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PAPER

Niche conservatism in non-native birds in Europe: niche unfilling rather than niche expansion

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ABSTRACT

Aim Niche conservatism, or the extent to which niches are conserved across space and time, is of special concern for the study of non-native species as it underlies predictions of invasion risk. Based on the occurrence of 28 non-native birds in Europe, we assess to what extent Grinnellian realized niches are conserved during invasion, formulate hypotheses to explain the variation in observed niche changes and test how well species distribution models can predict non-native bird occurrence in Europe.

Location Europe.

Methods To quantify niche changes, a recent method that applies kernel smoothers to densities of species occurrence in a gridded environmental space was used. This corrects for differences in the availability of environments between study areas and allows discrimination between 'niche expansion' into environments new to the species and 'niche unfilling', whereby the species only partially fills its niche in the invaded range. Predictions of non-native bird distribution in Europe were generated using several distribution modelling techniques.

Results Niche overlap between native and non-native bird populations is low, but niche changes are smaller for species having a higher propagule pressure and that were introduced longer ago. Non-native birds in Europe occupy a subset of the environments they inhabit in their native ranges. Niche expansion into novel environments is rare for most species, allowing species distribution models to accurately predict invasion risk.

Main conclusions Because of the recent nature of most bird introductions, species occupy only part of the suitable environments available in the invaded range. This signals that apart from purely ecological factors, patterns of niche conservatism may also be contingent on population-specific historical factors. These results also suggest that many claims of niche differences may be due to a partial filling of the native niche in the invaded range and thus do not represent true niche changes.

Keywords

Biological invasion, birds, climate/environment matching, DAISIE, Europe, niche conservatism, niche equivalency, niche shift, niche similarity, species distribution modelling.

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INTRODUCTION

Recently, much consideration has been paid to niche conservatism, which states that niches are conserved across space and time (Pearman *et al.*, 2008). Several authors have argued that

conservatism of the environmental niche is the norm (Peterson *et al.*, 1999). For example, during the last deglaciation, evolutionary adaptation played a minor role, as species have generally migrated rather than shift their niche (Huntley, 1991). In contrast, species can also rapidly adapt to changing conditions.

McGraw & Fetcher (1992), for instance, germinated century-old seeds of graminoid plants and found that, when growing them in common conditions with recent seeds, they exhibited significant differences in their physiological response to temperature. The degree to which species adapt to novel environments is important to a range of topics in ecology and evolution (Wiens *et al.*, 2010), but is of special concern for the study of non-native species. Given the limited possibilities for eradication, preventing the establishment of non-native species is paramount (Genovesi, 2005). Species distribution models (SDMs), which combine information from point occurrence data and geographically referenced environmental variables to predict the large-scale geographical distribution of species, have become the main tool for predicting invasion risk (Elith & Leathwick, 2009). SDMs assume that non-native species distributions can be predicted from the native-range niche. However, numerous examples of rapid adaptation in non-native species suggest that rapid evolution may be common during invasions (Holt *et al.*, 2005). Indeed, recent studies have detected a mismatch between potential distributions of native and non-native ranges derived from SDMs (e.g. Broennimann *et al.*, 2007).

However, results of niche conservatism tests have been shown to depend on underlying statistical and conceptual assumptions, and only recently, Warren *et al.* (2008) proposed a solid conceptual framework by showing that detection of niche conservatism entails testing two hypotheses, namely niche equivalency (whether native and non-native niches are indistinguishable) and niche similarity (whether niches are more similar than expected by chance). Moreover, Petitpierre *et al.* (2012) pointed out that studies should discriminate between 'true' niche shifts (expansions into novel environments) and 'niche unfilling' (partial filling of the native niche in the invaded range). Here, we use occurrences of non-native birds in Europe and in their native range to study niche conservatism during invasion. To quantify niche changes, we use a recent method that applies kernel smoothers to species occurrence densities in the environmental space constrained by the axes of an ordination on a number of environmental variables (Broennimann *et al.*, 2012). The use of a kernel smoother makes the process of moving from geographical space to multivariate environmental space (where the niche analyses are performed) independent of sampling effort and the choice of resolution in environmental space. The method allows us to obtain unbiased estimates of niche changes even when the availability of environments differs between the ranges occupied by native and non-native populations. It should also be noted that the niches considered here relate to the Grinnellian niche concept, i.e. the response of species to a set of non-consumable environmental variables that influence their large-scale geographical distribution (Soberón, 2007).

Further, we formulate hypotheses explaining the variation in observed niche changes among species. First, propagule pressure helps to overcome genetic bottlenecks and environmental and demographic stochasticity, and by introducing adaptive genetic variation for new areas it can also facilitate the colonization of novel environments (Simberloff, 2009). Moreover, higher propagule pressure can increase effective population size, enhancing

the evolutionary response to new selection pressures. We therefore expect propagule pressure to scale positively with the amount of niche expansion and overlap but negatively with unfilling. Second, high population growth rates positively influence invasion success and the rate of geographical spread (With, 2002). Reznick & Ghalambor (2001) also suggest that population growth is a crucial attribute of rapid adaptation. Therefore, we predict that niche expansion and overlap will be greater and unfilling smaller for species with life-history traits associated with rapid population growth. Third, species-rich habitats can, through efficient resource preemption or high predation pressure, prevent or limit the establishment of non-native species (Levine *et al.*, 2004). Biotic interactions are usually associated with the Eltonian niche, which is defined by resource–consumer dynamics and biotic factors. The Eltonian niche relates to the fine-grained structure of distributions but can modify the limits determined by the Grinnellian niche (Soberón, 2007). Recent studies indicate that biotic interactions may impact the coarse-scale distribution of species (e.g. Gotelli *et al.*, 2010). Therefore, we hypothesize that species introduced into species-rich habitats will exhibit a lower niche overlap and expansion and more unfilling. Fourth, we hypothesize that recently introduced species will be characterized by a larger amount of niche unfilling and lower values for expansion and overlap, reflecting the fact that they may still be in the colonization phase (Petitpierre *et al.*, 2012). Fifth, native niche breadth is a predictor of invasion success (Blackburn *et al.*, 2009), and we predict that species with a broader native niche will exhibit higher niche overlap and expansion and less unfilling. Lastly, Holt *et al.* (2005) argue that niche expansion will be more likely when introductions are performed in locations that are environmentally marginal relative to the native niche. To test this, we investigate whether the amount of niche expansion is related to the distance (measured in environmental space) between introduction locations and the centre of the native niche.

We conclude by investigating the importance of niche conservatism for the use of SDMs by testing how well native-range-based SDMs can predict non-native bird occurrences. We hypothesize that predictions will be more accurate for species characterized by high niche overlap and low niche expansion.

MATERIAL AND METHODS

Occurrences and environmental variables

The distribution of non-native birds in Europe was extracted from the DAISIE database (Chiron *et al.*, 2009), which holds information on the locations to and years in which non-native birds were introduced to Europe. It contains distribution data of 75 non-native birds at a 50 km × 50 km grid resolution. Native range occurrences were obtained from range maps (BirdLife International & NatureServe, 2011). For each species, we excluded the areas occupied only during the non-breeding season or during migration, or that were outside its known altitudinal distribution limits. The resulting ranges were converted to grids with a resolution of 0.5° (c. 50 km) and occur-

rences assigned to the centre of the cells were used to characterize the native niche. We minimized spatial autocorrelation by randomly removing occurrences within 0.5° of each other. Only 28 non-native birds met the minimum sample size of five occupied cells required by the kernel smoothers used (see below). All analyses were subsequently restricted to these 28 species (see Appendix S1 in Supporting Information). To describe the environmental niche we employed eight bioclimatic variables and a measure of human impact. Previous studies have shown that bird distributions are influenced by temperature and precipitation gradients (Root, 1988) and we derived the following variables from Hijmans *et al.* (2005): annual mean temperature, mean temperature of the warmest month, mean temperature of the coldest month, temperature seasonality, annual precipitation, precipitation of the wettest month, precipitation of the driest month and precipitation seasonality. We also included the global human footprint (Sanderson *et al.*, 2002), an index of human influence on the environment.

Statistical framework for quantifying niche overlap

Niche overlap was measured in environmental space using a technique that corrects for differences in the availability of environments between study areas (Broennimann *et al.*, 2012). We used a principal components analysis (PCA) to transform the environmental space of the nine environmental variables into a two-dimensional surface defined by the first and second principal components. The PCA was calibrated using environmental data at all sites comprising the native and invaded areas (i.e. background data). The two PCA axes captured on average $76.1 \pm 2.9\%$ (range 70.6–81.4) of the variation. The scores of the occurrences of each species were then projected onto a 100×100 PCA grid of cells bounded by the minimum and maximum PCA values in the background data. A smoothed density of occurrence for each species in each cell of the PCA grid was then estimated using a kernel density function (Broennimann *et al.*, 2012). To calculate niche overlap, we chose the D metric (Rödder & Engler, 2011) because it expresses an overall fit between niches over the full environmental space and determines whether we can infer the characteristics of the non-native niche from the native niche. The D metric varies from 0 (no overlap) to 1 (complete overlap). Besides a PCA, we used several alternative ordinations, but these gave similar results (Appendix S2). Following Petitpierre *et al.* (2012), we calculated a niche expansion and niche unfilling metric. Niche unfilling is the proportion of species occurrence densities in the native distribution located in environments other than the non-native distribution. Niche expansion is the proportion of densities in the non-native distribution located in conditions other than the native distribution. Note that these metrics are calculated only on the environmental space that is shared between both ranges, and that expansions measured in this way represent true niche shifts: expansion into environments new to the species but available in the native range. Tests of niche similarity and equivalency followed randomization tests as outlined by Broennimann *et al.* (2012). Rejection of niche equivalency means that the niches of

native and non-native populations are not statistically equivalent, while a rejection of niche similarity indicates that niches are more similar than expected at random. To verify whether the variability in selected species occurrences (i.e. the variability introduced by the procedure described above to reduce spatial autocorrelation) influenced our analyses, we repeated all modelling procedures a hundred times. This is important for niche equivalency and similarity as these are based on a *P*-value of 0.05, and depending on the exact set of species occurrences chosen, the results may fall just above or below the significance threshold.

When estimating niches in a geographical context, the choice of the extent of the study areas to be compared is a crucial decision (Barve *et al.*, 2011). In principle, this area should cover the entire set of areas the species could potentially have encountered during the time since it has been present in the region. However, most studies default to using an arbitrarily defined study area (Peterson, 2011). Here, we adopt two different definitions of the study area and first use the whole of Europe as extent (the default background). Second, for each species, we georeferenced each introduction event in ArcGIS 9.3 and buffered it with a distance equal to the minimum invasion speed recorded for birds ($4.59 \text{ km year}^{-1}$, calculated from Blackburn *et al.*, 2009) multiplied by the number of years since its first known introduction (the 'environmental' background, Appendix S3).

Recently, Peterson (2011) raised concerns about niche changes based on occurrence and spatial environmental data because: (1) they use an excessive number of variables to characterize the niche, (2) do not adequately account for the effects of sampling, (3) apply statistical methods overfitting the input data, and (4) delineate inappropriate extents of study area. Here, we focus on a limited number of variables known to influence bird distributions and further reduce dimensionality via a PCA. Also, by applying a kernel density function, our estimates of niche overlap are independent of sampling effort. Moreover, by using ordinations to quantify niches we avoid the sometimes overfitted niches produced by SDM-based techniques. Lastly, to correctly discriminate between suitable and unsuitable environments for the species, we test two different backgrounds. Therefore, we believe that the criticisms of Peterson (2011) do not invalidate our analyses.

Drivers of niche changes

We used the following variables as potential determinants of niche overlap between native and non-native populations: propagule pressure (at species and community level), introduction history, the capacity of the species for high population growth rates, native species diversity and biogeographical origin. We calculated two propagule pressure variables: the total number of introduction events per species, and community-level propagule pressure (Blackburn *et al.*, 2008). To quantify community-level propagule pressure, for each species, we selected all locations where it has been introduced and counted all other non-native species that have been introduced at those locations. To describe introduction history, we compiled the median introduction date

for each study species (Appendix S4). To estimate the capacity for high population growth rates, we derived six relevant life-history traits from the literature: the number of broods, clutch size, incubation and fledgling period, body mass and age at first breeding (Jeschke & Strayer, 2006). We used the first axis of a PCA on these life-history traits as an indicator of a species' propensity for high population growth rates, as this axis reflects a slow–fast continuum in life-history variation (Appendix S5). Based on range maps of birds (BirdLife International & NatureServe, 2011) and mammals (IUCN, 2009), we first calculated the native bird and mammal species diversity for each 0.5° cell in Europe. We then derived the average number of birds and mammals that are present in the current distribution area of each non-native species in Europe (Appendix S6). We included the biogeographical region of origin of each species because invasion success may be higher if species are introduced to an area from the same or nearby biogeographical regions (Appendix S1). To characterize native niche breadth, we calculated three independent measures: native range size (derived from range maps), the number of breeding habitats and the number of food types used by each species. Following Cardillo (2002), we considered as habitat types saltwater or estuarine, fresh water, forest, woodland and scrub, open habitats, cultivated farmlands and urban areas. The food type categories were leaves and stems, seeds and grains, fruit and berries, pollen and nectar, vertebrate carrion, vertebrate prey and lastly invertebrate prey (Appendix S5). To elucidate whether niche expansion is more likely when species are introduced to areas environmentally marginal relative to the native niche, we first obtained, in the environmental space, the native niche centroid and then calculated its average distance to all introduction events of a species.

To find out which factors determine the amount of niche change detected, we used a generalized least squares (GLS) model (R library nlme) with as fixed effects median introduction date, number of introduction events, community-level propagule pressure, the population growth axis, biogeographical region of origin, native species richness, native range size and the number of habitats and food types used. To account for possible phylogenetic non-independence, we included a species-level phylogeny as a correlation structure in the model (Freckleton *et al.*, 2002). Our tree topology was derived from the supertree developed by Davis (2008, <http://linnaeus.zoology.gla.ac.uk/~rpage/birdsupertree>; Appendix S8). We assumed equal branch lengths and varied Pagel's λ from 0 to 1. For all analyses, models with Pagel's $\lambda = 1$ were the best (i.e. lowest Akaike information criterion value corrected for small sample size, AIC_c) and all analyses were thus performed with λ set to 1. We used a model selection procedure based on the AIC (Burnham & Anderson, 2002) and calculated AIC_c values for all possible models. Models were ranked based on their AIC_c values, and parameter estimates were evaluated by model averaging and by computing predictor weights (Burnham & Anderson, 2002). Holt *et al.* (2005) postulated that populations introduced far from their native niche will go extinct because of a strongly negative growth rate but that niche expansion is more likely when a population is initially close to the bounds of its

niche, as it may be able to persist long enough to adapt. Thus, a curvilinear relationship is expected between niche expansion and the distance of introduction locations to the centre of the native niche (introductions close the centre are within the native niche, introductions too far from the centre result in extinction). To test for such a relationship, we compared generalized additive models (GAMs; R library gam) by varying the degrees of freedom from one to four (one is a linear model).

Species distribution modelling

To evaluate the importance of niche conservatism for generating SDM-based predictions of invasion risk, we investigated the relationship between the predictive accuracy of native-range based SDMs and the amount of niche overlap, unfilling and expansion measured. SDMs were fitted using the same species distribution and climate data as the niche analyses. To avoid extrapolation of models beyond training conditions, we removed all non-analogous climates as identified by the environmental PCA (PCA-env). To account for the differing performance of SDM techniques, we made predictions of non-native bird occurrence using four different techniques (GLMs, boosted regression trees, random forest and MAXENT; R libraries BIOMOD and dismo). To evaluate model performance, we used the Boyce index, a presence-only evaluation statistic that varies from -1 to $+1$ (higher values indicate better models; Hirzel *et al.*, 2006). To examine how the amount of niche overlap, expansion and unfilling influences SDM performance, we ran linear mixed models with the Boyce index as the dependent variable and niche overlap, expansion, unfilling or total niche change (unfilling + expansion) as fixed variables. SDM technique and species (nested within bird family) were included as random effects and *P*-values were generated by Markov chain Monte Carlo sampling (R library language).

RESULTS

Niche changes

Niche overlap values did not differ significantly between models run with an environmental ($D = 0.15 \pm 0.13$, range 0.001–0.42) and a default background ($D = 0.15 \pm 0.12$, range 0.0007–0.39; paired *t*-test, $t = -0.33$, d.f. = 27, $P = 0.75$). The same was true for the tests of niche similarity, as the number of times that this hypothesis was rejected did not differ between the backgrounds (paired *t*-test, $t = -1.47$, d.f. = 27, $P = 0.15$) and for niche equivalency (which was rejected for all species in each model repetition regardless of the background used). The fact that these metrics did not differ between backgrounds suggests that the method used here accurately controls for environmental availability and landscape constraints. Therefore, in the remainder of this paper we report the results of default background models only.

The amount of niche overlap detected was rather small for all species (i.e. $D = 0.15 \pm 0.12$, Fig. 1), and did not vary strongly

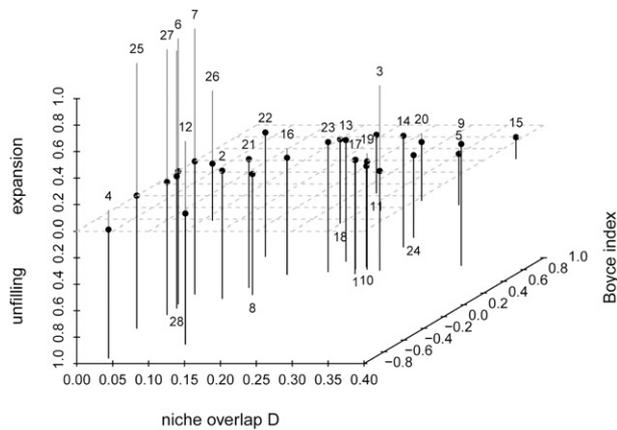


Figure 1 Niche changes and overlap between native and non-native ranges of 28 bird species that have invaded Europe. Vertical segments represent the magnitude of niche changes for each species. Extensions above (dark grey) and below (black) the zero plane indicate niche expansion and niche unfilling, respectively. Intersections with the zero plane are shown with filled dots. The horizontal plane represents a measure of niche overlap (the D metric) and the Boyce index, which evaluates how well native-range-based SDMs project onto analogue climates in the invaded range (i.e. Europe). For further explanation see the text. Key to species: 1, *Aix galericulata*; 2, *Aix sponsa*; 3, *Alectoris barbara*; 4, *Alectoris chukar*; 5, *Alectoris rufa*; 6, *Alopecurus aegyptiacus*; 7, *Amazona amazonica*; 8, *Anas acuta*; 9, *Anas penelope*; 10, *Anser anser*; 11, *Anser fabalis*; 12, *Anser indicus*; 13, *Athene noctua*; 14, *Aythya ferina*; 15, *Branta canadensis*; 16, *Branta leucopsis*; 17, *Colinus virginianus*; 18, *Estrilda astrild*; 19, *Leiothrix lutea*; 20, *Myiopsitta monachus*; 21, *Netta rufina*; 22, *Oxyura jamaicensis*; 23, *Passer hispaniolensis*; 24, *Perdix perdix*; 25, *Psittacula eupatria*; 26, *Psittacula krameri*; 27, *Syrnaticus reevesii*; 28, *Threskiornis aethiopicus*.

among the 100 model repetitions (Appendix S7). We found that only 29% (eight) of the species show more than 10% niche expansion whereas unfilling was much more common, as all species have more than 10% of their native niche unfilled in the non-native range (Fig. 1). Niche equivalency was rejected for all species, while the results of the niche similarity test are less straightforward, as for several species the results differed between runs (Appendix S7). For 12 species, niche similarity was never rejected, indicating that the native and non-native niches were no more similar to each other than expected by chance. Only two species (*Psittacula krameri* and *Leiothrix lutea*) always had non-native niches that were more similar to the native one than random expectations. For the remaining 14 species, the results were not univocal. For example, for Alexandrine parakeets (*Psittacula eupatria*), niche similarity was rejected in 52 out of 100 runs. The mean P -value of these similarity tests was 0.086 ± 0.11 (median 0.049), indicating that, depending on the exact set of occurrences selected and the way that the kernel smoothers are applied to the data, P -values fall just below or above the significance level.

Determinants of niche overlap, expansion and unfilling

Patterns of niche overlap were not explained by a single best model, since several models had similar AIC_c values (Appendix S8). However, AIC_c predictor weights showed that median introduction date was most frequently included in the best models (AIC_c weight 1.00), indicating that niche overlap is lower for more recently introduced species. All other variables had predictor weights lower than 0.57. A model with only median introduction date as a fixed effect explained 39.4% of the variance. Variation in niche unfilling was best explained by median introduction date (AIC_c weight 1.00) and the total number of introduction events per species (AIC_c weight 1.00). Niche unfilling is thus lower for species that were introduced earlier and more often. All other models had a $\Delta AIC_c > 2$ and the best niche unfilling model explained 39.0% of the variance. Niche expansion was not well explained by any model, as no variable had a predictor weight larger than 0.53. The relationship between the amount of niche expansion and the position of the introductions relative to the centre of the native niche was not curvilinear, as the best fit was obtained by a linear model (i.e. a GAM with one degree of freedom; $AIC = 32.1$, estimate and standard error 0.11 ± 0.063 , P -value 0.08). AIC values increased with increasing degrees of freedom, to $AIC = 35.9$ for four degrees of freedom).

Predictive performance of native-range based SDMs

The Boyce index varied from -0.77 to 0.85 (mean 0.38 ± 0.39 , median 0.41). This indicates that although the performance of native-range based SDMs varies strongly among species, in general, models reveal a fair transferability when used to predict non-native bird occurrences in analogue climates in Europe. As predicted, model performance correlated positively with niche overlap (1.79 ± 0.64 ; t -value 2.78, P -value 0.006) and negatively with niche unfilling (-0.95 ± 0.33 ; t -value -2.88 , P -value 0.005), niche expansion (-0.61 ± 0.19 ; t -value -3.14 , P -value 0.024) and total niche change (-0.53 ± 0.14 ; t -value -3.84 , P -value 0.0002). Similar results were obtained when calibrating the SDMs on the entire native range (Appendix S9).

DISCUSSION

Non-native birds in Europe do not occupy the same niche in the invaded range as in their native range, as niche overlap was low and niche equivalency was always rejected for each species. Niche similarity tests showed evidence for niche conservatism for up to 16 species, as their native and non-native niches were more similar to each other than random expectations in at least one model run. Differences between niches occupied in native and non-native ranges are mainly due to the fact that in the non-native range species occupy only a part of the available suitable environments. Expansion into novel environments is relatively rare, as only eight non-native birds in Europe have more than 10% of their non-native distribution outside their

native environmental niche. Thus, when taking into account the environments represented, non-native birds in Europe tend to occupy environments similar to the ones they inhabit in their native ranges, although only a subset of what is available.

This largely mirrors the findings of Petitpierre *et al.* (2012), who compared climatic niches of 50 plant invaders between Eurasia, North America and Australia and found that niche unfilling is more widespread than expansion. However, compared with our results, Petitpierre *et al.* (2012) found that plants showed more niche overlap ($D = 0.37 \pm 0.11$ for plants versus 0.15 ± 0.12 for birds; $t = -4.90$, d.f. = 33.7, $P < 0.0001$), and less unfilling (mean unfilling for plants 0.20 ± 0.21 versus 0.80 ± 0.22 for birds, Wilcoxon rank-sum test P -value < 0.0001) and expansion (mean plant expansion 0.051 ± 0.077 versus 0.26 ± 0.42 for birds, Wilcoxon rank-sum test P -value = 0.28). The differences between plants and birds could potentially be explained by their invasion histories: plants have been introduced earlier than birds (median introduction date for plants is the year 1750 compared with 1963 for birds). This implies that plants have had more time to spread and occupy the available environments while niche changes in birds more strongly reflect an ongoing colonization.

Indeed, when testing for the effect of introduction history, we find that birds that were introduced earlier exhibit a larger niche overlap. Given the relatively recent nature of most bird introductions, it is likely that dispersal limitations or lag-phase effects have prevented non-native birds from colonizing all suitable environments in Europe. Even when a species is introduced to a suitable location, several factors can hamper its expansion into otherwise suitable parts of the environmental space. Different processes such as Allee effects, dispersal barriers and biotic interactions can slow the spread of invaders (Okubo *et al.*, 1989; Taylor & Hastings, 2005; Sass *et al.*, 2010). Also, invasions often start with a small number of individuals, resulting in genetically impoverished populations, which hampers expansion. Indeed, populations often become invasive only after repeated introductions (Simberloff, 2009). The negative correlation between the total number of introduction events per species and the amount of niche unfilling suggests that introduction effort contributes to the degree to which niches are conserved during invasions. Increased propagule pressure can help a population expand its geographical range and environmental niche by buffering against environmental and demographic stochasticity and Allee effects. Moreover, when there is intraspecific variation in niche requirements across a species' native range, a non-native population that is drawn from a particular location may exhibit a niche that is only a subset of the species' entire niche (Peterson & Holt, 2003), resulting in a smaller overlap between native and non-native niches. Multiple introductions from a variety of sources can supply a more representative sample of the native genetic variation, enabling non-native populations to occupy an environmental space coinciding with the native niche. Also, the geographical disparity of introductions could influence the amount of niche unfilling. Indeed, the total number of introduction events per species is significantly correlated to the number of different grid cells and countries to which a species

has been introduced (Pearson $r = 0.96$ and 0.68 , respectively, $P < 0.0001$).

However, it remains unclear what drives differences in niche expansion among our study species. This may be at least partly due to the fact that only eight species showed niche expansion. Jeschke & Strayer (2005) found that when comparing birds native to Europe or North America introduced to the other continent, fewer North American birds spread in Europe than European birds in North America, and similar patterns have been observed for plants as well (Seastedt & Pyšek, 2011). Thus, the low prevalence of niche expansion found among non-native birds in Europe may reflect biogeographical patterns of invasibility of communities. In contrast with plant invaders, some of our species exhibit very high niche expansion values. An explanation might be that the distribution of birds is not as strictly governed by climate as it is for plants (Woodward, 1987; Beale *et al.*, 2008). Indeed, other factors such as brain size have been shown to increase invasion success by helping birds to cope with novel conditions (Sol *et al.*, 2005).

We did not find any relationship between niche change and native niche breadth. While niche breadth has been shown to enhance establishment success (Blackburn *et al.*, 2009), our result suggests that native niche breadth does not influence the colonization of novel environments beyond those present at the initial site of introduction. Niche change was also independent of native species richness. Empirical studies on biotic resistance to invasion have yielded conflicting results, which may be explained by covarying external factors at different spatial scales (Shea & Chesson, 2002). Several studies found that native and non-native species richness are positively correlated as they respond similarly to environmental gradients such as energy availability (Stohlgren *et al.*, 2003), while other findings suggest that conspecific attraction in concert with interspecific territoriality may result in spatially segregated distributions even at larger spatial scales (e.g. Gotelli *et al.*, 2010). Our results are in agreement with Chiron *et al.* (2009), who found that in Europe, native bird species richness is not correlated with non-native bird species richness, possibly because energy availability is more important at lower latitudes.

Clearly, more research on the ecology of non-native species in their new range is required to elucidate the conditions under which niche expansion can occur. Genetic admixture, hybridization and enhanced competitive strength have been suggested to facilitate or limit niche expansion (Petitpierre *et al.*, 2012), but it should be noted that also in the native range, dispersal barriers may prevent species from occupying suitable environments, leading to apparent niche expansion when these environments are colonized in the invaded range. Recently, Gallien *et al.* (2012) proposed a framework in which predictions of species presences and absences derived from a global model (built with all species occurrences using coarse-scaled bioclimatic variables) and regional distribution models (built with regional data only using fine-grained variables such as land use) are combined, whereby occurrences correctly predicted by regional models but not by the global model may indicate populations that are expanding their niche. The species showing niche expansions in

this study are prime candidates for such an analysis, although the availability of species distribution and environmental data at a finer scale is limited.

Despite the fact that over the last decades birds have been widely introduced across Europe and that rapid adaptation over comparable time-scales is not uncommon (e.g. see Urban *et al.*, 2007), niche expansion was relatively rare compared with unfilling. As the fundamental niche of a species cannot be quantified using empirical distribution data (Soberón, 2007), our analyses have compared the realized niches of native and non-native populations. The finding that realized non-native niches are, in the majority of cases, a subset of the realized native niche implies that SDMs can provide reliable predictions of invasion risk. Indeed, when building native-range based SDMs for non-native birds in Europe, we generally obtain fair model transferability.

CONCLUSIONS

Up to 16 of the 28 bird species that have invaded Europe show evidence for niche conservatism, but niche overlap was generally low. This is due to the fact that because of the recent nature of most bird introductions, species often occupy only a part of the suitable environments in the invaded range. Thus, apart from purely ecological factors, patterns of niche conservatism may also be contingent on population-specific historical factors. Colautti *et al.* (2006) argued that event-level factors such as propagule pressure should be accounted for before inferring process from patterns of invasion, and we suggest the same applies to the study of changes in the environmental niche during invasion. Niche expansion into novel environments was rare, suggesting that many claims of niche differences may be due to a partial filling of the native niche in the invaded range and thus do not represent true niche changes. An important avenue for future research is to identify the processes that give rise to true niche expansion, as the colonization of novel environments represents a real challenge for anticipating biological invasions.

ACKNOWLEDGEMENTS

D.S. is a post-doctoral researcher funded by the FWO Vlaanderen. O.B. was funded by the National Centre of Competence in Research (NCCR) Plant Survival, a research programme of the Swiss National Science Foundation. We thank the editors and two anonymous referees for their constructive comments.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Non-native bird species present in Europe.

Appendix S2 Niche overlap obtained by the alternative ordination techniques.

Appendix S3 Definition of the default background and the environmental background.

Appendix S4 Propagule pressure and invasion history variables.

Appendix S5 Life-history traits associated with population growth rates.

Appendix S6 Native bird and mammal species richness across Europe.

Appendix S7 Niche overlap, niche equivalency and niche similarity tests.

Appendix S8 Determinants of niche overlap, expansion and unfilling.

Appendix S9 Performance of native-range based species distribution models.

BIOSKETCH

Diederik Strubbe is a biogeographer at the Evolutionary Ecology Group of the University of Antwerp. He is mainly interested in biological invasions and in the use of species distribution models to test hypotheses about the factors controlling invasion success. Based on discussions with O.B., D.S. conceived the project, performed all analyses and led the writing. F.C. provided advice on the use of the DAISIE database and O.B. provided advice on the statistical methods used. All authors contributed substantially to the writing.

Editor: Vincent Devictor