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Towards a more mechanistic understanding of traits and range sizes

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ABSTRACT

Aim An important, unresolved question in macroecology is to understand the immense inter-specific variation in geographic range sizes. While species traits such as fecundity or body size are thought to affect range sizes, a general understanding on how multiple traits jointly influence them is missing. Here, we test the influence of a multitude of species traits on global range sizes of European passerine birds in order to better understand possible mechanisms behind macroecological relationships.

Location Global.

Methods We evaluated the effect of life-history traits (fecundity, dispersal ability), ecological traits (habitat niche, diet niche, migratory behaviour, migratory flexibility) and a morphological trait (body size) on the global range sizes of 165 European passerines. We identified hypotheses from the literature relating traits to range size and used path analysis to test them.

Results Fecundity, dispersal ability and habitat niche breadth had a direct positive effect on range size. Diet niche position had a direct negative effect on range size. Habitat niche breadth also had an indirect positive effect via higher fecundity. Migratory behaviour had an indirect positive effect via better dispersal ability. Body size had a strong positive direct effect which was reduced by negative indirect effects via several other traits.

Main conclusions Geographic range sizes of European passerines were influenced by life-history traits (fecundity and dispersal ability), ecological traits (habitat niche breadth, diet niche position and migratory behaviour) and by body size. Traits influenced range size both directly and indirectly. Body size effects were particularly complex, with positive and negative effects acting over different pathways. We show that it is necessary to disentangle the direct and indirect influence of multiple traits on range size to better elucidate the mechanisms that generate macroecological relationships.

Keywords

Birds, ecological traits, geographic range size, life-history traits, morphological traits, passerines, path analysis.

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INTRODUCTION

One of the fundamental traits of a species is the size of its geographic range (Brown *et al.*, 1996; Gaston & Fuller, 2009). Range size influences patterns of species diversity (Jetz & Rahbek, 2002; Soberón & Ceballos, 2011) and species with small ranges have a higher extinction probability (Brown, 1995; Lee &

Jetz, 2011), making range size one of the most important criteria for classifying the threat status of a species (IUCN Red List classification; IUCN, 2001).

Inter-specific range size variation can cover several orders of magnitude, even between close relatives (Brown *et al.*, 1996). Yet our understanding of the mechanisms that are responsible for this immense variation is limited (Lester *et al.*, 2007). Among

the most important factors that influence range size are species traits. Life-history traits, such as birth rate and dispersal ability (Holt *et al.*, 1997; Böhning-Gaese *et al.*, 2006), ecological traits, particularly habitat niche and diet niche (Brown, 1984; Gregory & Gaston, 2000) as well as migratory behaviour (Gaston & Blackburn, 1996), and morphological traits such as body size (Brown, 1995) have been shown to influence range sizes.

Brown *et al.* (1996) emphasized that several traits might influence range size simultaneously in a complex way, through direct as well as indirect effects. For example, large body size in birds may directly increase range size because of body size-dependent spatial interactions with resources and the environment (Brown, 1984). On the other hand, large-bodied species have lower fecundity which might lead to reduced range size (Gaston *et al.*, 1997; Böhning-Gaese *et al.*, 2000). Finally, large-bodied birds are less likely to be migratory (Hedenström, 2008) and thus might have lower dispersal ability and hence smaller ranges than small-bodied birds (Holt *et al.*, 1997; Dawideit *et al.*, 2009). The relative importance of traits can only be assessed by simultaneous analyses of multiple traits. Also, the apparent statistical significance of traits in individual tests may be caused by correlations with other, non-tested, traits (Shipley, 2000). Nonetheless, in most studies, traits have been tested individually.

For a more mechanistic understanding of the relationships between life-history traits, ecological traits, morphological traits and range size, as many traits as possible should be tested simultaneously and interactions among traits should be considered. One option for testing the direct and indirect effects of traits on a response variable is structural equation modelling, in particular path analysis (Mitchell, 1992; Shipley, 2000). Such models, while based on examination of correlational patterns (Shipley, 2000), have been used successfully to evaluate factors that directly or indirectly influence macroecological patterns such as species richness (Kissling *et al.*, 2007; Qian & Kissling, 2010) or extinction risk (Lee & Jetz, 2011).

Here, we tested the most comprehensive set of traits to date for their direct and indirect effects on the geographic range sizes of birds. We used birds in this analysis because traits and range sizes of birds are well documented and a number of studies have already tested individual relationships on which we can base a priori hypotheses (e.g. Gaston *et al.*, 1997; Böhning-Gaese *et al.*, 2006; Hurlbert & White, 2007). We incorporated traits reflecting the life history (annual fecundity, dispersal ability), ecology (habitat niche breadth, diet niche breadth and position, migratory behaviour and flexibility) and morphology (body size) of birds into our analysis.

We identified the following a priori hypotheses in the literature about the potential mechanistic relationships between these traits and range sizes of birds (see Methods for details). High annual fecundity and high dispersal ability lead to larger range sizes (Blackburn *et al.*, 2006; Böhning-Gaese *et al.*, 2006). Broader habitat niches and broader diet niches cause larger range sizes both directly and also indirectly via increasing annual fecundity (Brown, 1984; Hurlbert & White, 2007). Species with a diet niche position at higher trophic levels have smaller ranges (Gaston, 1994). There is a direct effect of migra-

tory behaviour on range sizes, for which both negative and positive relationships have been postulated in the literature (Gaston & Blackburn, 1996; Bensch, 1999). Migratory behaviour also influences range size indirectly via dispersal ability because migrants tend to be better dispersers, which in turn increases range size (Baldwin *et al.*, 2010). Species with higher migratory flexibility have larger ranges (Keitt *et al.*, 2001). Larger body size directly leads to larger range size (Brown, 1984). Additionally, body size is linked indirectly to range size via migratory behaviour, with large-bodied birds being less frequently migratory, and via annual fecundity, which is lower in large-bodied bird species (Böhning-Gaese *et al.*, 2000; Hedenström, 2008). We incorporated these hypotheses into a path model and estimated the strength of the direct and indirect effects of species traits on range sizes.

METHODS

Study species and area, geographic range sizes

We analysed the relationship between traits and global breeding range sizes of 165 European passerine bird species (see Appendix S1 in Supporting Information). The analysis was restricted to passerines because they share a similar body plan and because dispersal ability can be quantified comparatively easily from morphology (Dawideit *et al.*, 2009).

Global breeding range sizes of birds were calculated using data from a comprehensive global geographic bird range database at a resolution of $1^\circ \times 1^\circ$, following the approach described in Rahbek & Graves (2000, 2001). The dataset (version 30/06/2009) was an updated, more comprehensive version of the dataset used in the cited references by Rahbek & Graves (2000, 2001), collated and managed by co-author C.R. Maps represent a conservative extent-of-occurrence based on museum specimens, published sight records and spatial distribution of habitats, which have subsequently been validated by ornithological experts. Range size was quantified as the sum of the areas of all grid cells a species occupied. We considered only the land surface area of grid cells in square kilometres after applying a Behrmann global equal-area projection.

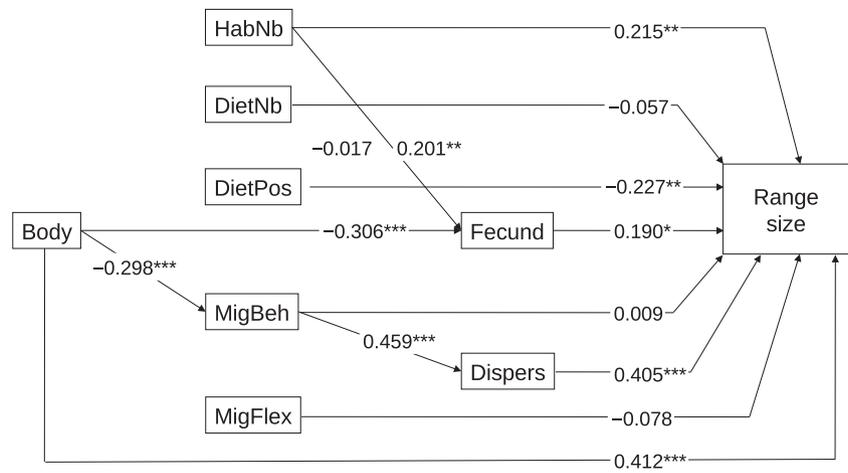
Species traits

The following traits and their potential relationships with range size have been derived from the literature. We use the traits and their relationships among each other and to range size to define a priori hypotheses on paths in the path diagrams (Fig. 1).

Annual fecundity

High annual fecundity (e.g. large clutches, many broods per year) may cause large geographic ranges as it could lead to high local abundances (Blackburn *et al.*, 2006) which are often correlated with large range sizes (Brown, 1984; Blackburn *et al.*, 1996; Gaston *et al.*, 1997; Borregaard & Rahbek, 2010; direct path from annual fecundity to range size in Fig. 1). We quanti-

Figure 1 Path diagram for path models relating avian traits to global range size ($n = 165$). Path coefficients and significance levels: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Body = log(body mass), HabNb = habitat niche breadth, DietNb = diet niche breadth, DietPos = diet niche position, MigBeh = migratory behaviour, MigFlex = migratory flexibility, Fecund = log(annual fecundity), Dispers = log(dispersal ability).



fied annual fecundity as the product of clutch size times the number of clutches per year using data from Ehrlich *et al.* (1994). For *Sturnus unicolor* the number of clutches per year was taken from Birds of the Western Palearctic interactive (BWPi, 2006) because data were missing in Ehrlich *et al.* (1994). For analysis, fecundity was \log_{10} -transformed.

Dispersal ability

Range filling, i.e. the ratio of realized to potential range size, can be limited by, amongst other factors, dispersal ability (Svenning & Skov, 2004). Accordingly, a positive relationship between dispersal ability and geographic range size has been shown in several studies (e.g. Dennis *et al.*, 2000; Böhning-Gaese *et al.*, 2006; direct path in Fig. 1).

We quantified dispersal ability as the quotient of Kipp’s distance (distance between the tip of the first primary to the tip of the wing) and bill depth (measured at the proximate edge of the nostrils). This measure has been shown to be the best morphological predictor of dispersal ability in European passerines (Dawideit *et al.*, 2009). We aimed to measure Kipp’s distance and bill depth for at least eight museum specimens per species. However, this was not always possible (mean 7.26 specimens; range 1–12 specimens). We took care to select adult, non-moulting specimens from localities as close as possible to the centre of the European geographic range and whose time of death was between April and July to avoid measuring wintering individuals. If fewer than eight suitable individuals were available, we relaxed the criteria on locality and time of death. For species that Svensson (1992) describes as sexually dimorphic we measured, if possible, four individuals per sex. For species with more than one subspecies in Europe, we measured the nominate species, as it is usually the most widespread. For species where subspecies had geographic ranges of similar size, we took measures of individuals from both and calculated the mean. All measurements were taken by the same person (H.K.). When calculating averages across specimens, we first calculated the quotient of \log_{10} (Kipp’s distance) and \log_{10} (bill depth) for each individual and then averaged over individuals.

Habitat niche breadth

Habitat niche breadth may be positively related to range size (e.g. Hurlbert & White, 2007; Carrascal *et al.*, 2008) as species that tolerate a wider range of conditions are able to colonize larger geographic areas (Brown, 1984; Gaston *et al.*, 1997; direct path in Fig. 1). Habitat niche breadth is also expected to increase fecundity, and hence indirectly increase range size (indirect path from habitat niche breadth to fecundity in Fig. 1), as species that are able to live under a wide variety of conditions and use a broad range of resources should also be able to obtain more resources locally and raise more young (Brown, 1984; Gaston *et al.*, 1997).

To quantify habitat niche breadth, the habitat use of a species was converted to a habitat gradient from closed forest to open country with values of 1 (closed forest), 2 (open forest), 3 (forest edge), 4 (orchards, gardens), 5 (shrub land), 6 (open country with single trees or shrubs, e.g. agricultural land with hedgerows), and 7 (open country without trees or shrubs, e.g. structurally simple arable land) using data from Ehrlich *et al.* (1994). A species was assigned up to three different values along this habitat gradient (Böhning-Gaese & Oberrath, 2003). Habitat niche breadth was calculated as the difference between the maximum and minimum value.

Diet niche breadth

Analogous to habitat niche breadth, species which use a broad range of food sources might be more widespread than more specialized species (direct path in Fig. 1). In addition, a broad diet niche may lead to increased fecundity, causing an indirect positive effect of diet niche breadth on range size (Brown, 1984; indirect path from diet niche breadth to annual fecundity, Fig. 1). Diet niche breadth was quantified by taking into account the range of food sources utilized. We classified all species as herbivorous, insectivorous or omnivorous using data from Ehrlich *et al.* (1994) (Böhning-Gaese *et al.*, 2000). We assigned species that were either herbivorous or insectivorous a diet niche breadth of 1 (38 species), species that were herbivorous and

insectivorous a value of 2 (120 species) and omnivorous species a value of 3 (7 species).

Diet niche position

We used the trophic level of a species as a measure of its diet niche position. Species at higher trophic levels are faced with lower food biomass and, consequently, might have lower local abundance and hence smaller range sizes than species at lower trophic levels (Gaston, 1994; direct path in Fig. 1). We defined the diet niche position of herbivorous species as 1 (29 species), of species that were herbivorous and insectivorous or that were omnivorous as 2 (35 species) and of insectivorous species as 3 (101 species).

Migratory behaviour

Equivocal results have been found for the effect of migratory behaviour on ranges size. On the one hand, migratory birds have been shown to have smaller geographic ranges than non-migrants, potentially because migrants are limited in extending their geographic ranges along a longitudinal axis within the Holarctic due to constraints caused by their migratory behaviour (Böhning-Gaese *et al.*, 1998; Bensch, 1999). On the other hand, long-distance migrants have been shown to have larger geographic ranges than sedentary birds in Anseriformes (Gaston & Blackburn, 1996). Here we tested for a potential direct effect of migratory behaviour, as well as for an indirect effect via dispersal ability (Fig. 1) because migratory birds show ecomorphological adaptations to long-distance flight also resulting in better dispersal ability (Winkler & Leisler, 1992; Dawideit *et al.*, 2009; Baldwin *et al.*, 2010). We classified the migratory behaviour of a species as 1 (residents, 51 species), 2 (short-distance migrants, with the centre of their non-breeding grounds south of the breeding grounds but north of the Sahara, 51 species) or 3 (long-distance migrants with the centre of their wintering grounds south of the Sahara; 63 species) (Böhning-Gaese *et al.*, 2000).

Migratory flexibility

Species with flexible migratory behaviour are more successful invaders than those with a fixed migratory programme (Sol & Lefebvre, 2000). Higher invasion success might lead to larger geographic ranges (Keitt *et al.*, 2001; direct path from migratory flexibility to range size in Fig. 1). For migratory flexibility we differentiated between species with an invariable migratory behaviour (value 0, residents or long-distance migrants, 114 species) and species with a flexible migratory behaviour (value 1, short-distance migrants, 51 species). Resident birds and long-distance migrants were classified very conservatively (Böhning-Gaese *et al.*, 2000) and included only species with no intra-specific variation in migratory behaviour within Europe, consequently defining all species *with* intra-specific variation in migratory behaviour as short-distance migrants.

Body size

Larger species interact with their environment at larger spatial scales than smaller species. Thus, smaller organisms are able to attain higher densities in small ranges, while larger ones tend to have less dense, more widely distributed populations (Brown, 1984, 1995; direct path in Fig. 1). We also expected species with large body size to be less migratory (indirect path to migratory behaviour; Fig. 1) because large birds may need more time to raise their young and to moult and hence have less time for migration and because body size constrains flight speed during flapping flight, the most common flight style of passerines (Hedenström, 2008). Furthermore, large bird species tend to have low fecundity (Böhning-Gaese *et al.*, 2000; indirect path to fecundity in Fig. 1). We used body mass as a measure of body size (Clark, 1979). Data were taken from BWPi (BWPi, 2006) and were \log_{10} -transformed.

Statistical analyses

Path analyses

In path analysis (Mitchell, 1992; Shipley, 2000), supposed mechanistic relationships between variables are delineated in a path diagram (Fig. 1). Direct effects are measured by the standardized partial regression coefficient (in the following path coefficient) for the direct link between a predictor variable and a response variable. Indirect effects are calculated by multiplying the path coefficients along a path between a predictor and a response variable, and then adding these products for all possible paths between the two, excluding the direct effect (Mitchell, 1992). We used the a priori hypotheses described above to define paths between species traits and geographic range size (Fig. 1). We allowed correlations between predictors if they were significantly correlated ($|r| \geq 0.15$; $P < 0.05$, $n = 165$) and if there was no information in the literature on traits and range size regarding the potential direction and cause of the correlation (Shipley, 2000). We thus fitted correlations between diet niche breadth and (1) dispersal ability, (2) migratory behaviour, (3) habitat niche breadth, (4) diet niche position and (5) body weight, between migratory flexibility and (1) fecundity and (2) habitat niche breadth, between diet niche position and (1) dispersal ability and (2) migratory behaviour, as well as between habitat niche breadth and dispersal ability (all $|r| < 0.55$). For clarity's sake, these correlations were omitted from Fig. 1. In addition, we examined generalized variance inflation factors (GVIF) from a linear model containing all predictors to assess the potential effect of multicollinearity on parameter estimates. GVIFs can be interpreted as the inflation in the size of the confidence ellipsoid for a parameter estimate in comparison with the confidence ellipsoid that would have been obtained for orthogonal data (Fox & Monette, 1992). A GVIF larger than 4 suggests collinearity (Fox, 2002). The path model was evaluated using the normed fit index (NFI) and the goodness-of-fit index (GFI) (Arbuckle, 2008). The NFI is calculated by comparing the fitted path model to a baseline model where all observed variables are

assumed to be uncorrelated (Bentler & Bonett, 1980). It ranges from 0 to 1 with values closer to 1 indicating a better fit. The GFI assesses how closely a model replicates the observed covariance matrix by calculating the proportion of variance that is accounted for by the fitted path model (Tanaka & Huba, 1985). The GFI ranges from 0 to 1 with larger values indicating a better fit. Path analyses were calculated using AMOS (Arbuckle, 2008).

Phylogenetic relatedness

Individual species do not necessarily represent independent data points, as closely related species tend to have more similar traits than distantly related species (Harvey & Pagel, 1991). To assess potential statistical issues arising from phylogenetic non-independence, we tested the residuals from a multiple regression of range size against all species trait variables (corresponding to the direct effects in the path model in Fig. 1) for phylogenetic autocorrelation (Revell, 2010). We used a published supertree for European birds (Thuiller *et al.*, 2011) which contains all of our study species except for *Sitta whiteheadii* and *Anthus petrosus*. All analyses were conducted in R 2.12.2 (R Development Core Team, 2011). We tested for phylogenetic signal in the residuals using the Abouheif test (Abouheif, 1999) with 999 randomizations as implemented in the package *ade4* (Jombart *et al.*, 2010) and by calculating Pagel's λ , a maximum-likelihood based measure of phylogenetic signal (Pagel, 1997), and testing for a significant difference to a lambda of zero (no phylogenetic structure), as implemented in the package *CAICR* (Freckleton, 2009).

RESULTS

The path model ($n = 165$ species) adequately described the data structure (NFI = 0.884, GFI = 0.95). The variables included in the model explained $R^2 = 0.253$ of the inter-specific variation in global range sizes. Species with higher fecundity, better dispersal ability, broader habitat niches, lower trophic level and larger body size had larger ranges (Fig. 2a–e). Habitat niche breadth had a positive effect on annual fecundity while body size had a negative effect. Body size had a negative effect on migratory behaviour and migratory behaviour positively affected dispersal ability (Fig. 1). GVI's were smaller than 2.7 for all predictors, indicating that parameter estimates were not affected by multicollinearity. Both tests on the potential influence of phylogenetic relatedness confirmed that there were no significant phylogenetic signals in the multiple regression residuals (Abouheif test, $P = 0.057$; likelihood ratio test for lambda = 0, $P = 1$), indicating that analyses of the data with non-phylogenetic methods were appropriate. Hence, our results were not affected by the phylogenetic relatedness of the species.

The standardized total effect size of each trait on range size could be split into direct and indirect effects (Table 1). The strong total effect of habitat niche breadth on range size was mostly caused by a direct positive effect on range size and only a weak indirect positive effect through higher annual fecundity. In contrast, the total effect of migratory behaviour on range size

Table 1 Standardized total effects, direct effects and indirect effects of bird traits on global range sizes of 165 European passerine species.

Bird traits	Total effect	Direct effect	Indirect effect
Fecundity	0.190	0.190	n.a.
Dispersal ability	0.405	0.405	n.a.
Habitat niche breadth	0.253	0.215	0.038
Diet niche breadth	-0.060	-0.057	-0.003
Diet niche position	-0.227	-0.227	n.a.
Migratory behaviour	0.195	0.009	0.186
Migratory flexibility	-0.078	-0.078	n.a.
Body size	0.295	0.412	-0.117

The correlation between predictor and response variable, the total effect, can be split up into direct effects and indirect effects via other dependent variables. Direct effects are measured by the standardized partial regression coefficients between a predictor variable and a response variable (i.e. the direct link). Indirect effects are calculated by adding the products of all path coefficients over all paths between a predictor and a response variable, excluding the direct effect (Mitchell, 1992). n.a., not applicable.

was driven by a stronger indirect effect through better dispersal ability, and a weak direct effect. The total effect of body size on range size was complex; its strong positive direct effect was counteracted slightly by two indirect negative effects, one via lower fecundity and the other via migratory behaviour and dispersal ability (Fig. 1), but still resulted in a significant positive total effect.

DISCUSSION

We tested the direct and indirect effects of a multitude of traits on the global breeding range sizes of European passerine birds. Path analyses revealed direct effects of fecundity, dispersal ability, habitat niche breadth, diet niche position and body size, as well as indirect effects of habitat niche breadth, migratory behaviour and body size on global range sizes.

Species which raised more offspring per year had larger geographic ranges (Table 1, Fig. 1). These results confirmed earlier studies that found positive relationships between fecundity and range size (e.g. Blackburn *et al.*, 1996; Gaston *et al.*, 1997). High fecundity might be linked to large range sizes through higher local abundance (Brown, 1984; Blackburn *et al.*, 2006). As a consequence, populations in sink habitats might be 'rescued' through regular immigration from source habitats, with the result that, on average, a larger proportion of habitat patches might be occupied (Gaston, 2003).

Better dispersers had larger geographic ranges. Poor dispersal ability may lead to a larger proportion of potentially suitable habitat remaining unoccupied (Lester *et al.*, 2007). Also, good dispersers should be able to sustain sink populations at longer distances to source populations than poor dispersers. Even for mobile species such as birds, and when multiple traits are tested simultaneously, dispersal ability has an influence on range size

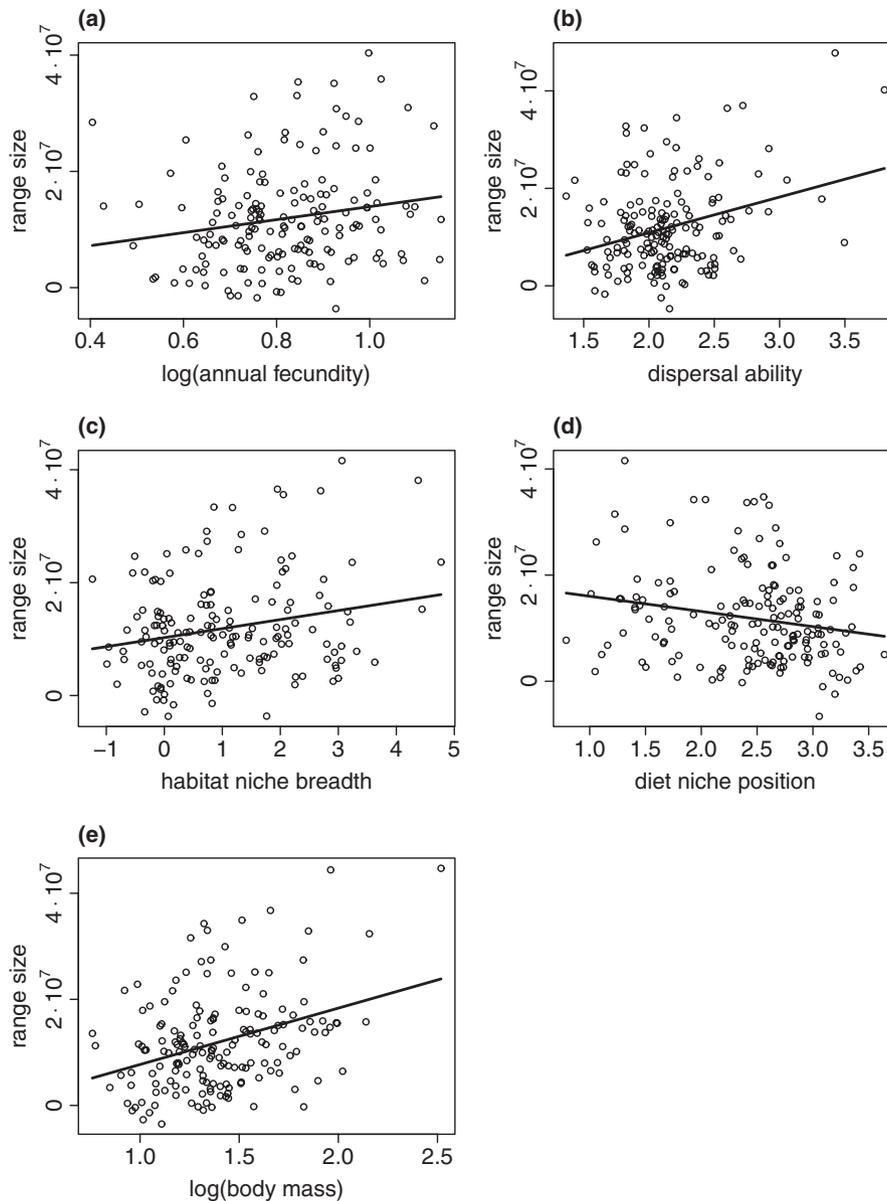


Figure 2 Leverage plots after Sall (1990) of bird traits with a significant direct effect on global range size: (a) log(annual fecundity), (b) dispersal ability, (c) habitat niche breadth, (d) diet niche position, (e) log(body mass), calculated from a multiple regression.

(Böhning-Gaese *et al.*, 2006). This suggests that not only trees, amphibians and reptiles (Svenning & Skov, 2004; Araújo *et al.*, 2008) but also birds might not have fully recolonized their potential geographic range since the last glacial period 20,000 years ago. It appears that, in the face of anthropogenic climate change, at least some bird species might not be mobile enough to track spatial shifts in their climate niche (Devictor *et al.*, 2008).

As shown by other studies (Hurlbert & White, 2007; Carrascal *et al.*, 2008), habitat niche breadth had a positive direct effect on range size, reflecting that the habitat niche directly constrains the area which can be colonized by a species. Species with a broad habitat niche also had higher fecundity, resulting in an additional positive indirect effect of habitat niche breadth on

range size. Species with broader habitat niches should find the optimal conditions for reproduction more frequently, achieving on average higher fecundity in a given area (Brown, 1984; Gaston *et al.*, 1997).

Contrary to habitat niche breadth, diet niche breadth did not have an effect on range size. Different food sources can occur side by side in the same site, while habitat types cannot. Therefore, it is not surprising that diet niche breadth is less limiting for a species' range size than habitat niche breadth. Furthermore, in regions intensively used and modified by humans, the ability to use anthropogenic food sources might be more important in determining range size than diet niche breadth (Böhning-Gaese & Oberrath, 2001). Finally, our classification of diet niche breadth was rather broad, and data taking the relative

consumption of finer classified diet items into account might give different results.

Bird species of a higher trophic level had smaller geographic ranges. This suggests that herbivorous birds indeed have more food biomass available than insectivores and are hence able to reach higher abundances and find enough food to sustain their populations in more places than insectivores. Note that no true carnivores (vertebrate-eating species) were included in this study. Inclusion of these species might give different results, as many carnivorous species (especially birds of prey) appear to have rather large geographic ranges (del Hoyo *et al.*, 1994).

We detected a positive indirect effect of migratory behaviour on range size, mediated via dispersal ability, while migratory flexibility had no effect. This link between migratory behaviour and dispersal ability has been described previously for passerines (Winkler & Leisler, 1992; Dawideit *et al.*, 2009).

By combining the traits in a path model it was possible to assess direct and indirect effects on range sizes. The benefit of such an analysis was best illustrated for habitat niche breadth, which had both direct and indirect effects on range size, by the presence of an indirect effect of migratory behaviour on range size in the absence of a significant direct effect and by body size showing direct and indirect effects influencing range size in opposite directions. The strong positive direct effect of body size on range size was moderated by two indirect negative effects, one via fecundity and the other via migratory behaviour and dispersal ability. The relationship between body size and range size has always been a matter of debate with published positive (Carrascal *et al.*, 2008), negative (Glazier, 1980), triangular (Brown & Maurer, 1987) and non-significant relationships (Virkkala, 1993). The present study demonstrates that a potential reason for these complex patterns might be the heterogeneity in mechanisms by which body size affects range size. Depending on the spatial scale of the analysis, the set of species analysed and other traits included in the study, this might result in positive, negative or no total effect of body size on range size.

Both life-history traits, three out of five ecological traits and one morphological trait showed significant direct or indirect effects on range size. Range size thus depended on the life history, ecology and morphology of species and ecological and morphological traits acted both via direct and indirect pathways. This underlines that range size is concurrently influenced by several traits via a number of different, simultaneously acting mechanisms.

Given that our path model was able to account for only a fraction of the total variability in range sizes, it is clear that important predictors were lacking from the model. We could not test three potentially important species traits in the model due to insufficient data: High relative brain size can influence the success of a species in a novel environment and the probability of exploiting novel food sources (Sol *et al.*, 2005) and may hence lead to large geographic ranges. Another trait that might influence range size is the position of a species' habitat niche: Species that prefer widespread habitats have larger geographic ranges than species preferring rare habitat types (Gregory &

Gaston, 2000; Hurlbert & White, 2007). Evolutionary age may also affect avian range size, with ranges increasing rapidly after speciation and then gradually declining again (Webb & Gaston, 2000). Furthermore, since our path model focused only on species traits, it does not incorporate a number of important factors which might also influence geographic range size: the climatic and geologic history of a species' habitat, the history of a species' distribution in space or biotic interactions with other species such as mutualism and pathogens (Orme *et al.*, 2006; Soberón & Ceballos, 2011).

In this study, we demonstrated how multiple, interacting traits have direct and indirect effects on range size. While our results apply to passerines, other bird groups may show different relationships between species traits and range size. Birds of prey, for example, have a high trophic level but frequently very large ranges. Looking beyond birds, it might be worthwhile to carry out similar studies with other groups of organisms for which similarly good data on traits and range sizes exist, e.g. mammals, amphibians, reptiles, butterflies or plants. For example, it has long been noted that, on average, birds generally have larger geographic ranges than mammals (Anderson, 1984), which might be explained by different direct and indirect effects of traits on the range sizes of the two groups. We expect that for other groups of organisms, other traits might prove to be important. For less mobile species, e.g. reptiles or plants, one may expect dispersal ability to have an even stronger effect than for birds, whereas for butterflies, diet niche breadth (of the larval stages) might potentially prove to be essential. While our path model represents a good hypothesis for how the species traits we measured influence range sizes, it is clear that those traits cannot fully explain inter-specific range size variation. We suggest that it is necessary to disentangle the direct and indirect influence of multiple other species traits and of factors related to the biogeographical and evolutionary history of species in order to better elucidate the mechanisms that generate macroecological range size patterns.

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Appendix S1 Study species.

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BIOSKETCH

Irina Laube is interested in understanding the interplay of species' ecology and evolution and how this influences range dynamics in space and time against the backdrop of past environmental change.

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