table A3b).

The univariate relationships between habitat specialization and particular species' traits were qualitatively similar to those obtained by model averaging in most cases. However, the diet specialization was insignificant and the effect of climatic niche breadth had the opposite direction (Supplementary material Appendix 1 Table A4a).

The relationships between habitat specialization and species' breeding area of occupancy in Europe, climatic niche breadth and the wing length/tail length ratio, respectively, were not affected by population trend of species (Supplementary material Appendix 1 Table A5). However, in the case of dietary niche breadth and migration distance, the relationships differed according to species' population trends (Supplementary material Appendix 1 Table A5). Specifically,

Table 1. Relationships between habitat specialization and species' traits in European birds as revealed by phylogenetic generalized least squares models for (a) all species and (b) passerines only. The parameter estimates were calculated using averaging across all models containing all combinations of the explanatory variables. All variables were standardized prior analysis to reveal comparable parameter estimates. The traits with confidence limits (CL) not overlapping zero are printed in bold.

Trait	Coefficient	Lower CL	Upper CL
(a) All species			
Breeding area of occupancy in Europe	**−0.54**	**−0.71**	**−0.37**
Diet specialization	**0.19**	**0.02**	**0.36**
Climatic niche breadth	**0.18**	**0.04**	**0.32**
Body mass	0.20	−0.31	0.71
Wing length/tail length ratio	**0.32**	**0.12**	**0.52**
Tarsus length/body length ratio	−0.11	−0.38	0.17
Migration distance	**−0.18**	**−0.34**	**−0.02**
(b) Passerines			
Breeding area of occupancy in Europe	**−0.92**	**−1.07**	**−0.76**
Diet specialization	0.14	−0.09	0.38
Climatic niche breadth	**0.51**	**0.33**	**0.69**
Body mass	0.10	−0.29	0.50
Wing length/tail length ratio	0.10	−0.09	0.28
Tarsus length/body length ratio	0.07	−0.27	0.42
Migration distance	**−0.20**	**−0.39**	**−0.02**

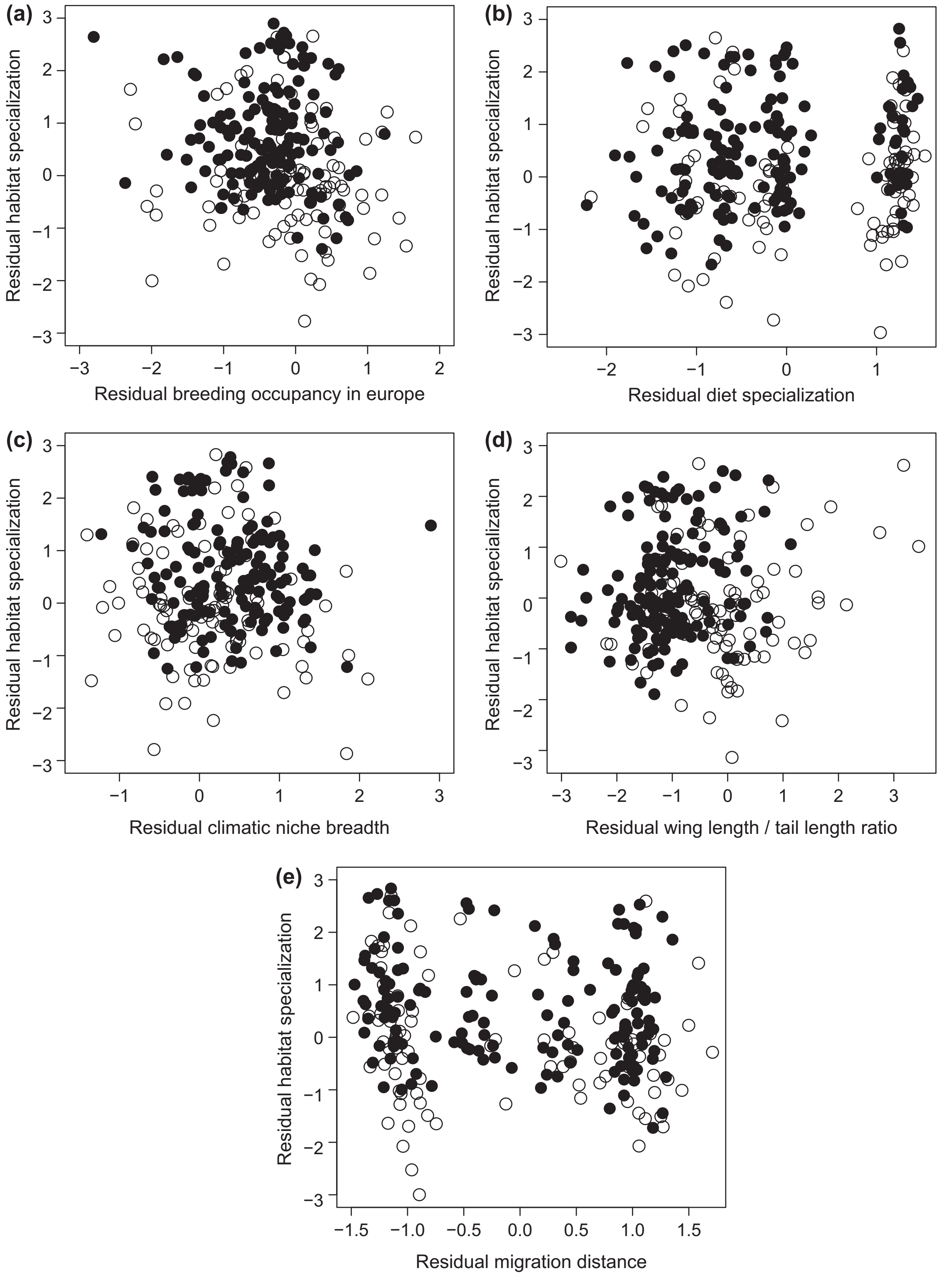

Figure 1. Relationships between habitat specialization and (a) breeding area of occupancy in Europe, (b) diet specialization, (c) climatic niche breath, (d) wing length/tail length ratio, (e) migration distance, respectively, in European birds. The relationship of habitat specialization and a given trait was calculated controlling for the effects of the other explanatory variables. The increasing values along the y axis indicate increasing habitat specialization. The increasing values along the x axis indicate increasing breeding area of occupancy in Europe, wing length/tail length ratio, diet specialization, climatic niche breath and migration distance, respectively. Open circles – non-passerines, filled circles – passerines.

the positive relationship between habitat and diet niches was significant only in species which were not declining and turned to insignificance in the case of declining species. The opposite was true in the case of migration distance, when its negative relationship to habitat specialization was driven largely by the declining species.

Passerines

After restricting the data set to passerines only, the results were somewhat different. The breeding area of occupancy in Europe remained the most important predictor of species habitat specialization but its effect was stronger than in the case of all species data set (Table 1b, Fig. 1a). Confidence limits of only two more variables did not overlap zero: climatic niche breadth and migration distance (Table 1b). Directions of these relationships were the same as in the case of all species: higher habitat specialization was associated with wider climatic niche (Fig. 1c) and shorter migration distance (Fig. 1e). By contrast, wing length/tail length ratio and diet specialization were no longer important (Table 1b). No relationship to habitat specialization also showed body mass and tarsus length/body length ratio (Table 1b).

When applying 10 instead of 15 habitat classes for the calculation of habitat specialization, the results did not change qualitatively (Supplementary material Appendix 1 Table A3c). Further reduction to eight habitat classes resulted in loss of the importance of the effect of migration distance (Supplementary material Appendix 1 Table A3d).

The univariate relationships between habitat specialization and particular traits were qualitatively similar to those obtained by model averaging in all but two cases. The effect of climatic niche breadth reverted from positive to negative and the wing length/tail length ratio became significant (Supplementary material Appendix 1 Table A4b).

The relationships between habitat specialization and the traits selected as important by model averaging were not affected by species' population trend (Supplementary material Appendix 1 Table A5).

Discussion

In this paper, we investigated how habitat specialization is related to species-specific traits in European birds. Habitat specialists had smaller breeding range, narrower diet niche, wider climatic niche, higher wing length/tail length ratio and migrated on shorter distances than habitat generalists. However, we found support neither for the relationship between habitat specialization and body mass, nor for relationship between habitat specialization and tarsus length/body length ratio. The absence of these relationships may be attributed to high level of phylogenetic conservatism in these traits (Barnagaud et al. 2014), reducing their effects in our phylogenetic analysis.

The effect of the area of occupancy was the strongest among all predictors and confirms that habitat specialization reflects species' space use at large spatial scales (Gaston et al. 1997). Because the range size is also related to several other ecological traits like diet niche, fecundity, body size or migration (Laube et al. 2013), we controlled for its effects in all models. Therefore, the relationships between habitat specialization and other traits can be viewed as not affected by unequal range sizes of the specialist and generalist species.

The higher diet specialization of habitat specialists suggests that the diet niche partly determines the habitat niche: the use of a wider variety of food resources enables species to occupy more habitats, and vice versa. A link between habitat and diet specialization is suggested for instance by recent observation of both habitat and diet specialization contributing in a similar way to the spatial patterns of bird species richness (Belmaker et al. 2012). Our finding also to some extend justifies the use a habitat niche as a surrogate for a general ecological specialization including also the diet one (Julliard et al. 2006, Devictor et al. 2008). However, the relationship was rather weak at the coarse spatial scale of our study. We suggest that even within a single habitat (e.g. the broad-leaved forest, as used as one habitat category in our dataset) a species can find various food resources (e.g. vertebrates, diverse insects, fruits and other plant tissues). As a consequence, species can be habitat specialist (occupying only one habitat) having a broad diet niche within this habitat at the same time. This applies particularly at the large spatial scales, where the habitats are defined broadly, and weakens the relationship between habitat and diet niche breadth. Therefore, although the habitat and diet niches are not independent, we advocate the use both of them in order to describe species' ecological specialization properly.

The relationship between habitat and diet specialization is stronger when all species were considered, than in passerines only. This is probably due to more diverse feeding strategies in non-passerine species with many highly specialized groups such as woodpeckers, pigeons or raptors. Indeed, a diet specialization in non-passerines (mean = 2.42, SD = 0.80) was significantly higher than in passerines (mean = 1.98, SD = 0.72; t-test: $t = 4.51$, $DF = 251$, $p < 0.001$) according to our data.

We found that habitat specialists are climatic generalists. Although it is not surprising that climatic and habitat niches are related because climate affects bird distribution through food and habitats (Ferger et al. 2014), the direction of the relationship we observed is quite unexpected. In contrast, the univariate relationship between habitat specialization and climatic niche breadth was negative in our data corresponding with a previous study on French birds (Barnagaud et al. 2012), i.e. habitat generalists occupy more climatic zones than habitat specialists. However, this relationship is quite weak and most likely driven by the range size effect: a large geographic range typically encompasses a wider range of temperatures than a smaller one (Gaston et al. 1997). After factoring out range size effect, the relation between habitat specialization and climatic niche breadth becomes positive. It may be caused by some specific habitats which host highly specialized species, such as farmland with *Alauda arvensis* and *Motacilla flava* or urban areas with *Passer domesticus* and *Delichon urbicum*, and are widely distributed over different climatic zones. However, when correcting habitat specialization for habitat availability, this explanation is not supported because the specialists to widespread habitats do not have broad climatic niches (Supplementary material Appendix 1 Results). As an alternative (but not mutually exclusive) explanation, we suggest that the positive relationship between habitat specialization and climatic niche breadth may be driven by species breeding in mountain areas. Such species have narrow habitat niches, but also face a large climatic variability within limited geographic distribution which makes their climatic niches relatively wide. Indeed, species like *Lagopus muta*, *Gypaetus barbatus*, *Eremophila alpestris* or *Hirundo* *rupestris* seem to be representatives of these attributes according to our data. To test this idea formally, within the species in our dataset we identified 25 species (Supplementary material Appendix 1 Table A1) as mountain-breeding according to the information in BWPi (Cramp 1977–1994). These mountain-breeding species had relatively higher habitat specialization (mean = 2.83, SD = 0.86) than the remaining species (mean = 2.61, SD = 0.75), albeit not significantly so (t-test: t = 1.33, DF = 251, p = 0.183), and significantly wider climatic niches (mountain-breeding species: mean = 8.20, SD = 2.14; remaining species: mean = 6.57, SD = 3.38; t-test: t = 2.36, DF = 251, p = 0.019).

As for the morphological traits, the wing length/tail length ratio was the only important predictor of species' habitat specialization. The higher wing length/tail length ratio of habitat specialists suggests that such species depend more on manoeuvrability of the flight (Norberg 1995) and thus likely forage more in the air or live in more open habitats than habitat generalists. This pattern can be caused by several mechanisms. First, many forest species are able to occupy even small patches of their habitat, whereas the open habitat species require relatively large areas of habitat (Hořák et al. 2010, Desrochers et al. 2011). One can speculate that this disproportion in spatial requirements can be caused by a three-dimensional character of forest compared to two-dimensional open habitats such as grassland or semi desert. In consequence, open habitat specialist species are better adapted for frequent flying by having higher wing/tail length ratio. Second, lower habitat specialization of species with lower wing length/tail length ratio can also coincide with a recent expansion of several originally forest species (e.g. *Columba palumbus*, *Turdus merula*, *Garrulus glandarius*) into new environments created by humans such as urban habitats (Evans et al. 2010). Third, it is possible that the higher habitat specialization of open land species can be produced by our a priori definition of habitats. However, we do not think this effect can entirely explain the importance of wing length/tail length ratio in our analysis. The relationship between habitat specialization and wing length/tail length ratio was observed even after reduction of habitat classes to 10 and was marginally insignificant after further reduction to 8 habitat classes, when we discriminated only two types of open and forest habitats, respectively. The relationship between habitat specialization and wing length/tail length ratio was not detected after narrowing the dataset to passerine species only. We suggest that passerines lack the high variability in morphological adaptations to habitats that drove the relationship over all species (e.g. relatively long wings/short tail in open habitat).We observed low habitat specialization in long-distance migrants. Long-distance migrants meet many different habitats en route and on their wintering grounds (Salewski and Jones 2006) and they could maintain broad habitat niches during breeding season, too. This can be advantageous especially when they arrive late to breeding grounds and territories are already taken by residents (Berthold 2001). Besides, some studies suggest that the migratory behaviour originated in tropical species with broad habitat niches (Levey and Stiles 1992, but see Bruderer and Salewski 2008) and thus the low habitat specialization of the present-day long-distance migrants could be a residue of this origin. Alternatively, differences in habitat specialization need not to be mechanistically connected with migratory behaviour and can be just a by-product of differences in distribution of species with different migration strategies determined by other factors (Brändle et al. 2002).

The analysis discriminating species undergoing long-term population decline in Europe (BirdLife International 2004) showed that most of the relationships described above hold true irrespective to species' population trend. However, there were two exceptions. First, declining species did not show positive relationship between habitat and diet specialization. It is possible that the link between niche axes can be weakened by reduction of number of occupied habitats resulting from population reduction. Second, declining species had stronger relationship between habitat specialization and migration distance than the other species. This effect can be attributed to high number of long distance migrants among declining species (Sanderson et al. 2006).

We should bear in mind that the data on habitat specialization, diet specialization, climatic niche breadth and the area of occupancy used in our study are restricted to the breeding period only. While there are important practical and biological reasons for such a restriction (see the Materials and methods section), it has potential limitations. First, species are generally more specialized during breeding in terms of habitat use and especially diet (Cramp 1977–1994). It is thus possible that observed relationships would weaken after considering the non-breeding niches. Second, niches of migratory species, particularly the climatic niche, widen much more towards the non-breeding periods than the niches of resident species (Cresswell 2014). Since we showed that migrants are habitat generalists, it is possible that the unexpected positive relationship between habitat specialization and climatic niche breadth would disappear if the non-breeding ranges were taken into account.

Our analyses were made separately for passerines and for all birds together. We aimed to assess, whether ecological variation within passerines is ample enough to support trends observed for the whole European avifauna, which is assumed (and largely untested) in numerous studies. Although several traits showed the same relationships to habitat specialization, some others did not. As discussed above, there are good biological reasons for these differences between datasets. However, from the perspective of representativeness, it is clear that in the case of traits showing relatively lower variability in passerines, a narrow taxonomic focus may hamper revealing trends observed over larger taxonomic scale. This is likely caused by considerable ecological differentiation among lineages deeper in avian phylogeny.

In this study, we expressed the habitat specialization at the level of individual species. This approach can mask differences among populations or even individuals within species (Bolnick et al. 2003). For example, a generalist species can either consist of different local populations, each being specialized to different habitat, or from populations (or individuals) exploiting a wide range of habitats locally. Discrimination between these types of habitat specialization could be a subject of the future studies. They can test whether the patterns described here still hold when we estimate habitat specialization at species-, population- or individual-level.

Conclusion

Our study showed that together with the widely reported positive relationship between geographic range size and habitat niche breadth, several other traits had important independent effects on species' habitat specialization. This suggests that the habitat specialization can be to some extent, at least in European birds, treated as a broad surrogate of a general ecological specialization covering also other niche dimensions such as diet specialization. However, a negative relationship between habitat and climate niche breadth implies that niche estimates differ along climate and habitat axes. This finding might be important for deeper understanding of the effect of predicted climatic changes on geographical distributions of species. We can speculate that, habitat specialists may be less affected by climate change than might be actually assumed as their preferred habitats can be found across climatic zones. This also implies that impacts of climate change may mechanistically differ between specialists and generalists being mediated stronger by habitat change in the former group. Irrespective to the exact mechanisms, it seems that for complete view of climate impacts on species' distributions it is important to measure both climatic and habitat niche breadth. To sum, we have shown that species' distributions across habitats are informative about their positions along other axes of ecological space and can explain states of particular functional traits. However, the links between different niche estimates cannot be always straightforwardly predicted.

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Supplementary material (available online as Appendix oik-02276 at <www.oikosjournal.org/appendix/oik-02276>). Appendix 1.