Research Article

Human-habitat associations in the native distributions of alien bird species

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Summary

1. The role of human tolerance is increasingly being proposed as a key driver of invasion success by alien species. Human habitat associations may first facilitate transport, making a species more available for introduction, and also facilitate establishment by creating environmental matching between human-altered habitats at the sites of origin and introduction. Nevertheless, the assumption that alien species exhibit associations with human habitats in their native ranges has been largely overlooked.

2. We conduct the first global assessment of the relative importance of human habitat associations in shaping the native distributions of species introduced worldwide, in relation to other key important drivers, i.e., climate and land-use. For this, we applied deviance partitioning analysis and species distribution models (SDM) to 776 introduced alien bird species from five continents.

3. While an independent effect of climate, and a joint effect of climate and non-urban land uses, appear as major factors governing alien species distribution in their native ranges, significant independent contributions of anthropogenic variables were found for most species. The effect of anthropogenic variables was mostly positive, or concave with highest responses at intermediate values. Notably, human-habitat associations in the native distributions of alien birds were significantly higher than expected relative to a pool of available species from the same bird families (N=3,565). Thus, introduced alien birds are a non-random sample with respect to their association with human-

altered habitats. Nevertheless, an increase in introduction rates of species showing no response, or a negative response, to human influence has occurred over recent decades.

4. To prevent invasions, understanding which species are most likely to become successful aliens outside their native range is essential. Our results support the hypothesis that association with humans may be an important driver of alien bird species distribution in their native ranges, and thus increase the likelihood that these species will end up being introduced and established. To provide policymakers with robust predictions of invasion risk, we recommend including human habitat associations in invasion risk assessments, and accounting for them in species distribution models.

Keywords: anthropocene, biological invasions, human-tolerant species, invasive exotic birds, environmental-matching, SDM, transport

Introduction

Biological invasions are a concern because they impose significant negative impacts on native species, ecosystems and human societies (Millennium Ecosystem Assessment 2005; Vilà *et al.* 2010). Many thousands of species have established alien populations worldwide, and there is no evidence that the rate of accumulation of aliens is slowing down (Seebens *et al.* 2017). Awareness of the negative impact of biological invasions and the critical need for effective management have led to an extended body of research assessing the factors driving invasion success so as to predict invasion outcomes (e.g., Blackburn *et al.* 2009; Vall-Llosera and Sol 2009; Dyer *et al.* 2017).

Event-level factors, such as propagule pressure or time since first introduction (Blackburn, Lockwood & Cassey 2015; Abellán *et al.* 2017), and species-specific life history traits (Sol *et al.* 2012) have been described as key drivers of the invasion process, determining both the establishment success of introduced species, and the subsequent extent of spread of established species across the new environment (Blackburn, Lockwood & Cassey 2015; Dyer *et al.* 2016; Abellán *et al.* 2017). Additionally, the hospitability of the environment where a species is introduced might greatly affect invasion success (Duncan *et al.* 2014; Abellán *et al.* 2017). Climate – and in particular climate matching to native ranges – is generally considered as a major environmental range-limiting factor of invasive species distribution, especially at large spatial scales (Cardador *et al.* 2016; Abellán *et al.* 2017). Other biotic and abiotic factors have also been widely recognized to influence invasion process but are less well-understood (Levine, Adler & Yelenik 2004; Gallardo, Zieritz & Aldridge 2015). One factor that has recently attracted attention is the extent to which being associated with human-altered environments allows organisms to better negotiate the different stages of the invasion process.

Growing evidence suggests that alien species tend to proliferate in human-altered habitats in introduced ranges that most native species are unable to use (Sax & Brown 2000). This pattern has been classically explained in terms of human-related alterations making the environment easier to invade by reducing biotic resistance and offering new niche opportunities (Sol *et al.* 2017b). However, the pattern can also be interpreted as reflecting the variety of ways human activities may influence the invasion process. These include an increased chance of repeated introductions and large propagule pressure in humanized environments (McKinney 2002; Gallardo & Aldridge 2013). Human activities may also facilitate environmental matching by increasing the likelihood that a species that relies on human-altered environments in their area of origin ends up established in such type of environments after being introduced. For birds, for example, there is increasing evidence that traits associated with tolerance to urbanization in introduced alien species' native ranges (Evans *et al.* 2011; Sol *et al.* 2014, 2017b) are also related to the establishment success of human-driven introductions. While these alternative hypotheses are theoretically sound, the crucial assumption that alien species exhibit human habitat associations in their native ranges has surprisingly been largely overlooked (with the exception of plants, for which a high proportion of naturalised alien species show associations with human-disturbed environments in their native ranges, Kalusová *et al.* 2017).

Understanding the relationship of alien species with human-altered habitats in their native distributions is not only essential to unravel the pathways of invasions, but it is also relevant because critical biological adaptations in relation to human activities that might favour invasions might also occur within introduced alien species' native ranges

(Rey *et al.* 2012; Hufbauer *et al.* 2012). For some insects, for example, human alterations have been shown to lead to major evolutionary changes (i.e., thermotolerance adaptation) within species' native ranges that might later constitute prior adaptations when introduced in new areas (Foucaud *et al.* 2013). Moreover, better understanding the relationship of human factors to species' native distributions also has relevance for predictions of invasion risk. Notably, species distribution models (SDMs, phenomenological models that statistically relate observed species occurrences to environmental variables) play a critical role in invasion risk assessments, relying mostly on an assumption of conservatism of the climatic niche (Jiménez-Valverde *et al.* 2011; Guisan *et al.* 2014). However, recent studies have shown that this approach could be hampered by apparent mismatches between native and invasive distributions derived from SDMs. While such differences are often interpreted as niche shifts reflecting evolutionary changes, mismatches may be also contingent upon the environmental variables used (Strubbe & Matthysen 2014). In particular, the failure to incorporate relevant factors of species distribution, such as human factors, that might modify distributional limits set by climate might lead to poor predictions (Strubbe *et al.* 2015).

In this study, we conduct the first global assessment of the relative importance of human habitat associations in shaping the native distributions of 776 alien bird species introduced worldwide, in relation to other key important drivers of species distributions, i.e., climate and land-use. For this, we used deviance partitioning analysis to identify the pure and joint contributions of these variable sets on environmental suitability obtained from SDMs. We then assessed whether the role of human-habitat associations is more important in introduced species than expected by chance relative to a pool of available species from the same bird families (N=3,565). As species adapted to human-altered habitats are likely to increase in abundance within areas frequented by humans, we expected that they were more likely to have been captured and transported to a novel range (Hufbauer *et al.* 2012; Sol *et al.* 2017b) and thus, overrepresented in the alien species pool. Similarly, we assessed whether human-habitat associations are more frequent within established species (N = 330), as would be expected if larger propagule pressure or environmental-matching between original habitats and introduction sites occur (Hufbauer *et al.* 2012; Sol *et al.* 2017b). Finally, we evaluated whether the relevance of human-habitat associations across species introduced worldwide has changed over recent centuries, as changes in the main introduction pathways and source pools of alien bird species have occurred (Dyer *et al.* 2017; Seebens *et al.* 2018).

Materials and methods

Species distribution and environmental data

Our analyses focused on all bird species that have been reported as introduced in the wild in at least one non-native locality worldwide (N = 971) (Dyer, Redding & Blackburn 2017). Occurrence data at the species level for analysis were compiled from the Global Biodiversity Information Facility (GBIF, http://www.gbif.org) and then checked and classified as pertaining or not to the introduced alien species' native breeding range according to BirdLife International and NatureServe range maps (2014). Birdlife International and NatureServe range maps comprise polygons mostly based on the Digital Chart of the World as a basemap (1:1,000,000 scale). Species distributions on these maps are derived from a systematic and thorough search of the data available in all regions of the world (including a variety of sources such as museum data, bird observation datasets and webpages, published literature, survey reports and other unpublished sources, distribution atlas, distributions maps in field guides and other handbooks and expert opinion). While information provided is likely to be complete and up-to-date for most species, data may be incomplete for some species, probably due to intrinsic geographic or taxonomic biases in the available data (Collen *et al.* 2008; Hortal *et al.* 2008). However, both geographic origin of species and taxonomy are accounted for in our analyses (see below), and thus these sources of bias should not affect our results. Occurrence data were aggregated at 5-arcminute resolution, which corresponds approximately to 10 × 10 km. This resolution was considered to be representative of smallest city sizes and thus adequate to capture main responses of bird species to humanized environments with acceptable computing time. Samples with reported geographic issues, location uncertainty above 5 km or with central grid coordinates of atlases of >10km resolution were removed from analyses. Duplicate samples at the 5-arcmin resolution were handled as single observations. Only introduced species with more than 50 locations in their native breeding range (N = 794) were retained for subsequent analyses (Stockwell & Peterson 2002) Disregarding species with lower sample sizes is unlikely to affect our main results, as preliminary analyses showed overall consistent patterns when considering species with increasingly larger sample sizes (Table S1 & S2 in Supplementary Material). The mean number of locations for selected species was 8,074 (SD = 17,571, range = 51 – 141,810).

As descriptors of human altered environments we considered two variables: (1) the Global Human Influence Index, which provides a weighted 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 (2) the percentage of urban habitats as a more specific descriptor of urbanization. Although species may respond similarly to both variables, different responses are also possible: for example, a species can respond positively to the Global Human Influence Index because its distribution is mostly associated with agricultural habitats, such that it then shows no response to urbanization). Percentage of urban habitats (including urban and built-up areas) at the 5-arcmin resolution was derived from data provided by the USGS Land Cover Institute (LCI) (https://landcover.usgs.gov/) at 500m resolution.

We also compiled information on climate and non-urban land uses given their key role in bird species distributions. As non-urban land use variables we derived the percentage of woodlands and open lands (including shrubland, grassland and savannas) using the same data source and methodology as for the percentage of urban habitats. As climate variables we considered eight bioclimatic variables (obtained from WorldClim, http://www.worldclim.org/) (Hijmans *et al.* 2005), which are known to affect bird distributions (Strubbe *et al.* 2015; Cardador *et al.* 2016): annual mean temperature, temperature seasonality (standard deviation of monthly values × 100), 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 (coefficient of variation of monthly values). However, annual mean temperature and temperature seasonality were highly correlated with minimum temperature of the coldest month ($r \geq 0.90$) and thus we only retained this last variable for analyses to reduce the number of variables the maximum. Annual precipitation was also highly correlated with precipitation of wettest month (and more correlated with the rest of variables), and thus removed from analyses (Table S3 in Supplementary Material). Both the linear and quadratic forms of variables were considered to account for non-linear relationships. For 18 species of the 794 species analysed, problems arose with model convergence and hence these were disregarded in subsequent analyses.

Factors affecting species distributions

We conducted generalized linear models (GLM) for each introduced species containing all combinations of the variable sets (i.e., human, climate and non-urban land uses) and with species occurrences as the response variable (binomial error distribution and logit-link function). Models were run with a single set of pseudo-absences including locations from all biomes covered by each introduced alien species' native range to ensure the most biologically meaningful fit between species occurrence and predictor variables (Guisan *et al.* 2014). To reduce uncertainty caused by sampling artefacts, we conducted 10 replicates for each model by randomly selecting 70% of each species' data (including presences and pseudo-absences) for each replicate (but see consistent results for models considering total sample size, Table S4-S6 in Supplementary material). A stepwise approach based on the Akaike's information criterion (AIC) was used to avoid model overfitting in GLMs. However, results from models including all variables were highly consistent according to preliminary analyses (Table S7 in Supplementary Material). To reduce the potential effect of sampling biases in the data, a bias file was created by retrieving from GBIF occurrence data at the family level for each introduced species (Elith, Kearney & Phillips 2010; Gallardo & Aldridge 2013). 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-arcminute resolution using ArcMap 10.5 to be included in all models.

Deviance partitioning analyses were then used to assess the relative roles of human-habitat associations, climate and non-urban land-uses on introduced alien species' native ranges. Deviance partitioning is a quantitative statistical method which separates the amount of deviance explained by the independent effects of each explanatory variable set in a model from the amount explained by joint effects that cannot unambiguously be attributed to one variable set or another due to spatial collinearity (Heikkinen *et al.* 2005). It entails the calculation of incremental improvements in model fit due to the inclusion of each variable set in every possible model. Negative values in pure effects were interpreted as zeros as they correspond to cases where the explanatory variables explain less variation than random normal variables would (Legendre 2008). As a null model for deviance partitioning analyses for each species we used a GLM with species occurrences as the response variable and containing sampling bias as unique predictor.

Response to humans and introduction rate

Results of GLMs considering human, climate and non-urban land uses (see above) were used to classify introduced species in categories according to their different responses (no response, positive, negative, convex or concave) to human variables (i.e., Global Human Influence Index and percentage of urban habitats) in their native ranges. We then evaluated whether the influence of human variables in shaping introduced alien species' native range differed from that expected at random using randomization procedures. For this, the observed frequency of different types of responses to human variables of introduced species was first compared against a null distribution of 10,000 simulated values obtained by randomly sampling an equal number of species within the same taxonomic families. A total of 3,565 species (including the 776 introduced species, as we were interested in the pool of available species) were considered for randomizations. To tackle possible geographic biases in introduction patterns (Duncan *et al.* 2003), we generated a second null model for randomizations in which we considered both species' taxonomic family and geographic origin. Geographic origin was the realm (Oceania, Afrotropic, Neartic, Palaeartic, Australasia, Indomalayan or Neotropical) occupied by most of the introduced alien species' native range (>50%) according to BirdLife International and NaturServe (2014). If no dominant realm occurred, geographic origin was classified as "multiregion" (1.9 % of species). GLMs for non-introduced species were conducted using the same procedure as for introduced species (see above).

Response to humans and establishment

We then compared the frequency of different types of responses to human variables of established species against species introduced by generating 10,000 simulated values obtained by randomly sampling an equal number of species within the same taxonomic families. As established species we considered those that have been reported as established in the wild in at least one non-native locality (Dyer, Redding & Blackburn 2017). Introduced species for which no information on establishment success was available, and the small number with extirpated populations (Dyer, Redding & Blackburn 2017), were not considered for analyses.

Temporal variation of response to humans

We tested for differences in introduction periods among introduced alien species showing different responses to humans in native ranges. For this, we used a randomization approach in which species' first introduction dates were randomised, and the geometric mean of each type of response (no response, positive, negative, convex or concave) calculated. This was repeated 10,000 times to give the expected distribution of geometric means for each type of response. The mean, minimum, maximum and percentiles of the 10,000 geometric means for each category were then extracted. The actual geometric means for each category were then compared with the expected distributions. Information on first introduction date was available for a total of 599 from the 776 introduced species with estimated response to human variables. Since introduction dates before 1500 were scarce (n = 7) and 1500 is a standard cutoff point for studying biological invasions (Dyer *et al.* 2017), we censured our analyses to years after 1500 to avoid an excessive noise of extreme values.

Results

Factors affecting species distribution

Of the 776 introduced species analysed, 725 ± 5 (93 ± 0.5 %) presented native distributions significantly affected by human-altered environments (note that mean ± SD values refer to results obtained across 10 model replicates), whether by the Global Human Influence Index (149 ± 6, 19 ± 1%), percentage of urban habitats (69 ± 4, 9 ± 1%) or both (507 ± 8, 65 ± 1%). The effects were mostly positive or concave both for the Global Human Influence Index (31 ± 1 % and 46 ± 1 % of the total 776 species, respectively) and the percentage of urban habitats (15 ± 1 % and 53 ± 1 %, respectively). Positive or concave responses mean that occurrence probability is highest at high or intermediate values of human variables, respectively (Fig. 1). Negative and convex responses were uncommon (< 5%).

Deviance partitioning analyses showed that the pure contribution of human variables to models averaged 14 ± 13% (mean ± SD) across the 776 species and replicates (Fig. 2). Climate explained a larger fraction of the variation in distribution patterns (54 ± 18 %), followed by the joint effect of climate and non-urban land uses (20 ± 14%) and human variables and non-urban land uses (11 ± 9%). Contributions of the pure effect of non-urban land uses and other joint effects were low (< 5%). The total deviance explained by the three variables sets was 16 ± 9 %.

Human-habitat associations and invasion stages

Introduction rates were higher than expected by chance for species with concave or positive responses to the Global Human Influence Index and lower than expected for species showing no response, with slight variations according to the modelling approach used (Tables 1, S4 and S8). Some support for lower introduction rates than expected for species showing negative responses was also found. Results were overall consistent for percentage of urban habitats, although lower support for the effect of positive and negative responses on introduction rates was found, with some variation across modelling approaches (Tables 1, S4 and S8). Among established species, species responding positively to high or intermediate values of the Global Human Influence Index and percentage of urban habitats, respectively, were also over-represented (Table 2 and S5). Regarding temporal variation, randomization procedures showed later first introduction dates for species showing no response or a negative response to the Global Human Influence Index and earlier for species showing positive responses (but see some variations across replicates, Table 3 and S6 and Figure 3). Support for later introduction dates for species showing no response to urban environments was also found (Table3).

Discussion

Our results support the hypothesis that association with humans may be an important driver of alien bird species distribution in their native ranges, increasing the likelihood that these species will end up being introduced and subsequently established. While an independent effect of climate, and a joint effect of climate and non-urban land uses, appear also as major factors governing distribution in introduced alien species' native ranges, significant independent contributions of anthropogenic variables were consistently found for most species. Human-habitat associations in the native distributions of alien bird species were significantly higher than expected by chance, indicating that introduced and established alien birds are not a random sample with respect to their association to human-altered environments (as occurrs with plants, Kalusová *et al.* 2017).

The independent positive effect of our two metrics of human-altered environments on species occurrence probability in native ranges might reflect the capacity of some species to use and thrive in those environments. This may be related to phenotypic plasticity, evolutionary response to such environments or non-random sorting due to habitat pre-adaptations (Sol, Lapiedra & González-Lagos 2013). In turn, the use of human environments may allow such species to gain access to new resource opportunities such as supplementary feeding (Robb *et al.* 2008; Clergeau & Vergnes 2011) or different microclimatic or microhabitat conditions with respect to natural areas

(Pickett *et al.* 2001) that could modify physiological and resource limitations locally imposed by climate and non-urban land uses. However, it is worth noting that a large fraction of the species in this study only responded positively to moderate levels of human alterations (concave responses). More extreme conditions may act as stronger environmental filters selecting for only a low fraction of species that can tolerate such conditions (Sol *et al.* 2017a).

Human habitat associations in introduced alien species' native range can in turn have important effects on invasion risks. Thus, in our study, higher introduction rates were observed for species responding positively to high or intermediate levels of human alterations, compared with species not responding or responding negatively to them. This pattern might be explained by different processes. First, species adapted to human-altered environments are likely to increase in abundance within areas frequented by humans and thus are more likely to be captured and transported to new regions (Hufbauer *et al.* 2012; Sol *et al.* 2017b). Additionally, species habituated to humans could also have higher chances to pass selection filters imposed by captivity and transport (Mueller *et al.* 2017). It is also possible that given that birds are commonly chosen for particular purposes – i.e. most introduced species are game or ornamental cage birds (Duncan *et al.* 2003; Abellán *et al.* 2016) – people would prefer to choose species with which they are more familiar. This has certainly been argued to drive specific cases of naturalisation (Blackburn, Lockwood & Cassey 2009), and would potentially favour species more common in human-modified environments.

As introduced species constitute the pool of species from which establishment, and thereafter spread, can take place, species showing tolerance to human altered environments are also likely to be overrepresented in subsequent invasion stages (Duncan *et al.* 2003). In turn, the likelihood of establishment of such species may increase, for example, because of higher colonization and propagule pressures, as species associated with humans are expected to be introduced more frequently but also in higher numbers. Additionally, environmental matching due to the introduction of such species to human-altered environments to which they are already adapted may also enhance establishment (Hufbauer *et al.* 2012; Sol *et al.* 2017b).

Nevertheless, temporal trends of species introduced worldwide show that an increase in introduction rates of species showing no response, or a negative response, to human influence has occurred through time. These temporal patterns occur in parallel to changes in the main origin of introduced species (Dyer *et al.* 2017; Seebens *et al.* 2018), suggesting that changes in the type of species introduced in relation to their tolerance to humans could be related to increased accessibility to more pristine areas with globalization and technology development. While ‘historical’ bird introductions mostly involved species originating from Europe and related to deliberate releases by early acclimatisation societies, most recent bird introductions concern unplanned releases of birds from the pet trade, and involve species originating from more tropical regions (Abellán *et al.* 2016; Dyer *et al.* 2017). Different urbanization histories in regions of origin of introduced species would have posed different selective pressures in relation to human alterations, with species in less exposed areas having had less opportunity to colonize human-modified environments. Our results contrast with previous expectations suggesting that the ever-increasing rates of human-transformations worldwide, could be related to increased transport and introduction of species adapted to human alterations (Hufbauer *et al.* 2012). However, it is important to note that the influence of human-habitat associations on the transport probability of birds could be lower than those of other species (e.g. insects (Foucaud *et al.* 2013)), which unlike birds, are involuntarily introduced in long-distance transport channels.

The data used in this study are the best currently available for an entire major taxon, but nonetheless come with caveats (Dyer *et al.* 2016; Dyer, Redding & Blackburn 2017). The species analysed are likely to be at different stages of the invasion process (Blackburn et al., 2009), and thus some of them may establish or die out in the future. The documentation of introductions and established species may be influenced by higher or lower recording effort in certain regions or throughout time. The estimates of responses to human habitats mostly rely on species current distributions, assuming that these responses have remained constant throughout time. All of these issues add noise to our analyses, although we do not believe that they will have generated any of the results we present here as artefacts.

In the Anthropocene era, it is increasingly acknowledged that human activities interact with ecological processes in multiple ways. Our work contributes to the growing evidence that human-habitat associations can play an important role in the native distributions of alien bird species, with important effects on introduction Therefore, accounting for human-habitat associations in introduced alien species' native ranges is essential to provide a more thorough assessment of invasion risk. Invasion risk assessment represent the primary approach to support and prioritise policies and actions (e.g. importation bans or quarantines) aimed to prevent the introduction of species posing a high risk of invasion. A common approach to risk assessment uses species distribution models to predict the probability of establishment in a new region, according to climatic constraints in a species' native range and/or invaded regions (Thuiller *et al.* 2005). While these models have been described as effective first-screening tools, they often assume that broad limits of species distributions are determine by climate, with the effect of other factors being insignificant. The key role of anthropogenic variables in shaping alien species' native ranges in our study shows that this assumption can be violated. Thus, to provide more robust predictions of invasion risks, incorporating anthropogenic variables into species distribution models is highly recommended to guide effective management. Our results also have applied relevance for the application of assessments mostly based on species traits, as they provide empirical support to previous trait-based species risk assessments assuming that human associations can be used as a reliable predictor of invasion risks (Vall-Llosera & Sol 2009).

Authors' contributions

L.C. and T.B conceived the ideas, L.C. analysed the data with inputs from T.B, L.C. and T.B. discussed results, contributed critically to the drafts and gave final approval for publication. L.C. led the writing of the manuscript.

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Data accessibility

All data used in this manuscript have already been published or archived and can be accessible from Figshare (*http://dx.doi.org/10.6084/m9.figshare.4234850*) (Dyer, et. al 2017), GBIF database (*https://www.gbif.org/*), WorldClim (*http://www.worldclim.org/bioclim*), USGS Land Cover Institute (LCI) (*https://landcover.usgs.gov/*) and BirdLife International & NatureServe (2014) (*http://datazone.birdlife.org/species/requestdis).*

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Table 1. Results for randomization procedures assessing the response to the Global Human Influence Index and urbanization of alien birds relative to a pool of available species from the same bird families (N=3,565). Note that as species response classifications are based on 10 replicated models, 10 randomization procedures were conducted. In each, run the observed frequency of different types of responses (observed) of alien birds was compared against a null distribution of 10,000 simulated values. The averaged values ± SD of the mean, minimum and maximum of the 10,000 simulated geometric means across different runs are shown. The number of runs with significant results at α = 0.01 and α = 0.05 are shown. Results are based on a randomization stratified approaches considering only species' family.

Response	**Mean**	**Min**	**Max**	**Observed**	**P < 0.001**	**P < 0.05**
Global Human Influence Index						
Concave	335 ± 8	305 ± 7	367 ± 7	360 ± 9	9	10
Convex	23 ± 2	12 ± 2	34 ± 3	23 ± 3	0	0
Negative	33 ± 2	19 ± 3	48 ± 2	28 ± 2	0	3
Positive	224 ± 4	197 ± 4	254 ± 4	244 ± 7	3	10
Tolerant	161 ± 7	132 ± 7	189 ± 7	120 ± 6	10	10
Urban						
Concave	354 ± 5	324 ± 4	386 ± 3	411 ± 5	10	10
Convex	21 ± 3	12 ± 2	32 ± 4	16 ± 3	2	5
Negative	34 ± 4	20 ± 4	48 ± 4	31 ± 4	0	0
Positive	110 ± 6	89 ± 6	132 ± 6	119 ± 7	0	2
Tolerant	257 ± 5	226 ± 4	287 ± 4	199 ± 7	10	10

Table 2. Results for randomization procedures assessing the response to the global human influence index and urbanization of established alien birds against introduced bird species. Note that as species response classifications are based on 10 replicated models, 10 randomization procedures were conducted. In each, run the observed frequency of different types of responses (observed) of alien birds was compared against a null distribution of 10,000 simulated values. The averaged values ± SD of the mean, minimum and maximum of the 10,000 simulated geometric means across different runs are shown. The number of runs with significant results at α = 0.01 and α = 0.05 are shown. Results are based on a randomization stratified approaches considering species' family and geographic origin.

Response	**Mean**	**Min**	**Max**	**Observed**	**P < 0.001**	**P < 0.05**
GHII						
Concave	147 ± 4	128 ± 5	168 ± 5	150 ± 5	0	0
Convex	11 ± 1	3 ± 1	17 ± 2	9 ± 2	0	0
Negative	13 ± 1	5 ± 1	19 ± 2	10 ± 1	0	1
Positive	113 ± 4	95 ± 4	132 ± 4	124 ± 4	3	8
Tolerant	46 ± 3	34 ± 3	59 ± 4	37 ± 4	6	8
Urban						
Concave	174 ± 4	155 ± 4	193 ± 4	189 ± 5	7	10
Convex	8 ± 1	2 ± 1	12 ± 2	7 ± 2	0	0
Negative	13 ± 2	6 ± 2	20 ± 3	12 ± 2	0	0
Positive	50 ± 4	36 ± 4	63 ± 5	51 ± 5	0	0
Tolerant	84 ± 5	68 ± 5	101 ± 5	70 ± 4	9	9

Table 3. Results for randomization procedures assessing the first introduction date of alien bird species showing different types of responses to the global human influence index (GHII) and urbanization. Note that as species response classifications are based on 10 replicated models, 10 randomization procedures were conducted. In each run, the observed geometric mean of first introduction dates of alien birds (observed) was compared against a null distribution of 10,000 simulated values. The averaged values ± SD of the mean, minimum and maximum of the 10,000 simulated geometric means across different runs are shown. The number of runs with significant results at α = 0.01 and α = 0.05 are shown.

Response	**Mean**	**Min**	**Max**	**Observed**	**P < 0.001**	**P < 0.05**
Global Human Influence Index						
Concave	1914 ± 0.02	1901 ± 1	1928 ± 1	1911 ± 1	0	0
Convex	1914 ± 0.07	1830 ± 10	1970 ± 5	1928 ± 13	0	2
Negative	1915 ± 0.08	1836 ± 6	1967 ± 1	1945 ± 7	2	5
Positive	1914 ± 0.02	1893 ± 3	1934 ± 1	1900 ± 3	3	9
Tolerant	1914 ± 0.04	1880 ± 6	1943 ± 1	1939 ± 4	10	10
Urban						
Concave	1914 ± 0.02	1901 ± 1	1927 ± 1	1911 ± 2	0	1
Convex	1914 ± 0.14	1800 ± 11	1980 ± 5	1898 ± 8	0	0
Negative	1914 ± 0.11	1837 ± 7	1965 ± 4	1927 ± 6	0	0
Positive	1914 ± 0.05	1878 ± 4	1943 ± 2	1906 ± 4	0	0
Tolerant	1914 ± 0.05	1891 ± 2	1937 ± 2	1925 ± 3	0	4

Figure captions

Figure 1. Partial response curves showing the response to the Global Human Influence Index of introduced alien birds in their native ranges. Responses are based on GLMs modelling the probability of species occurrence in native ranges and are grouped into different categories depending on whether only the linear or the quadratic term of variable is significant in models, and on the sign of estimate. Positive refers to a positive relationship between human influence and species' probability of occurrence; negative to a negative relationship. In concave relationships, occurrence probability increases at intermediate values, whereas in convex relationships, occurrence probability increases at low or high values. Results based on models using all available occurrence data are shown.

Figure 2. Deviance partitioning analyses for the probability of occurrence of alien bird species in their native ranges (panel a). Results are expressed as a percentage of the total deviance explained by the model (panel b). Deviance is explained by three groups of predictors: climate, non-urban land uses and human variables; (a), (b), and (c) are pure effects of climate, non-urban land uses and human variables respectively; while (d), (e), (f) and (g) are fractions indicating their joint effects. Results for 10 replicates models for each species (N = 776) are shown.

Figure 3. Trends in first introduction dates of alien bird species after year 1500 according to response to the Global Human Influence Index in native ranges. Yearly proportions of total newly introduced species per response category are provided. Results based on models using all available occurrence data are shown.

Figure 1.

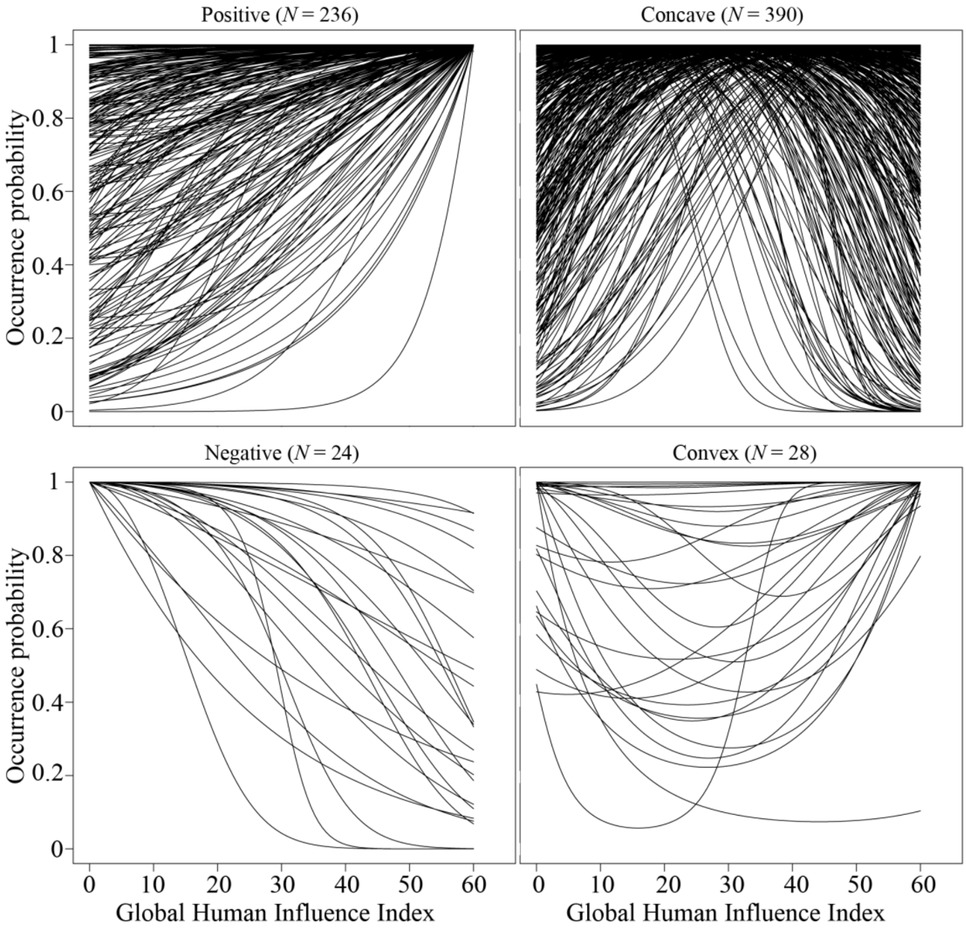

Positive (*N* = 236)
Concave (*N* = 390)
Negative (*N* = 24)
Convex (*N* = 28)
Occurrence probability
Occurrence probability
0
0.2
0.4
0.6
0.8
1
0
10
20
30
40
50
60
Global Human Influence Index
Global Human Influence Index

Figure 2.

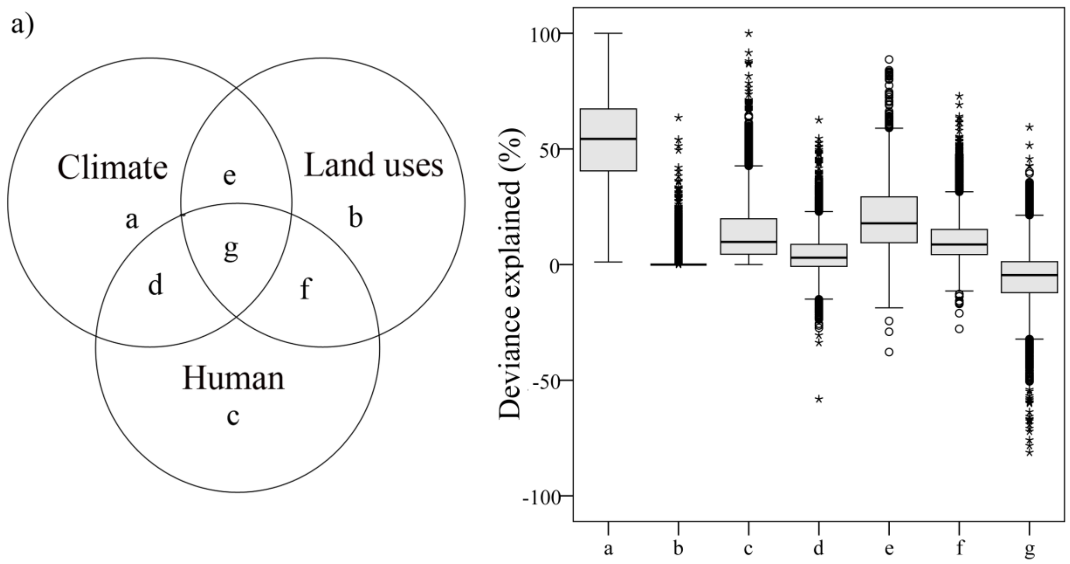
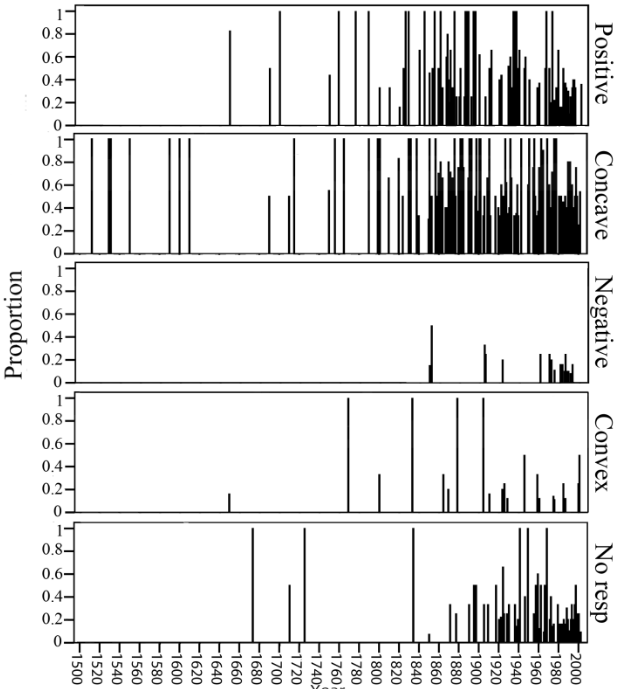

a)
Climate
e
Land uses
a
b
g
d
f
Human
c
Deviance explained (%)
100
50
0
-50
-100
a
b
c
d
e
f
g

Figure 3.


Proportion
Positive
Concave
Negative
Convex
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0
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1
1500
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1920
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