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A global assessment of human influence on niche shifts and risk predictions of bird invasions

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Abstract

Aim: Estimating the strength of niche conservatism is key for predictions of invasion risk. Most studies consider only the climatic niche, but other factors, such as human disturbance, also shape niches. Whether occupation of human habitats in the alien range depends on the native tolerances of species remains unexplored. We assessed niche conservatism in climatic and human spaces for bird species showing different responses to humans in native ranges and evaluated whether considering anthropogenic niche variables affects invasion predictions.

Location: Global.

Time period: From 500 CE to the present day.

Major taxon studied: Birds.

Methods: We assessed niche conservatism by comparing the native and alien distributions of 150 bird species. We differentiated “niche expansions” into environments new to the species and “niche unfilling”, whereby a species fills its native niche only in part. Global predictions of alien bird distribution were generated using species distribution models (SDMs).

Results: Climatic niche similarity was higher than random expectation in 56% of species, and human disturbance niche similarity in 43%. Only 34 and 15% of species had >10% of their alien distribution in climates or human conditions, respectively, different from those of native ranges. Climatic niche expansions mostly involved colonization of colder and less seasonal climates. Human niche expansions involved colonization of more disturbed environments by species not responding positively to human influence in native ranges. Climatic and human niche unfilling was more common than expansions and was lower for species introduced earlier and those responding positively to human influence. Models including human variables do equally well for all species.

Main conclusions: Alien birds tend to invade areas with similar climatic and human conditions to their native range, but niche unfilling and expansions occur and relate to species native tolerances to human-modified habitats and first introduction year. Incorporation of human-related variables in SDM results in more accurate predictions for all species.

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KEYWORDS

alien species, climate, human disturbance, human tolerance, invasion risks, niche expansion, niche overlap, niche unfilling, species distribution models

1 | INTRODUCTION

Invasive species are a growing concern because of their significant deleterious effects on co-occurring native species (Millennium Ecosystem Assessment, 2005; Vilà et al., 2010) and on human socio-economic activities. Invasive species impose U.S.\$ billions in losses per year through their impacts on ecosystem services that are crucial to human health (e.g., clean water supplies) and the loss of natural resources, amenities (e.g., nature tourism) and agricultural production (Millennium Ecosystem Assessment, 2005; Vilà et al., 2010). As a consequence, policy-makers face increasing pressure to apply effective prevention and control measures to deal with biological invasions (Leung et al., 2002, 2012).

Species distribution models (SDMs; correlational techniques using associations between the environment and species occurrences to assess habitat suitability) have become major methodological tools for invasion risk assessments. Species distribution models are often used to estimate the geographical distribution of climates suitable for invasive species in adventive regions based on those used in native areas (and/or previously occupied alien ranges; Broennimann & Guisan, 2008), as a means of assessing the risk of invasion (Cardador et al., 2017; Thuiller et al., 2005). These models rely on ecological niche theory, which predicts that for relatively recent events, such as biological invasions, conservatism of the climatic niche is expected (Araújo & Peterson, 2012; Peterson, 2011). Although this framework seems to hold for a large fraction of naturalized populations in different taxa (Liu et al., 2017; Petitpierre et al., 2012; Strubbe, Broennimann, Chiron, & Matthysen, 2013), evidence is accumulating that some species can still have notable success in areas climatically distinct from those occupied in their native ranges (Broennimann et al., 2007; Early & Sax, 2014). For example, colonization of alien areas where conditions were different to those occupied in native ranges was apparent for nearly 30% of alien bird species established in Europe (Strubbe, Broennimann, Chiron, & Matthysen, 2013), for 14% of 50 Holarctic terrestrial alien angiosperms (Petitpierre et al., 2012), 55% of 22 globally invasive insect species (Hill, Gallardo, & Terblanche, 2017) and 33% of 30 Indo-Pacific tropical fishes invading the Mediterranean Sea (Parravicini, Azzurro, Kulbicki, & Belmaker, 2015).

Mismatches between broad-scale climatic conditions occupied in native and alien distribution ranges are often interpreted as evidence of species adaptations in response to selection pressures imposed by the novel environment. However, species occurrences and spatial climatic data used to characterize species niches by SDMs reflect the realized (i.e., the occupied) niche, not the fundamental niche: the locations in which species are found might not represent the full suite of climatic conditions in which the species can survive indefinitely, owing to constraints imposed by dispersal, biotic

interactions and the characteristics of the accessible habitat (Guisan, Petitpierre, Broennimann, Daehler, & Kueffer, 2014; Soberon & Peterson, 2005). Also, niche shifts may be contingent upon the environmental variables used (Strubbe & Matthysen, 2014). The heavy reliance of SDMs on macroclimatic variables might fail to account for other relevant factors, thus, leading to poor predictions. In particular, association with human-modified habitats in alien ranges has been proposed as one potential cause explaining the presence of alien species in areas climatically distinct at a broad scale from those occupied in their native ranges (Mori et al., 2020; Strubbe, Jackson, Groombridge, & Matthysen, 2015). This could occur because human-altered environments can allow species to gain access to new resource opportunities, such as supplementary feeding (Clergeau & Vergnes, 2011), or different microclimatic or microhabitat conditions with respect to more natural areas (Pickett et al., 2001) that might allow species to overcome physiological and resource limitations locally imposed by broad-scale climate. The inclusion of human-related variables in SDMs has thus been proposed as a simple and direct way to improve invasion risk predictions (Cardador & Blackburn, 2019; Strubbe, Jackson, et al., 2015).

However, whether all species have the same probability of occupying human habitats in alien ranges or whether this depends on the tolerances of species for anthropogenic environments in their native ranges remains poorly understood. This knowledge gap can have important implications for SDM performance, particularly when calibrated in native ranges. Thus, relying for predictions on human-habitat relationships from SDMs calibrated in native ranges fails to acknowledge that new relationships between species distributions and human variables might arise in alien ranges. This might be particularly the case for species that neither select nor avoid human habitats in their native ranges, because theory suggests a shift in occupancy towards more altered habitats and landscapes in the alien ranges (González-Moreno, Díez, Richardson, & Vilà, 2015). Phenotypic plasticity, evolutionary response to novel selection pressures or non-random colonization processes attributable to higher rates of alien species introduction (colonization pressure) and greater propagule pressure in human-altered environments could favour such a pattern (Blackburn, Lockwood, & Cassey, 2015; Lockwood, Cassey, & Blackburn, 2009).

In this study, we conduct the first global assessment of niche conservatism in climatic and human disturbance spaces for species showing different types of responses to human-modified habitats in their native ranges. For this, we compare the native and established alien ranges of 150 bird species that have alien populations worldwide. We analyse two distinct phenomena that may explain non-similarity in realized niches: “niche expansion” into environments new to the species and “niche unfilling”, whereby the species only fills its niche in part in the invaded range. It should be noted that the niches

considered here mostly relate to the Grinnellian niche concept, that is, the response of species to a set of non-consumable environmental variables that influence their large-scale geographical distribution (Soberón, 2007). We also assess how accounting for human-habitat variables in the native ranges can affect the performance of invasion risk (i.e., probability of occurrence) predictions derived from SDMs for different species. To that end, we conduct SDMs calibrated on occurrence data and climatic variables in native ranges that either ignore or incorporate human-related environmental variables to generate predictions of invasion risks and contrast them against real occurrence data in alien ranges. We test two alternative hypotheses. The first hypothesis is that human disturbance niche is conserved in alien ranges. If so, we expect higher accuracy for models integrating human-related predictors. Niche expansions in the climate space might be caused, in part, by human disturbance buffering against climate mismatches for species showing a positive response to disturbance only. The second hypothesis is that the human disturbance niche expands towards more altered environments in alien ranges. If so, we expect that niche expansions in climate space might occur because human disturbance buffers against climate mismatches for all species.

2 | METHODS

2.1 | Data compilation

We focused on all bird species that have been reported as established in the wild in at least one alien locality worldwide and for which mapped distributions were available (Cardador & Blackburn, 2019; Dyer, Redding, & Blackburn, 2017). Occurrence data at the species level for analyses were compiled from the Global Biodiversity Information Facility (GBIF, GBIF.org, 2018; for a complete list of GBIF occurrence downloads, see Supporting Information Table S1) and classified as pertaining to the breeding native range or invasive range according to BirdLife International and NatureServe (2014) and the Global Avian Invasions Atlas (Dyer, Redding, et al., 2017), respectively. Only data for the period 2000–2017 were used in analyses to match the temporal scale of human variables. Occurrence data were aggregated at 5 arcmin resolution, which corresponds approximately to 10 km × 10 km, which was considered to be adequate to capture the main responses of bird species to humanized environments (Cardador & Blackburn, 2019). Samples with reported geographical issues, location uncertainty >5 km or with central grid coordinates of atlases of >10 km resolution were removed from analyses. Duplicate samples at the 5 arcmin resolution were handled as single observations. Only introduced species with >50 locations (i.e., 5 arcmin cells) in native ranges were retained for subsequent analyses to maximize modelling accuracy (Stockwell & Peterson, 2002). Additionally, species with fewer than five locations in their alien range were disregarded, because this is the minimum sample size required for niche analyses proposed by Broennimann et al. (2012) using the library *ecospat* in R (see subsection 2.2). Final

occurrence data averaged $8,786 \pm 17,085$ locations in native ranges (mean \pm SD, range: 72–105,620) and $1,803 \pm 9,122$ (range: 5–66,749) in alien ranges ($n = 150$ species).

To describe the climatic niche, we considered eight bioclimatic variables (obtained from WorldClim, <http://www.worldclim.org/>; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) that are known to affect bird distributions (Cardador, Carrete, Gallardo, & Tella, 2016; Strubbe, Jackson, et al., 2015): annual mean temperature, temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation, precipitation of the driest month, precipitation of the wettest month and precipitation seasonality. However, annual mean temperature, temperature seasonality and annual precipitation were highly correlated with other climate variables ($r \geq .90$), and thus, removed from analyses (Cardador & Blackburn, 2019). As descriptors of human transformed environments, we considered two variables: (a) the Global Human Influence Index, which provides a weighed composite map of anthropogenic impacts including urban extent, population density, land cover, night lights and distance to roads, railways, navigable rivers and coastlines (Sanderson et al., 2002); and (b) the percentage of urban habitats, as a more specific descriptor of urbanization. The percentage of urban habitats at the 5 arcmin resolution was derived from data provided by the USGS Land Cover Institute (LCI) (<https://landcover.usgs.gov/>) at 500 m resolution.

2.2 | Niche analyses

We compared the realized climatic and human disturbance niches of species in the native ranges with the niches occupied by the same species in the alien ranges using the framework proposed by Broennimann et al. (2012). These analyses involved the following four steps: (a) definition of a two-dimensional gridded environmental space; (b) calculation of the density of occurrences along the two-dimensional environmental space using kernel smoothers; (c) measurement of niche overlap between native and alien densities of occurrence along the environmental space; and (d) statistical tests of niche similarity using randomization approaches. For climatic niche analyses, the gridded environmental space was that formed by the first two axes of a principal components analysis (PCA) on the five climatic variables considered (see above) in 5 arcmin pixels across the world. These axes explained 86% of the inertia. The first PCA axis (51%) predominantly represented temperature gradients (with higher values representing colder climates), whereas the second axis (34%) mostly represented precipitation gradients (with higher values representing drier climates with higher precipitation seasonality; Table S2). For the human space, the two axes represented the two human-related variables considered (i.e., the Global Human Influence Index and the percentage of urban environments). We then applied kernel smoothers to calculate the occurrence density across the environmental gradients for each species. Overlap between occurrence densities in native and alien ranges was measured using the Schoener's *D* metric (Broennimann et al., 2012; Warren,

Glor, & Turelli, 2008). This index indicates the overall match between environmental conditions covered by occurrence densities in native and alien ranges, that is, how much the realized niche in the native area is similar to the niche in the alien range, and ranges between zero (no overlap) and one (complete overlap).

Following Petitpierre et al. (2012), we also divided non-overlap situations into cases of “niche expansion” into environments new to the species and “niche unfilling”, whereby the species fills its niche in the alien range only in part. Niche expansion was calculated as the proportion of alien occurrence densities in conditions different from those covered by the native distribution, and niche unfilling as the proportion of native occurrence densities in conditions not occupied in the alien range. To define native and alien ranges for analyses, we considered the complete gradient of climatic and human conditions that the study species could have reasonably encountered, including consideration of dispersal ability and major biogeographical barriers (Barve et al., 2011; Soberon & Peterson, 2005). In the case of alien ranges, we expected that the area accessible for newcomers would be affected most by the time and distance since first introduction, and thus, we used the methodology proposed by Strubbe et al. (2013; Strubbe, Jackson, et al., 2015) to define these ranges; that is, we buffered each alien occurrence locality with a distance equal to the minimum invasion speed recorded for birds [i.e., 4.59 km/year, derived from Blackburn, Lockwood, & Cassey (2009)] multiplied by the number of years since introduction. In contrast, in native areas dispersal is not expected to be so limited by time, but by major biogeographical barriers. Thus, we considered all biomes occupied by each species in its native ranges (Cardador et al., 2017; Strubbe, Jackson, et al., 2015). Finally, we assessed niche conservatism by conducting niche similarity tests. Similarity tests assessed whether the observed overlap between realized niches in the alien and native ranges was greater than would be expected by chance. For this, a measured niche overlap was compared against a null distribution of 100 simulated overlap values (obtained by drawing occurrences in the alien range at random). Note that niche expansion and unfilling were calculated only on the environmental space that was shared between native and alien ranges, and that expansions measured in this way represent true realized niche shifts (i.e., expansion into environments new to the species but available in the native range).

2.3 | Species distribution modelling

Invasion risk predictions were derived from an ensemble model of three techniques (generalized linear models, MAXENT and random forest) using the R library biomod2. Ensemble models reflect the central tendency of individual models and reduce the uncertainty related to particular modelling approaches (Araújo, Whittaker, Ladle, & Erhard, 2005; Zhu & Peterson, 2017), although they do not always outperform individual models (Qiao, Soberón, & Peterson, 2015; Zhu & Peterson, 2017). To address our question, we followed a hierarchical approach and ran models with two different combinations of the predictors, namely: (a) climatic models that included only

climatic predictors (CLIM); and (b) full models that included both climatic and human-related predictors (CLIM + HUM). Both the linear and quadratic terms of the predictors were considered. Models were calibrated using only occurrence data in native ranges. Although it is generally accepted that the potential range distribution of invasive species is best addressed using its global coverage (Broennimann & Guisan, 2008), we used only native information for model calibration because the focus of this study was not to produce the best-fitting model in the alien range, but to determine the role of climatic and human-disturbance similarity between native and alien ranges on model predictions. Models were run with a single set of 10,000 pseudo-absences randomly drawn from all biomes occupied by each species across its native ranges (Cardador et al., 2017; Strubbe, Jackson, et al., 2015). Presences and pseudo-absences were weighted as such to ensure neutral (0.5) prevalence. To reduce the potential effect of sampling biases in the data, a bias file was created by retrieval from GBIF occurrence data at the family level for each species (Cardador & Blackburn, 2019; Elith, Kearney, & Phillips, 2010). Occurrence data from species in the same taxonomic family are expected to suffer from the same detection limitations, reducing the effect of sampling biases in observed distribution patterns. We derived a kernel density map of sampling bias at a 5 arcmin resolution using ArcMap v.10.5 to be included in all models. To account further for uncertainty in the data, we conducted 10 replicates for each model by dividing the occurrence data into random training (70%) and test (30%) data sets. For each species, ensemble models were generated as averaged means of all models conducted. Ensemble models showed good performances in the training region (area under the receiver operating characteristic curve > 0.8 and true skill statistic \geq 0.6 for all species) and were thus used to generate predictions in the adventive regions. Sampling bias was set to its maximum value for model predictions.

The SDM-based predictions were tested against real occurrence data in alien ranges using the Boyce index, which ranges from minus one to plus one, with higher values indicating higher match (Hirzel, Gwennarëlle, Helfer, Randin, & Guisan, 2006). As background points for such analyses, we followed the framework proposed by Strubbe et al. (2013; Strubbe, Jackson, et al., 2015) as for niche analyses (see subsection 2.2).

2.4 | Effect of species responses to humans in native ranges on niche shifts and prediction accuracy

Species were classified in different categories according to their responses to the Global Human Influence Index (hereafter, referred to as “response to human influence”) and percentage of urban land (hereafter, “response to urbanization”) in their native ranges, following Cardador and Blackburn (2019). Five types of responses were considered for human influence and urbanization responses [no response, positive, negative, convex (i.e., positive response to high and low values) and concave (i.e., positive response to intermediate values)]. This classification was based on linear and quadratic estimates of the response to human influence and percentage of urban land

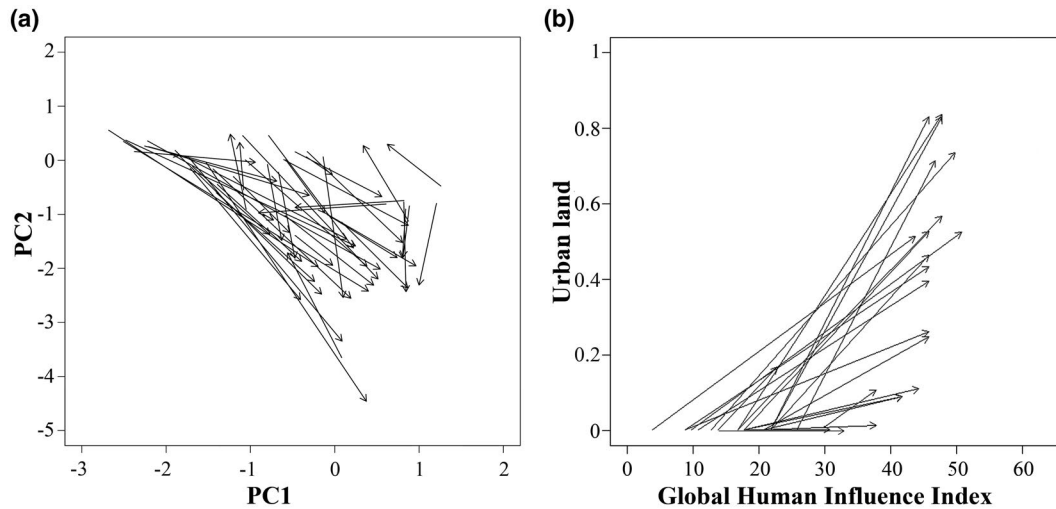


FIGURE 1 Shifts of the niche centroids between native and alien species distributions. Arrows link the centroids of the native and alien distributions of those alien bird species showing >10% niche expansion in climatic (a) and human disturbance (b) spaces. PC, principal component

fitted in generalized linear models (GLMs) also containing climate variables and sampling bias (as described above) as fixed effects and with species occurrences as the response variable (binomial error distribution and logit-link function) (Cardador & Blackburn, 2019). Models were run with a single set of pseudo-absences including locations from all biomes covered by the native range of each species, as in previous analyses. We conducted 10 replicates for each model by randomly selecting for each replicate 70% of the data for each species. A stepwise approach based on Akaike's information criterion was used to avoid model overfitting in GLMs [but results from models including all variables were highly consistent (Cardador & Blackburn, 2019)]. Final model predictions were generated as averaged means across replicates.

We assessed whether niche overlap, expansion and unfilling in climatic and human disturbance spaces (response variables) varied according to species responses to human influence and urbanization in native ranges (categorical variables with five levels) by using GLMs (Hill et al., 2017; 2015; Strubbe, Jackson, et al., 2015). To account for potential effects of differences in introduction histories among species (Strubbe et al., 2013), we also included the year of first introduction of each species as a covariate in models (Strubbe, Beauchard, et al., 2015). This information was available for 148 of the 150 species in the study by Dyer, Redding, et al. (2017).

Prediction accuracy measured by the Boyce index was also compared among species showing different types of responses to human influence and urbanization in native ranges by using GLMs including the model (CLIM versus CLIM + HUM), the type of response to human influence and urbanization, and their interactions as fixed effects. To avoid overparameterization, we conducted two different GLMs, considering alternatively the interaction: (a) between the model and response to human influence; and (b) between the model and response to urbanization in native ranges. First introduction year was also included in these GLMs as a control variable. To assess whether improvements in model performance were better than

expected by chance due to the inclusion of any two variables, we repeated our analyses by considering a third type of model (CLIM + RAND) including climate variables and two null variables obtained by assigning the worldwide values of urban percentage and human influence at random.

3 | RESULTS

3.1 | Climatic niche shifts

Climatic niche overlap between native and alien ranges was more similar than expected by chance (niche similarity tests $p < .05$) for 56% of considered species (Schoener's D : mean \pm SD, $.20 \pm .15$, $n = 150$). The magnitude of climatic niche expansion averaged $12 \pm 20\%$ ($n = 149$ because one species showed no shared environmental conditions in native and alien ranges and expansion was not computed), with >10% climatic niche expansion observed for 34% (50) of species. Niche unfilling (mean \pm SD, $26 \pm 29\%$, $N = 149$) was more common, with 54% of the species (81) having >10% of their native niche unfilled in the alien range. For most species, climatic niche expansions were related to shifts along both the first and second PCA axes of the climate space, indicating colonization of colder and less seasonal areas with respect to their native distributions (Figure 1a; Supporting Information Figure S1). No significant relationship between climatic niche expansion and response to human influence (Figure 2a) or urbanization in native ranges or year since first introduction was observed (Supporting Information Table S3). In contrast, year of first introduction had an influential effect on climate niche overlap (estimate = -0.0003 ± 0.0001 , $p < .001$) and unfilling (estimate = 0.0005 ± 0.0001 , $p < .001$), with higher amounts of niche overlap and lower niche unfilling (Figure 3a) observed for species introduced earlier (Supporting Information Tables S4 and S5). A significant effect of the response to human influence in native

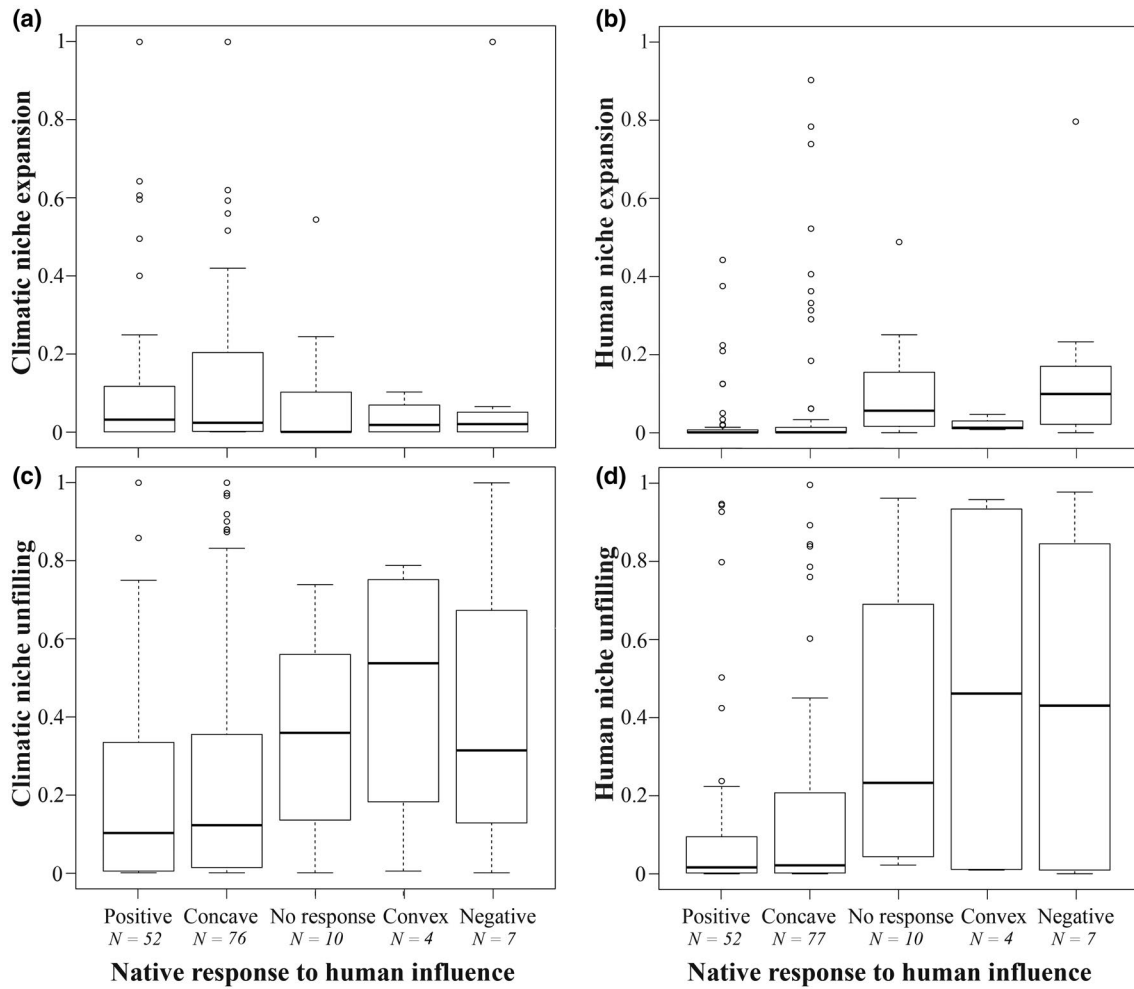


FIGURE 2 Niche expansions (a,b) and unfilling (c,d) in climatic (a,c) and human disturbance (b,d) spaces in relationship to responses to human influence in native ranges are shown. *n* = sample size for each category

ranges on climatic niche overlap and unfilling was also observed (Supporting Information Tables S4 and S5). Species showing positive responses to high (positive responses) or intermediate (concave responses) values of human influence showed a higher amount of niche overlap and lower climatic niche unfilling (Figure 2c; Supporting Information Tables S4 and S5).

3.2 | Human disturbance niche shifts

Niche overlap in the human disturbance space was more similar than expected by chance for 43% of considered species (Schoener's *D*: mean ± *SD*, .29 ± .17, *n* = 150). The magnitude of human disturbance niche expansion averaged 6 ± 16%, with >10% human disturbance niche expansion observed for 15% (22) of species. Niche unfilling (mean ± *SD*, 18 ± 29%) was more common, with 35% of the species (52) having >10% of their native niche unfilled in the alien range. Niche expansion mostly involved the colonization of more disturbed environments in terms of human influence and urbanization (Figure 1b; Supporting Information Figure S2) and was significantly lower for species showing positive responses (estimate: -0.17 ± 0.07,

p = .013) to human influence in their native ranges (Figure 2b; Supporting Information Table S6). Support for greater expansions in species with later introduction dates (estimate: 0.00014 ± 0.00007, *p* = .042) was also observed. The year of first introduction also influenced niche overlap (estimate: -0.0003 ± 0.0001, *p* < .001) and unfilling (estimate: 0.0005 ± 0.0001, *p* < .001) (Figure 3b; Supporting Information Tables S7 and S8). Significantly higher human niche overlap for species showing positive responses to human influence in native ranges (Supporting Information Table S7), and lower niche unfilling for species showing positive responses to high (positive) or intermediate values (concave), was also observed (Figure 2d; Supporting Information Table S8).

3.3 | Human-habitat associations and invasion risk predictions

When considering climatic variables only, the performance of SDM predictions in alien ranges measured by the Boyce index averaged .21 ± .53 (mean ± *SD*; median: .29). The inclusion of human-related variables in models improved model performance

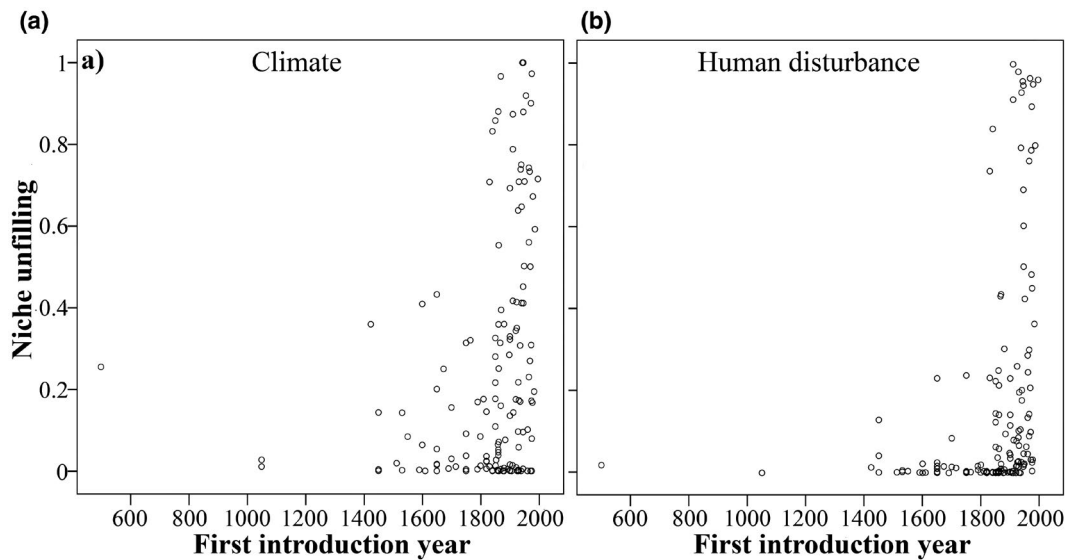


FIGURE 3 Relationship between niche unfilling in climatic (a) and human disturbance (b) niche spaces versus the year of first introduction of each species

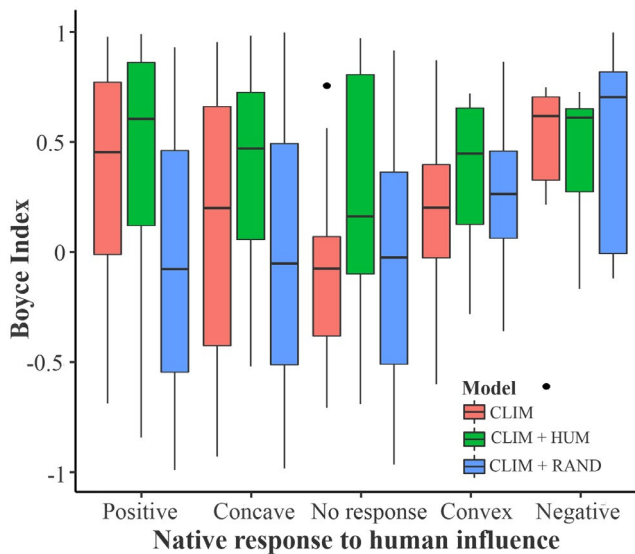


FIGURE 4 Accuracy of predictions in alien ranges according to variables used in models (only climate, climate plus human variables or climate plus random variables) and species responses to human influence in native ranges

($p \leq .001$; Figure 4; Supporting Information Table S9), with the resulting Boyce index averaging $.43 \pm .44$ (mean \pm SD; median .50). Increases in model performance were significantly better than expected by chance ($p < .001$; Figure 4). No significant interaction between model (CLIM versus CLIM + HUM) and the type of response to human influence or urbanization in native ranges was found (Supporting Information Table S9), but model performance was significantly better for species showing positive responses to human influence (Figure 4; Supporting Information Table S9).

4 | DISCUSSION

Alien bird species show a strong propensity to conserve their native niche in their alien ranges, in terms of associations with both climate and human disturbance. Although niche overlap between alien and native ranges was, in general, low and not more similar than expected by chance for all species, niche expansions into novel environments were relatively rare. Only 34 and 15% of species had $>10\%$ of their alien distribution in climates or human disturbance conditions different from those occupied in their native ranges, respectively. The observed niche differences appeared to be, thus, largely related to the fact that bird species occupied only a part of all suitable habitats in the alien ranges (Petitpierre et al., 2012; Strubbe et al., 2013). These results are in agreement with previous findings for other taxonomic groups and geographical scales (Petitpierre et al., 2012; Strubbe et al., 2013) and are probably related, at least in part, to time-limited population growth and dispersal from introduction locations, as suggested by the significant effect of year of first introduction (Supporting Information Tables S4–S5 and S7–S8). Notably, the species response to human influence in the native ranges appears to be a relevant (albeit not the only) factor influencing niche changes.

The positive effect of the response to human influence in native ranges on climatic niche overlap, and its negative effect on niche unfilling (Figure 2b), might reflect the benefit of environmental matching for these species, owing to their introduction to human-altered environments to which they are already adapted (Hufbauer et al., 2012; Sol, González-Lagos, Lapedra, & Díaz, 2017). Other species are able to expand their niche towards more disturbed environments in alien ranges, but it might be the case that only those with prior adaptations are able to use human resources efficiently, meaning that they can attain higher population sizes and spread towards suitable areas more rapidly. Species tolerant to human-modified environments can also possess particular traits that allow them to

deal better with novel environments in general, such as enhanced behavioural plasticity (Sol, Lapiedra, & González-Lagos, 2013; Sol et al., 2017), which might, in turn, favour geographical expansion. Given that species selecting human habitats in native ranges are expected to be introduced more frequently and also in higher numbers (Cardador & Blackburn, 2019; Hufbauer et al., 2012), higher propagule pressure could also favour geographical expansion towards suitable climatic and human conditions, and thus, lower niche unfilling, by avoiding stochasticity and population demographic processes (e.g., Allee effects) in newly colonized sites (Blackburn et al., 2015; Facon et al., 2006).

As expected, expansion in human disturbance space mostly involved colonization of more disturbed environments by species not responding positively to human influence in their native ranges (Figure 1b). Such a pattern could be explained by different factors. Colonization pressure and propagule pressure are higher in humanized environments, increasing the probability of introduction and establishment in such environments in alien ranges. Although establishment success has previously been shown to be lower for species not affected or negatively affected by human habitats in their native ranges (Cardador & Blackburn, 2019), it is possible that the few species that succeed do so in humanized environments. Behavioural or evolutionary responses to new selection pressures could be behind such shifts. In the case of species not responding to human influence in native ranges (i.e., those whose native distribution is mostly influenced by climate), it is also possible that as those species come from more natural areas, the low exposure to human-altered environments in native ranges has provided those species with relatively few opportunities to colonize such environments (and thus, human tolerance is not captured by their realized niche), even if they are capable of exploiting human-modified habitats (i.e., they are part of their fundamental niche). It is also possible that at least some of these latter species simply do well in both types of environments (human or not).

Given that invasion is a dynamic process, it is also worth noting that some of the species analysed might spread or die out in the future. This seems likely to explain the major role of the year of first introduction in present-day unfilling rates, but also the support for a positive effect of the year of first introduction in human disturbance niche expansions. Thus, for more recently introduced species, current distributions might reflect the characteristics of the new introduction localities rather than optimum environmental conditions, which might be more likely to be moved into during spread (Abellán, Tella, Carrete, Cardador, & Anadón, 2017). Variation in the type and origin of species transported over recent centuries could also be behind temporal differences (Cardador & Blackburn, 2019; Dyer, Cassey, et al., 2017).

Regarding climatic niche expansions, neither response to humans in native ranges nor year since first introduction appears to be a good predictor of current observed patterns. For most species, climatic niche expansions were related to colonization of colder and less seasonal areas with respect to their native distributions (Figure 1a). This pattern is in agreement with recent studies showing

that physiological tolerances to cold are less conserved than tolerances to heat (Araújo et al., 2013). However, the observed broad-scale climatic mismatches might not necessarily reflect real shifts in physiological tolerances. In this sense, associations with human habitats in alien ranges could also explain the observed pattern in part. The heat island effect is one of the best-documented climatic features of human settlements (Pickett et al., 2001). Human habitats might also provide supplementary food provisioning and low predator/competitor densities with respect to natural areas (Clergeau & Vergnes, 2011; Pickett et al., 2001; Sax & Brown, 2000). These conditions might be especially favourable for birds during winter, when climatic conditions are harsh and food is in poor supply.

From an applied point of view, accounting for human variables in SDMs resulted in significant improvements in predictions of invasion risk. Although the performance of SDMs varies strongly among species, models accounting for both climatic and human factors have, on average, a fair transferability to adventive regions, particularly taking into account that a large portion of suitable habitats might still not be occupied (Cardador et al., 2016; Petitpierre et al., 2012; Strubbe et al., 2013). This result supports and generalizes the conclusion of Strubbe, Jackson, et al. (2015), based on the invasion of the ring-necked parakeet in Europe, that the incorporation of data about human influence in models calibrated in native ranges might result in a more accurate assessment of invasion risks. Although differences in responses to human influence in native ranges seem to affect the magnitudes of realized niche expansions, no significant differences in model improvements across species responding differently to humans were found. This might be explained, at least in part, by the low magnitude and proportion of species showing niche expansions. However, model performance was better for species responding positively to human environments for which niche unfilling and expansion were lower.

Estimation of the strength of niche conservatism and its potential drivers is relevant to predicting the fate of introduced species (Early & Sax, 2014; Perret, Leslie, & Sax, 2018; Strubbe et al., 2013). Although most studies of niche shifts consider only broad climatic niches, our results support the idea that niche shifts are rare but might also occur at other relevant environmental niche axes (i.e., those related to the presence of human habitats) (González-Moreno et al., 2015; Hill et al., 2017). Studies attempting to understand the role of human activities in invasion success have mostly focused on the introduced range of alien species. There, the often-found relationship between alien species occurrence and human-altered habitats (Sax & Brown, 2000) has been interpreted as the result of increased chance of repeated introductions and large propagule pressure in humanized environments (Gallardo & Aldridge, 2013; McKinney, 2002), the reduction of biotic resistance and predation from the more species-poor recipient native communities (Case, 1996) and the availability of diverse niche opportunities in human-altered habitats (Hobbs & Huenneke, 1992; Sol, Bartomeus, & Griffin, 2012). Our results support the hypothesis that associations with human-altered environments in alien ranges could also reflect the ability of some

alien species to use and thrive in those environments in their native ranges, with important consequences for climatic niche filling. Taking into account that ever-increasing rates of human-induced transformations worldwide are expected to lead to an increase in the transport and introduction of species adapted to human-modified environments, particularly for taxa introduced involuntarily in long-distance transport channels (Hufbauer et al., 2012), increasing rates of invasion and geographical expansion could occur in the future. Additionally, further expansions to more natural habitats would be expected, because the alien geographical ranges of current alien bird species might be limited by time (Abellán et al., 2017; Cardador et al., 2016; but see Dyer, Franks, et al., 2016). Our findings help to fill the current gap in our understanding of the mechanisms that might allow alien species to fill and expand their niches at new locations and might help to improve our capacity to assess invasion risks accurately.

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DATA AVAILABILITY STATEMENT

All data used in this manuscript have already been published or archived and can be accessed via Figshare <http://dx.doi.org/10.6084/m9.figshare.4234850> (Dyer, Redding, & Blackburn, 2016), GBIF.org (2018) (for a complete list of GBIF occurrence downloads, see Supporting Information Table S9), the WorldClim database (Hijmans et al., 2005), available for download from <http://www.worldclim.org>, 0.5 km MODIS-based Global Land Cover (Broxton, Zeng, Sulla-Menashe, & Troch, 2014), available for download from https://archive.usgs.gov/archive/sites/landcover.usgs.gov/global_climatology.html, and BirdLife International & NatureServe (2014), available for download from <http://datazone.birdlife.org/species/requestdis>

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BIOSKETCHES

Laura Cardador is a post-doctoral researcher interested in spatio-temporal patterns of species distribution and the ecological mechanisms driving these patterns, paying particular attention to the conservation and management implications.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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