

## Forum

### Invasion success and tolerance to urbanization in birds

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Cities are considered hotspots of biological invasions, yet it remains unclear why non-indigenous species are so successful in environments that most local native species do not tolerate. Here, we explore the intriguing possibility that humans may be unintentionally introducing species preadapted to persist in such environments. Combining data on historical introductions with information of avian assemblages along urban–wildland gradients, we found that avian species that in their native range proliferate in human-altered environments have been more likely to be transported and introduced to new locations than species confined to the wildland. We also found that such urban dwellers had higher chances to become established because they already had adaptations to cope with novel environments. These findings suggest that the pathway of introduction selects for species preadapted to persist in novel environments, providing an explanation for why non-indigenous birds are so successful in cities. Because the tendency to introduce species associated with human-altered environments continues, there is an urgent need to develop new regulations to prevent future introductions.

Keywords: Anthropocene, biological invasions, global change, life history, urban ecology



#### Introduction

Despite growing concern over the environmental and socio-economic problems caused by biological invasions (Vilà et al. 2011, Díaz et al. 2019), the reasons why non-indigenous species (NIS, hereafter) can be so successful in novel environments to which they have had little opportunity to adapt are insufficiently understood (Sax and Brown 2000, Sol et al. 2012a, Redding et al. 2019). The success of these NIS is puzzling because exposure to novel conditions commonly generates mismatches between the environment and the organisms' phenotype, causing maladaptation and extinction (Bell 2017, Maspons et al. 2019). A popular explanation for this paradox is that the success of NIS results from their capacity to exploit human-altered environments that most local native species rarely use, an idea known as the 'disturbance hypothesis' (Elton 1958, Case 1996, Sax and Brown 2000, McKinney 2002, Nordheimer et al. 2018).



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Among different types of disturbances, the long-lasting and relatively permanent environmental changes associated with urbanization may be particularly beneficial to NIS establishment (Sol et al. 2012a, Cadotte et al. 2017). Urban environments are novel to native species and rarely used by them, either because they cannot persist there or because they have not yet been colonized (Aronson 2014, Sol et al. 2014, Møller and Díaz 2017, Santini et al. 2019). Released from competitors and enemies, NIS that can capitalize on resource opportunities created by human activities can largely increase in numbers and become invasive (Sax and Brown 2000, Sol et al. 2012a, McLean et al. 2017). Because NIS are more likely to be introduced in urban environments – whether intentionally or accidentally through the pet trade (Abellán et al. 2017, Padayachee et al. 2017, Lockwood et al. 2019) or horticulture (Hulme 2009) – the ‘disturbance hypothesis’ provides a plausible explanation for the unexpected success of many biological invasions. Although evidence is accumulating that NIS attain higher success in human-altered environments compared to less modified areas (Cadotte et al. 2017, Nordheimer et al. 2018; but see Redding et al. 2019), the ‘disturbance hypothesis’ is insufficient to resolve the paradoxical success of NIS because it does not explain why they are able to exploit environments that most local native species do not tolerate (McKinney 2006, Evans et al. 2011, Sol et al. 2014, Cadotte et al. 2017, Ducatez et al. 2018, Santana Marques et al. 2020).

Recently, it has been suggested that the proliferation of NIS in urban environments, and hence their success in the new region, might reflect that species preadapted to persist in cities are more likely to transition throughout the different stages of the invasion process – that is the capture, transport, introduction, establishment, and spread (reviewed in Sol et al. 2017b). On the one hand, species that in their native range proliferate in human-altered environments – particularly urban areas – should be easier to obtain and better predisposed to cope with the hurdles of transport and introduction (Duncan et al. 2003). For example, habituation to humans may make it easier to capture and keep animals in captivity to be transported to other regions (Mason et al. 2013). It follows that species that live in close proximity to humans in their native ranges should be more likely to be introduced – and in larger numbers – than those living in other environments (Duncan et al. 2003, Cardador and Blackburn 2019). On the other hand, because these species may already have adaptations to living close to humans (Hufbauer et al. 2012), they should be more likely to settle, establish, and prosper in urban environments after being introduced (Ehrlich 1989, Evans et al. 2011). It is increasingly appreciated that the pathways by which NIS become introduced highly influence subsequent stages of the invasion process (Hulme et al. 2008). However, the hypothesis that species frequently occurring in human-altered areas in their native range are more likely to be introduced and to establish in new regions has rarely been considered to explain the success of NIS (Hufbauer et al. 2012, Cadotte et al. 2017).

Here, we present a comprehensive test of this hypothesis in birds. Based on a worldwide dataset of >200 well-characterized bird assemblages along local urban–wildland gradients, we first ask whether NIS attain greater success in urbanized environments compared to nearby less modified areas. We then combine data on global historical introductions with information on the habitats in which bird species occur in their native ranges to explore underlying explanations. We start by asking whether avian species associated with human-altered environments in their native range are more often introduced by humans. Then, we address the complementary hypothesis that once introduced, species associated with human-altered environments in their native range are more likely to establish themselves in the new region than those species restricted to wildland areas. We also investigate whether this is because urban-dwellers tend to be introduced in larger numbers (i.e. high introduction effort) or because they have traits that preadapt them to persist in their new environment (i.e. preadaptations).

To address the latter issue, we focus on three general preadaptations that have previously been shown to facilitate the persistence of birds in novel environments in general, and urban areas in particular, that is, a broad niche, enhanced behavioral plasticity and a future returns life history strategy (Duncan et al. 2003, Sol 2007, Sol et al. 2014) (Supporting information for additional justification). Because we found that the probability that a species is introduced and establishes itself in a novel environment increases if the species tolerates urban habitats in their native range (i.e. measured as increases in abundance in highly urbanized habitat compared to nearby less modified areas), we use international bird trade data to investigate whether there is a trend to introduce these species nowadays.

## Material and methods

### Data

#### *NIS along urban–wildland gradients*

To examine to what extent the association between NIS and urbanized environments is general, as expected from the ‘disturbance hypothesis’, we used a dataset of well-characterized avian assemblages available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.2rbnz7jff>> (Sol et al. 2020). In this dataset, avian assemblages within each study locations are assigned to one of five land-use classes: 1) highly urbanized environments (HUR) dominated by buildings and little or absent vegetation (i.e. city centers); 2) moderately urbanized environments (MUR) including residential areas with single family houses and associated gardens (i.e. suburbs); 3) little-urbanized environments (LUR) with few buildings and abundant vegetation (e.g. urban parks); 4) native vegetation (NVG); and 5) rural areas (RUR). For the present study, we focused on locations that met two criteria: 1) information was available for both urbanized (LUR, MUR, and HUR) and nearby areas that

were less modified by comparison (RUR and NVG); and 2) at least one of the assemblages of the location was invaded by one or more NIS. The resulting dataset included presence/absence and abundances per unit area or unit time for 58 NIS in one or more of 36 study locations (range from 1 to 17 species) from Africa, Australia, Asia, Europe, North America, and South America (for information on habitat definitions and assignments see Sol et al. 2014, 2017b, 2020).

#### ***Occurrence in human-altered environments***

We used the habitat classification scheme from the International Union for Conservation of Nature (IUCN) to assess whether NIS occurred in human-altered environment in their native ranges. This classification scheme includes data for habitat occurrence of 9903 bird species (see IUCN habitat classification scheme 3.1; <[www.iucnredlist.org/technical-documents/classification-schemes](http://www.iucnredlist.org/technical-documents/classification-schemes)>). The IUCN data allowed us to classify bird species as occurring or not across any type of artificial terrestrial habitat such as arable land, pastureland, plantations, rural, urban, and subtropical/tropical heavily degraded former forest ( $n=4515$  species occurring in these human-altered environments). We also classified species as occurring or not in urban areas – the most modified environments ( $n=905$  species) (Supporting information).

#### ***Tolerance to urban areas in the native range***

Because occurrences of avian species in urban environments depend in part on their abundance in nearby rural and natural habitats, we used the dataset of avian assemblages previously described to compute two metrics of urban tolerance. The first metric was estimated as the log–log difference in the mean number of individuals of a species recorded between highly urbanized habitat (HUR) and nearby natural vegetation (NVG) of a given study location (hereafter urban tolerance index or UTI, Sol et al. 2017b). High positive values of the index indicate high tolerance to the environmental alterations associated with urbanization while low negative values indicate species less tolerant to urbanization (Evans et al. 2011). Values close to zero are more uncertain as they may indicate either no effect of urbanization or that the species is too scarce in the region to assess its tolerance (Sol et al. 2014). To tackle this issue, we used a second, more restrictive, metric to estimate urban tolerance based on community simulations (hereafter exploiter/avoider metric, Sol et al. 2014). This allowed us to effectively separate species that tolerate urbanization (exploiters) from those that do not (avoiders). A species was considered an urban ‘exploiter’ if its observed abundance in the highly urbanized habitat was equal to or greater than the 95th percentile of the abundance expected by chance, and an urban ‘avoider’ if it was equal to or lower than the 5th percentile; the species for which information was insufficient to be assigned to one or another category (i.e. their abundances in urban areas were distributed as expected by random) were not considered. Because we were interested in the intrinsic ability of a species to tolerate urbanization, we considered a species as an exploiter when at least one of its native populations was classified in this category (Supporting

information). This was justified because previous evidence in birds showed that urban tolerance is a species-level characteristic that shows significant phylogenetic signal (Sol et al. 2014, 2017b).

#### ***Historical introductions***

We used the Global Avian Invasion Atlas, GAVIA available at Figshare data repository: <<https://doi.org/10.6084/m9.figshare.4234850.v1>> (Dyer et al. 2016a, 2017) to analyze whether species associated with human-altered environments in their native range are more often introduced outside their native range. The dataset covers >27 000 introductions events of 971 bird species spanning the period 6000 BCE – AD 2014, and hence provides unique information on the frequency at which species have been introduced. We used the GAVIA dataset to extract information on whether a bird species was ever introduced, as well as the frequency of introductions (i.e. number of times that a species was recorded as being introduced to a given location and the average number of introductions per country;  $n=961$  species).

#### ***CITES information on bird trade***

Because patterns of introduction change over time, pathways that were rare in the past, like the trade-in pet birds, are now the most common (Abellán et al. 2016, Dyer et al. 2017). To test whether there is an ongoing trend to introduce species that are associated with humans in their native ranges, we used information on the total number of live individuals per species that were legally traded from 1975 to 2013 according to the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) data ( $n=1074$  species; <[www.cites.org](http://www.cites.org)>). While CITES information is not exempt from potential bias such as underrepresentation of some taxonomic groups or occasional failures in the estimation of the number of individuals involved in trade, it still represents the only global formal convention tracking data on international trade in wildlife in a structured and verifiable way (Reino et al. 2017). Indeed previous analyses have shown a direct link between trade and introduction numbers (Reino et al. 2017, Cardador et al. 2019). For each CITES trade event, information on the number of traded individuals came from the importer country (28.7%), the exporter country (19.6%), or both (51.7%). This is not likely to affect our results, since when available, information provided by the importer and the exporter countries was highly correlated (Pearson correlation coefficient:  $r=0.91$ ,  $p > 0.001$ ,  $n=7606$ ). In these cases, the maximum number of individuals reported was used for analyses (Supporting information).

#### ***Establishment success***

GAVIA provides information on successes and failures of many introductions, but this information is insufficient to determine species-specific ‘invasion potential’ (i.e. tendency of a species to succeed wherever it is introduced, Supporting information analyses) in the absence of introduction effort data (e.g. number of individuals released) (Duncan et al. 2003). We instead used another global data source of

historical avian introductions from a previous study (Sol et al. 2012b). This dataset provides information on establishment success (i.e. whether a given introduction event was successful or failed to produce a self-sustaining population) and introduction effort for 832 events for 202 bird species (data available at <<https://doi.org/10.1126/science.1221523>> as Supporting information).

### **Preadaptations**

We gathered information from previously assembled data sets for species traits that preadapt birds to cope with novel environments (Sol et al. 2012b, 2017a, Sayol et al. 2016) and could also affect urban tolerance (Sol et al. 2014, 2017a). The traits considered were 1) the brood value, an index that represents the value of current reproduction with respect to the value of future reproduction (Bókonyi et al.

2009), estimated as  $\log_{10} \left\{ \frac{1}{\text{broods per year} \times \text{lifespan}} \right\}$ ;

2) relative brain size, which is a surrogate of behavioral flexibility (Lefebvre et al. 1997, Reader and Laland 2002) and was estimated as the residuals of a phylogenetically corrected least squares log-log regression between brain and body size using the `phyl.resid` function of the `phytools` R-package (Revell 2009); and 3) niche breadth, characterized by the frequency of use (not used=0, occasionally used=0.1, frequently used=0.5 and almost exclusively used=1) of different categories of habitat and diet, expressed as Rao's quadratic entropy (De Cáceres et al. 2011). The categories used to define habitat breadth were forest, woodland, open vegetation (including tundra and grassland), and aquatic habitats (including marshes and wetlands; Wilman et al. 2014). For diet breadth, we considered the percentage of use of invertebrates, endotherms, ectotherms, fishes, scavengers, fruits, nectar, seeds, plants, and unknown items (Supporting information).

Although other traits may also be relevant (Sol 2007, Capellini et al. 2015), they were not used because their association with both establishment success and urban tolerance is less firmly supported (Sol et al. 2017a) (Supporting information).

### **Phylogenetic relationships**

For analyses where it was necessary to control for possible non-independence of observations due to common ancestry, we used a maximum clade credibility consensus tree. This tree was built with the `TREEANNOTATOR` software (Drummond et al. 2012) using 1000 random sampled phylogenies from the pseudo-posterior distribution of trees available in <[www.birdtree.org](http://www.birdtree.org)> (Jetz et al. 2012).

### **Statistical approaches**

We analyzed the data using a Bayesian generalized mixed model (BGLMMs) approach, as implemented in the `MCMCglmm` (Hadfield 2010) and `brms` packages (Bürkner 2017). BGLMMs provide a flexible framework to accommodate a variety of response variables (e.g. richness and

abundance of NIS, introduction status, introduction frequency, establishment success, and traded individuals), as well as to include random factors to deal, when appropriate, with geographic (e.g. study location, country of introduction) and phylogenetic non-independence of data. A detailed description of the response variables, predictors, potential confounding effects, and error distribution of adjusted models are provided in the Supporting information.

Because we did not have a priori information about parameter distributions for our models, we used weakly informative priors; thus, all the information in the analysis comes from the data (Hadfield 2010). `MCMCglmm` models were run for 50 010 000 iterations with a burn-in of 10 000 and a thinning interval of 500, which guaranteed convergence and mixing for all our models. Model convergence and mixing were assessed visually, plotting the traces of each of the model parameters and checking that the effective sample size for all estimates was equal to or larger than 1000 (Hadfield 2010; Supporting information). Fixed effects were considered statistically significant when 95% credible intervals (CI) did not span zero, that is, Bayesian p-values (p-MCMC) were lower than 0.05 (Hadfield 2010).

We investigated whether introduction effort or preadaptation to novel environments explains the relationship between urban tolerance and establishment success as follows. To analyse the introduction effort, we use gaussian BGLMMs to model the mean number of individuals per species released as a function of the two metrics of urban tolerance described above. To evaluate the importance of preadaptations, we combined phylogenetic principal component analyses (Revell 2009) and path analyses based on phylogenetic generalized least squares models (PGLS) (Hardenberg and Gonzalez-Voyer 2013, van der Bijl 2018). For these analyses we estimated the 'invasion potential' as the random effect coefficients from a binomial BGLMMs controlling for taxonomy and country as random effects and introduction effort as fixed effect (Supporting information). All analyses were performed using R Statistical Software ver. 4.0.3 (<[www.r-project.org](http://www.r-project.org)>) in R Studio (RStudio Team 2020). R script and the details on the structure of each model are available as Supporting information together with the associated data.

## **Results**

### **Are non-indigenous birds more common in the more urbanized environments?**

The analysis of avian assemblages (n=220) confirmed that non-indigenous birds were mainly restricted to urbanized environments (Fig. 1a). Indeed, NIS richness tended to be higher in urbanized areas than in less modified environments (Fig. 1b, p-MCMC < 0.001; Supporting information model M1). Importantly, NIS only achieved high densities in the most intensively urbanized areas (Fig. 1c, p-MCMC < 0.001, Supporting information model M2).



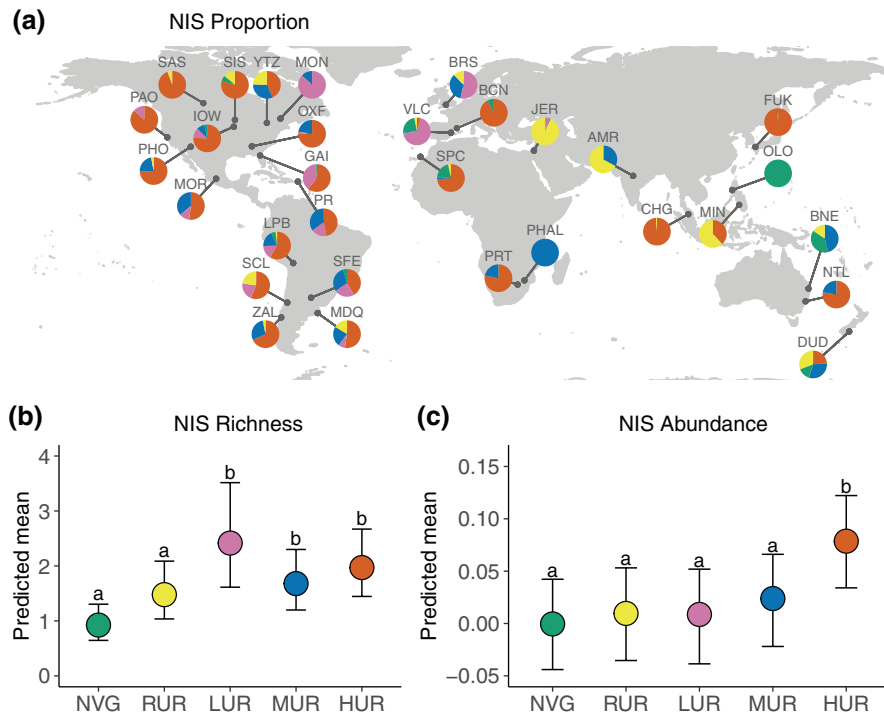


Figure 1. The Success of NIS along the urban–wildland gradient. (a) Worldwide study locations showing the proportion of non-indigenous individuals in bird assemblages located in land-use classes with different intensities of human disturbance. Predicted mean (solid points) of (b) richness and (c) relative abundance for 58 NIS as a function of the land-use class of bird assemblages ( $n = 220$ ). The lower and upper bounds of 95% credible intervals are depicted by vertical lines. These parameters come from Bayesian mixed models which accommodates differences in intercepts among study locations. Land-use classes representing the urban–wildland gradient are indicated by different colors (NVG: wildland; RUR: rural; LUR: low urbanized; MUR: moderately urbanized; and HUR: highly urbanized habitat). Letters 'a' or 'b' are used to denote land-use classes with significant (different letters) or non-significant (same letters) differences in (a) the richness or (b) abundance of NIS. Abbreviations for the study locations are in Supporting information.

### Are avian species associated with human-altered environments in their native range more often introduced by humans?

Two lines of evidence suggest an affirmative answer to this question. First, species classified as occurring in human-altered environments in their native ranges were more likely to have been historically introduced in regions outside their native range ( $p\text{-MCMC} < 0.001$ ;  $n = 9904$  species; Fig. 2a; Supporting information model M3). Second, the frequency of introductions among the species that had been introduced at least once in the past was higher if the species occurred in human-altered habitats in its native range than if it did not ( $p\text{-MCMC} = 0.007$ ;  $n = 971$ ; Fig. 2b; Supporting information model M4). This pattern persisted even when the frequency of introductions was estimated as the average number of introductions per country ( $p\text{-MCMC} < 0.001$ ;  $n = 971$  species; Fig. 2c; Supporting information model M5).

### Are urban dwellers more likely to be introduced by humans?

To further interpret the above results, we asked whether the probability of a species being introduced was contingent on the intensity of the human alteration. We found that the

frequency of introductions among the species that had been introduced at least once in the past was higher if the species occurred in urbanized areas in its native range than if it did not ( $p\text{-MCMC} < 0.001$ ; Supporting information model M8).

### Is the tendency of NIS to originate from human-altered environments observed in contemporary introductions?

When focusing on the most recent introductions (CITES trade data), we found that species occurring in human-altered environments in their native range were traded in larger numbers than those not occurring in such environments ( $p\text{-MCMC} < 0.001$ ,  $n = 978$  species; Fig. 2d; Supporting information model M6). The conclusion holds when considering as a predictor the occurrence in urban areas ( $p\text{-MCMC} < 0.01$ ; Supporting information model M10).

### Are avian species associated with human-altered environments in their native ranges more likely to be established after being introduced?

The analysis of successes and failures in historical introductions did not provide evidence that species occurring in human-altered habitats in their native range were more

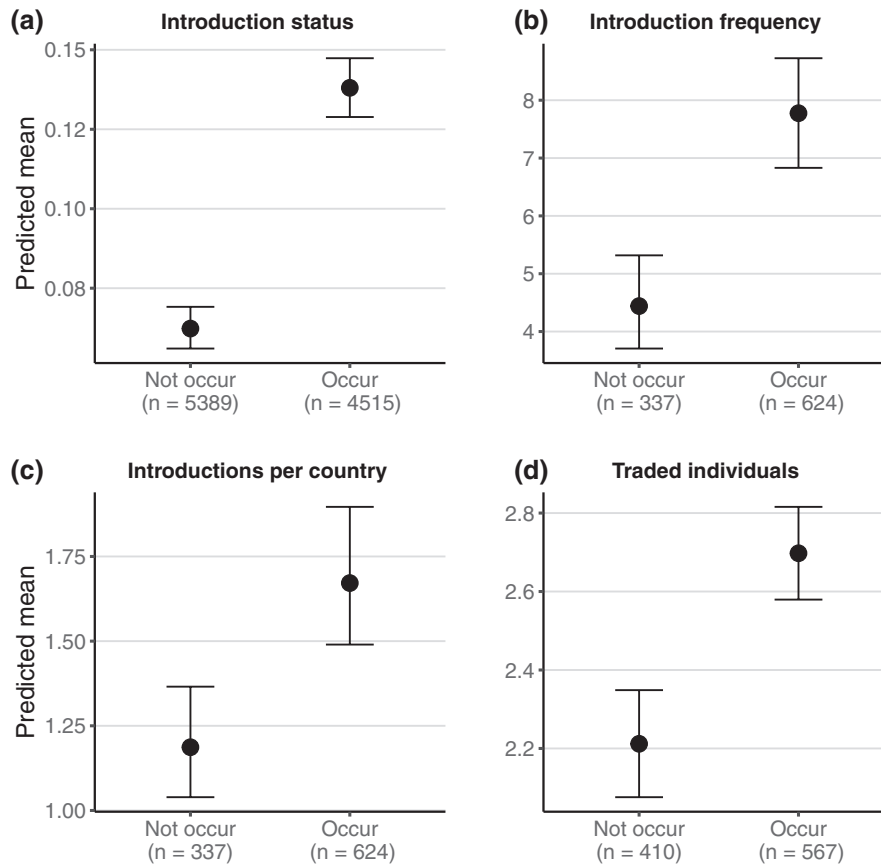


Figure 2. Predicted differences of introduction pressure between species that do or do not occur in human-altered environments in their native range. Introduction pressure was assessed by (a) the introduction status (i.e. whether or not the species has been recorded as introduced at least once), (b) the frequency at which it has been introduced (i.e. the number of times the species has been introduced), (c) the number of introductions per species per country and (d) the number of individuals traded. The solid points display the predicted mean and vertical lines the 95% CI of the response variable as a function of occurrence in human-altered environments conditional on all other predictors (Supporting information). Parameters were obtained from Bayesian phylogenetic mixed models that included phylogeny, species identity, and country of introduction as random factors. The number of species involved in each category is depicted in brackets.

likely to succeed when introduced to a new region than those that had not been reported to occur in these habitats ( $p\text{-MCMC}=0.811$ ;  $n=202$  species; Table 1, Supporting information model M11). However, we did find evidence that species that occurred in the most intensively human-altered environment (i.e. urban areas) were marginally more likely to succeed ( $p\text{-MCMC}=0.09$ ,  $n=202$  species; Table 1). The pattern was clearer when considering finer measures of urban tolerance. Comparing successes and failures in historical avian introductions, the likelihood of establishment was higher for urban tolerant species, regardless of the method used to measure it (UTI:  $p\text{-MCMC} < 0.01$ ;  $n=86$  species; exploiter–avoider:  $p\text{-MCMC} < 0.01$ ;  $n=72$  species; Table 1, Supporting information model M13 and M14).

### Why do avian species that proliferate in human-altered areas in their native range tend to establish self-sustaining populations when introduced to regions outside of their native ranges?

Our finding that species that tolerate urban areas in their native range attained higher establishment success did not

simply reflect that these species were introduced in larger numbers. The analysis of historical introductions for the subset for which introduction effort was available indicated that species that tolerate urban areas were not introduced in larger numbers (UTI:  $p\text{-MCMC}=0.865$ ,  $n=86$ ; exploiter–avoider:  $p\text{-MCMC}=0.833$ ,  $n=72$  species; Supporting information). In addition, the conclusion that urban tolerant species were more likely to succeed when introduced held even when introduction effort was included as a covariate in the models (Table 1c, d).

Instead, we found evidence that the enhanced establishment success of urban dwellers was related to the possession of traits that facilitate persistence in novel environments. A phylogenetic principal component analysis of introduced species loaded invasion potential, urban tolerance, relative brain size, and the brood value in the same axis (first principal component, PC1), reflecting that these variables co-varied and that this co-variation was not merely caused by phylogenetic relationships. The PC1 represented 31.8% of the variation and characterized successful invaders by high tolerances to urbanization, larger brains, and lower brood values (Fig. 3 and Supporting information). A broader habitat niche also loaded

Table 1. Establishment success of avian species according to their association with human-altered environments in the native range. The association with human-altered environments is presented as (a) occurrence in human-altered environments in native range (halt-occurrence=occurrence in human-altered versus absence as reference factor) (n=202 species); (b) occurrence in urban areas in native range (urb-occurrence=occurrence versus absence as reference factor) (n=202); (c) urban tolerance, estimated by the urban tolerance index (UTI) (n=86 species) and (d) by community simulations (exploiter versus avoider as reference factor) (n=72 species). CI is the credible interval (lower and upper 95%) in the Bayesian generalized linear mixed model and pMCMC is the posterior probability for the parameter not being different from zero. Credible intervals do not overlap zero. Significant (< 0.05) pMCMC values are in bold.

|  | Posterior mean       | Lower-95% CI          | Upper-95% CI         | Sampling effect | pMCMC            |
|--|----------------------|-----------------------|----------------------|-----------------|------------------|
| (a) Occurrence in human-altered environments |                      |                       |                      |                 |                  |
| Fixed  |                      |                       |                      |                 |                  |
| Halt-occurrence                              | 1.47 <sup>e-01</sup> | -1.01 <sup>e+00</sup> | 1.35 <sup>e-01</sup> | 100 000         | 0.81             |
| Introduction effort                          | 3.20 <sup>e-05</sup> | 5.40 <sup>e-06</sup>  | 6.10 <sup>e-05</sup> | 2127            | <b>&lt;0.001</b> |
| Random                                       |                      |                       |                      |                 |                  |
| Phylogeny                                    | 3.57                 | 2.58 <sup>e-07</sup>  | 9.70                 | 58 982          | –                |
| Species                                      | 4.91                 | 1.73                  | 8.68                 | 67 155          | –                |
| Location                                     | 4.15                 | 0.28                  | 9.60                 | 81 560          | –                |
| (b) Occurrence in urban environments         |                      |                       |                      |                 |                  |
| Fixed  |                      |                       |                      |                 |                  |
| Urb-occurrence                               | 1.09                 | -2.04 <sup>e-01</sup> | 2.38                 | 94 992          | 0.09             |
| Introduction effort                          | 3.12 <sup>e-05</sup> | 4.28 <sup>e-06</sup>  | 5.91 <sup>e-05</sup> | 2066            | <b>0.001</b>     |
| Random                                       |                      |                       |                      |                 |                  |
| Phylogeny                                    | 2.41                 | 1.05 <sup>e-09</sup>  | 7.53                 | 59 513          | –                |
| Species                                      | 4.84                 | 1.77                  | 8.42                 | 69 719          | –                |
| Location                                     | 4.21                 | 0.37                  | 9.73                 | 79 784          | –                |
| (c) Urban tolerance index                    |                      |                       |                      |                 |                  |
| Fixed  |                      |                       |                      |                 |                  |
| UTI  | 2.69 <sup>e-01</sup> | 7.56 <sup>e-02</sup>  | 4.74 <sup>e-01</sup> | 100 000         | <b>0.006</b>     |
| Introduction effort                          | 3.29 <sup>e-05</sup> | 5.73 <sup>e-06</sup>  | 6.22 <sup>e-05</sup> | 2044            | <b>0.001</b>     |
| Random                                       |                      |                       |                      |                 |                  |
| Phylogeny                                    | 1.06                 | 1.75 <sup>e-11</sup>  | 4.76                 | 74 019          | –                |
| Species                                      | 3.47                 | 0.57                  | 7.13                 | 84 768          | –                |
| Location                                     | 4.98                 | 0.22                  | 12.87                | 84 146          | –                |
| (d) Exploiter–avoider                        |                      |                       |                      |                 |                  |
| Fixed  |                      |                       |                      |                 |                  |
| Exploiter                                    | 3.11                 | 0.95                  | 5.34                 | 83 497          | <b>0.002</b>     |
| Introduction effort                          | 0.03 <sup>e-02</sup> | -0.02 <sup>e-02</sup> | 0.09 <sup>e-02</sup> | 97 727          | 0.229            |
| Random                                       |                      |                       |                      |                 |                  |
| Phylogeny                                    | 2.23                 | 2.23 <sup>e-07</sup>  | 9.56                 | 58 804          | –                |
| Species                                      | 9.43                 | 2.08                  | 19.43                | 57 677          | –                |
| Location                                     | 8.57                 | 0.57                  | 22.49                | 63 135          | –                |

in the same axis of the invasion potential and urban tolerance, although its contribution was lower (Supporting information).

We explored the causal structures linking the above variables with a phylogenetic path analysis (Fig. 4a–c, Supporting information). Two causal models provide a good fit to the data ( $\Delta\text{CICc} \leq 2$ , Supporting information). These models were nested, sharing the same paths except one. The top-ranked causal model fits with a scenario in which the existence of traits to cope with novel environments enhances the invasion potential and improves, in turn, tolerance to urban environments (Fig. 4c and Supporting information). The alternative models tested showed relatively poorer fit to the data, with  $\Delta\text{CIC}$  values always  $>3.65$ .

## Discussion

Growing evidence for plants, invertebrates, and vertebrates indicate that NIS mostly proliferate in human-altered environments, notably urban areas, and rarely expand to less

modified environments (Case 1996, Cadotte et al. 2017, Nordheimer et al. 2018; this study; but see Redding et al. 2019). A recent meta-analysis for instance showed that NIS from taxa such as plants and invertebrates reach their highest abundances in urban areas (Cadotte et al. 2017). Evidence is also accumulating that successful NIS are often associated with human-altered environments in their native ranges (Sol et al. 2002, Møller et al. 2015, Kalusová et al. 2017, Cardador and Blackburn 2019). Among European plants, for example, species that occur in human-altered habitats had a higher probability of naturalization than species confined to wildland areas (Kalusová et al. 2017). Our comprehensive analysis does not only confirm these patterns for birds but also provides novel insights into the underlying causes. First, we found that birds associated with human-altered environments in their native range were more frequently transported and introduced from one location to another than species that are restricted to less modified environments. Their broad distribution (Dyer et al. 2016b), high abundance near human settlements (Møller and Díaz 2017), and their habituation to

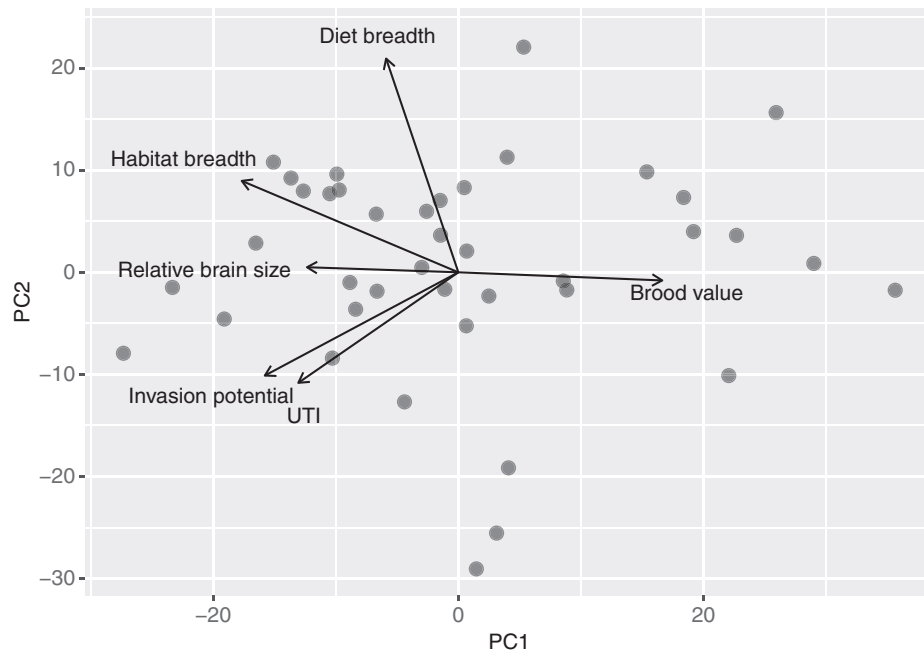


Figure 3. Phylogenetic principal components analysis showing the loading of invasion potential, urban tolerance, relative brain size, brood value, habitat, and diet breadth. The first two phylogenetic principal components are showed (31.8% for PC1 and 19.6% for PC2). Points represent 40 avian introduced species for which data for all variables were available. The length of arrows represents the loading of each variable on the phylogenetic principal components (Supporting Information).

people (Mason et al. 2013) may facilitate their progression through the stages of capture, captivity, and transport during the invasion process. Second, we found that species that proliferate in urban areas in their native range were also more

likely to become established when introduced to non-native regions worldwide compared to species that avoid urban environments. Our results not only generalize previous findings by Møller et al. (2015), who reached similar conclusions

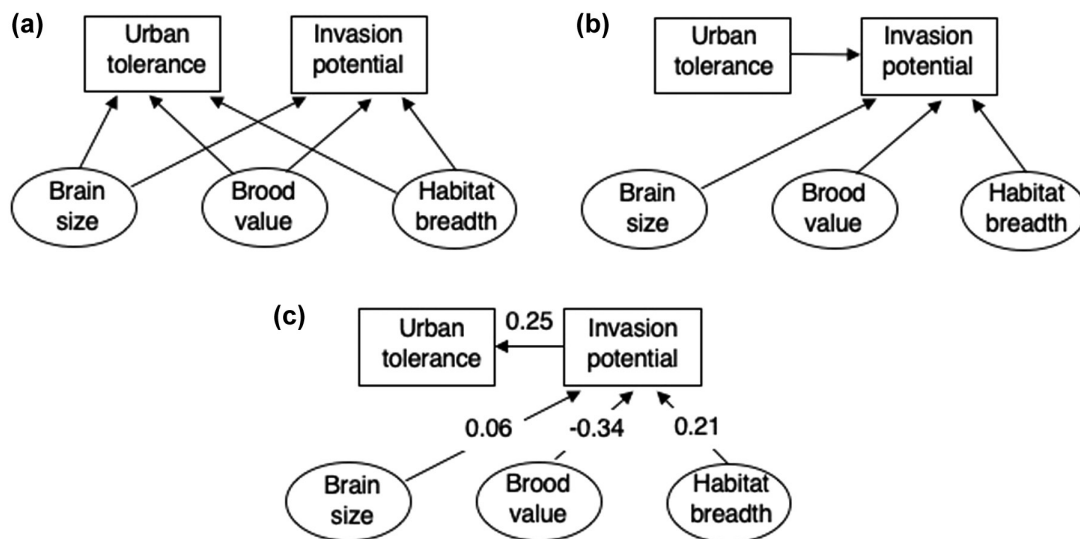


Figure 4. General structures of path models potentially explaining the link between invasion potential and urban tolerance. We tested all these path models, plus all the variants that arise of causally combining the traits. (a) Common causal scenario in which the association between urban tolerance and invasion potential arises because both attributes are affected by similar traits. This is to be expected if there exist traits that confer advantages to cope with novel environments in general. (b) Direct effects scenario in which urban tolerance has a direct effect on the invasion potential, indicating the existence of unmeasured traits that enhance the invasion potential by enabling to fill particular niches created by human activities. (c) Indirect effects scenario in which the traits affect the invasion potential, which in turn affects urban tolerance (best-supported model;  $\Delta\text{CIC}$  values  $< 2$ ). Arrows show direct effects; the direction and strength of the effect are indicated with the sign and numerical values (i.e. the standardized path coefficient). The effect of diet breadth has also been investigated but it was not included in the top-ranked model and for the sake of simplicity is not presented here.



in an analysis of birds introduced to Pacific islands, but also suggest that the pattern does not merely reflect that urban tolerant species are introduced in larger numbers. Rather, our analyses support the existence of some attributes of species that preadapt them to cope with new environments in general, among them urbanized environments.

Urban areas are novel in many ways: natural vegetation is replaced by built-up structures, resource opportunities become mostly of anthropogenic origin, and human disturbances become very frequent (McKinney 2002). Coping with the challenges of ‘anthropogenic niches’ (sensu Hulme-Beaman et al. 2016) thus requires traits that help reduce adaptive mismatches and environmental uncertainties (Sol and Maspons 2016). One of these traits can be a large brain, relative to body size, which is thought to confer enhanced learning abilities (Lefebvre et al. 1997, Reader and Laland 2002, Overington et al. 2009). Behavioral adjustments, for instance, are considered to be particularly important to successfully confront urban environments, where persistence largely depends on the animal’s capacity to improve resource use, communication, and disturbance avoidance (reviewed by Sol et al. 2013). Our results also support the view that a broad habitat niche should be part of such a life history strategy to cope with environmental changes (Sol et al. 2016). A broad niche is widely thought to facilitate persistence in novel environments, including urban areas (Evans et al. 2011, Sol et al. 2014), because it increases the likelihood of finding an appropriate niche in a novel context. Finally, our results align with previous evidence that a life history that prioritizes future over present reproduction (i.e. a low brood value) may be beneficial to invade novel, human-altered environments. Such a strategy reduces the fitness cost of a reproductive failure and provides more time to acquire environmental information and develop behavioral responses, facilitating population persistence when individuals are exposed to adaptive mismatch and environmental uncertainties (Sol et al. 2012b, 2014, Sol and Maspons 2016).

Our analyses do not deny the case-by-case importance of adaptive specializations to thrive in urban environments. Although other tested models show relatively poorer fit to the data (as the  $\Delta\text{CIC}$  values are  $> 2$ ), the possibility that it is the urban tolerance which influences invasion potential or that both are influenced by the common effect of the traits cannot be discounted (Hardenberg and Gonzalez-Voyer 2013). However, the best supported models indicated that general adaptations to cope with novel challenges are more important.

Our findings thus align with recent work suggesting that most urban species are not urban specialists nor restrict themselves to artificial habitats; rather, they are capable of using a wide array of natural habitats in their native ranges (Ducatez et al. 2018). Therefore, the observation that NIS did not generally expand toward natural vegetation does not necessarily reflect that they cannot persist in such habitats. Alternative explanations may include strong biotic resistance, behaviorally induced preferences for urbanized environments and/or time lags in more recent introduction events (e.g. wildlife trade) (Abellán et al. 2017, Tsang et al. 2019).

There is a long-running line of enquiry in invasion biology about the relative importance of species traits versus characteristics of the recipient environment (Duncan et al. 2003, Redding et al. 2019, Evans et al. 2021). Our study highlights the importance of considering both to fully understand the success of biological invasions. Thus, a species that is preadapted to exploit urban environments is more likely to be transported to other regions and be introduced to environments with similar features. This presents them with ecological opportunities that are unavailable to many natives species. Released from enemies, these species may proliferate and expand. Our results also highlight the importance of considering the features of introduction events and how they interact with species traits and community characteristics. Thus, by determining which, where and how species are introduced, human activities may be facilitating the successful proliferation of many NIS. This framework improves our understanding as to why many non-indigenous birds are so successful when introduced in novel environments.

Anthropogenic activities are interfering with ecological processes in many ways (McGill et al. 2015). Our results add to this growing literature, highlighting that the pervasive influence of human activities may explain why some NIS are so successful in novel urban environments. The implications of our results for preventing and mitigating the impact of biological invasions are important, as urban areas are predicted to continue to expand (Seto et al. 2012) and our results suggest that the trend to introduce species preadapted to urban environments is not diminishing.

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(equal); Writing – review and editing (equal). **Daniel Sol Rueda**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Software (supporting); Supervision (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

## Transparent Peer Review

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## Data availability statement

Data are available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.dr7sqv9zr>> (González-Lagos et al. 2021).

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