



Vacant niches help predict invasion risk by birds

Pamela González-del-Piiego¹ | Manuel Mendoza² | Joana Santana^{3,4} | Joana Ribeiro⁴ |
Luís Reino^{3,4} | Miguel B. Araújo^{1,2}

¹Rui Nabeiro Biodiversity Chair, MED Institute, Universidade de Évora, Évora, Portugal

²Department of Biogeography and Global Change, National Museum of Natural Sciences (CSIC), Madrid, Spain

³CIBIO/InBIO, Research Centre in Biodiversity and Genetic Resources, University of Porto, Vairão, Portugal

⁴CIBIO/InBIO, Instituto Superior de Agronomia, Universidade de Lisboa, Lisbon, Portugal

Correspondence

Pamela González-del-Piiego, Rui Nabeiro Biodiversity Chair, MED Institute, Universidade de Évora, Évora, Portugal.
Email: pgonzalezdelpiiego@gmail.com

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Abstract

Aim: If communities have a ceiling determining the number of species that can coexist, then the ability of alien species to establish at any given location should be related to the quantity of vacant niches available. We developed a new approach to estimate the extent to which niches are vacant and then explored the relationship between vacant niches and alien species.

Location: Global with focal tests in Europe and North America.

Taxon: Birds.

Methods: Drawing on a global classification of trophic structures for birds, we calculated a 'vacant niche ratio' metric to quantify the expected level of saturation (i.e. number of vacant niches) for each 1° × 1° grid cell globally, based on the difference between expected and observed numbers of bird species for all trophic guilds. Next, we used random forests to examine if the presence of plant-invertivore (whose food source represents plants, seeds, fruits and invertebrates) and granivore alien bird species was associated with the vacant niche ratio across well-sampled regions.

Results: In Europe, we found a significant relationship between alien species and vacant niches, with greater numbers of alien species being found in communities that offered greater numbers of vacant niches overall, and across habitat types. In North America, we found no significant relationship between plant-invertivores and vacant niches, while for granivores, we found that areas with fewer vacant niches had greater numbers of alien species, especially in forests. However, vacant niches alone correctly predict 69% of the presence of alien bird species when combining both regions and trophic guilds.

Main Conclusions: Most regions of the world have unsaturated bird communities, with the level of saturation in communities varying within regions and trophic guilds. We found that although often-neglected, vacant niches are likely to be, at least partially, related with the successful establishment of alien bird species.

KEYWORDS

alien species, avian, trophic guilds, trophic structure, unsaturated communities, vacant niches

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1 | INTRODUCTION

The idea that nature sets a limit to the number of individuals and species that coexist in any given place has been discussed for over half a century (Elton, 1958). Implicit is the notion, which is consistent with the first law of thermodynamics, that communities are limited by the quantity of energy or resources available to producer and consumer species (MacArthur, 1970). Yet, the idea of community saturation is hard to formalise let alone measure empirically. Issues raised in the literature range from questioning the very existence of a maximum ceiling for species coexistence (Harmon & Harrison, 2015; Herbold & Moyle, 1986) to discussions regarding its association, if any, with the establishment of alien species (Herbold & Moyle, 1986; MacArthur, 1970). The related concept of 'vacant niche' (=empty/unsaturated) refers to unused but potentially usable resources in communities (Elton, 1958; Hardy, 1967); a concept that regained interest in studies of the processes triggering biological invasions (Dong et al., 2020; Gauzere et al., 2020; Gray et al., 2019). If one accepts that assemblages have varying degrees of saturation (Rohde, 2008) (for a summary of ideas on saturation see Table 1) and resources set an upper limit on diversity (MacArthur & Levins, 1964), then it follows that the ease with which alien species establish in a community relies upon the number of vacant niches available in a given community (Johnstone, 1986; Rohde, 2005; Sax et al., 2002). These are not new ideas. The influential ecologist MacArthur (1970) proposed that 'where the utilizations [of resources] fall slightly below the production, a new species can enter [a community] if the addition of one pair (or propagule) will make the total utilisation closer to the

available production. For this reason, more productive environments will hold more species'. It follows from this view that the risk of establishment of alien species should increase with increased availability of unused (vacant) resources (niches). Recent studies have provided empirical support to this view showing that a positive relationship between vacant niches and biological invasions can be found (Brym et al., 2011; Dong et al., 2020).

However, difficulties in quantifying the degree of saturation within communities have restricted understanding of the patterns and processes underlying niche vacancy; thus, limiting the ability to firmly establish links between vacant niches and biological invasions. To address this issue, we develop a novel methodology that estimates biogeographic-level saturation within communities. The approach begins with a characterisation of trophic structures, describing how species are distributed within trophic guilds and how guilds coexist with each other (Mendoza & Araújo, 2019). Here, we used six well defined community trophic structures that were estimated by analysing bird species feeding preferences and their global distributional co-occurrence (Mendoza & Araújo, 2022). Our working hypothesis is that for any given community trophic structure (i.e. grid cells on the map belonging to the same trophic structure), the maximum number of observed species across communities represents the saturation point. Any departure from this estimated saturation would thus result in a quantity of niche vacancy (Figure 1). We note that saturation might not be realised anywhere in the world (Harmon & Harrison, 2015; Mateo et al., 2017), in which case the estimated maximum saturation is not absolute but relative to existing configurations of trophic

TABLE 1 Summary of ideas supporting the notion that communities have varying degrees of saturation.

Main idea	Brief description	References
Exceeding carrying capacity can collapse a population	Reindeer <i>Rangifer tarandus</i> population exceeded the carrying capacity and caused the population to crash	Klein (1968)
Communities are unsaturated	Communities of plant-feeding insects are not fully saturated with species, indicating that there are unutilised or partially unutilised resources (vacant niches)	Lawton (1982) and Lawton and Price (1979)
High proportion of vacant niches	Between 12% and 54% of niches of marine invertebrates are vacant	Walker and Valentine (1984)
Opportunity window	The successful establishment of alien species increases with the availability of vacant niches in their non-native range	Johnstone (1986)
Exceeding carrying capacity can decline a population	Alien species may experience a rapid increase in population density, followed by a decline. Examples of such species include the Little owl <i>Athene noctua</i> , the Rhododendron lace bug <i>Stephanitis rhododendri</i> , the Canadian pondweed <i>Elodea canadensis</i> and the Red-billed leiothrix <i>Leiothrix lutea</i> .	Berger (1981) and Williamson and Brown (1986)
Exceeding carrying capacity can result in local extinction	When an alien species population surpasses the carrying capacity of the environment, it can suffer local extinctions. A very frequent example of such species is the rabbit <i>Oryctolagus cuniculus</i> .	Thompson and King (1994)
Carrying capacity can be reached	Bird species richness, in some islands, has reached its carrying capacity, as the number of native species that have gone extinct is comparable to the number of established alien species.	Sax et al. (2002)
Not all communities are at carrying capacity or saturated	Plant species richness, in some islands and counties is still increasing, indicating that they have not reached their carrying capacity	Sax et al. (2002) and Stohlgren et al. (2008)
Alien species can reach a peak of population density	An alien species that is highly successful shortly after its introduction can get reduced in its population or even become extinct	Simberloff and Gibbons (2004)

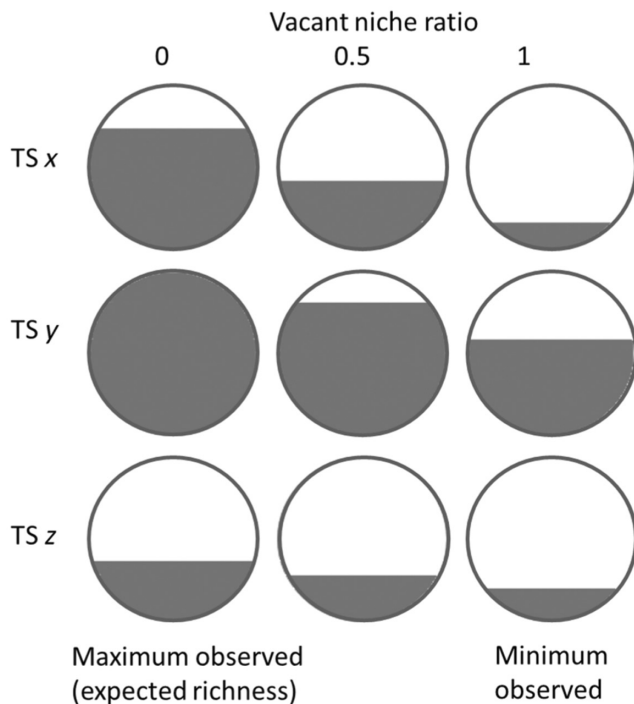


FIGURE 1 Vacant niche ratio. Representation of vacant niche ratio calculation for a given guild. Each row represents a trophic structure (TS x, y and z). The filling (grey) represents maximum observed richness per trophic structure (left column) and minimum richness (right column) across grid cells (circles). All grid cells in the middle column show a vacant niche ratio of 0.5 yet they have different species richness (grey filling) due to the differences in the maximum and minimum observed richness across trophic structures (see Section 2.5).

structures. With that potential caveat in mind, we calculated a 'vacant niche ratio' [see Equation (1) in Section 2] to quantify the relative level of saturation for each guild and trophic community at grid-cell level globally, with values ranging from 0 (saturated community) to 1 (unsaturated). Next, we used Random Forests (Breiman et al., 1984) to assess if the incidence of alien species was associated with vacant niche ratio in the two regions where reasonably good data for alien bird species exists (Europe and North America). For this analysis, we focused on plant-invertivores and granivores since they are the groups with the greatest numbers of alien species worldwide. We then examined how well models of niche vacancy predicted the binary classification of presence of alien bird species across these regions and habitat types.

2 | MATERIALS AND METHODS

2.1 | Overview

We classified all birds into nine trophic guilds based on their feeding preferences. Then, we obtained six global trophic structures for birds, within a global $1^\circ \times 1^\circ$ grid system, obtained from clustering groups of coexisting guilds weighted by the numbers of species

found within each guild. The maximum number of species recorded per guild and trophic structure was used as the saturation point. At each location, the departure from saturation was interpreted as an estimation of the quantity of vacant niches for both grid cells and guilds. Additionally, we gathered and mapped the distribution of alien bird species across the grid system. We used random forests (Breiman et al., 1984) to assess if the presence of alien species is related to the level of saturation across two well-sampled regions (Europe and North America) and expressed models' outputs as accuracy, that is a metric of how accurately models correctly predict the binary classification of presence of alien bird species. Finally, we assessed if the relationship of the presence of alien species with the number of vacant niches differed within the most common habitat types used by alien species (forests and croplands).

2.2 | Native spatial data

We used birds because they have been recorded over broad temporal scales and across their native and alien distribution (GBIF, 2020; IUCN, 2020). We extracted the native global distribution ranges of 9993 bird species from (Birdlife, 2014), and plotted their geographical distribution in a world terrestrial $1^\circ \times 1^\circ$ grid system, totalling 18,418 grid cells. Bird occurrences within each grid cell were used to produce a presence-absence matrix with all bird species as columns and all grid cells as rows. No records for species occurring in Antarctica were used.

2.3 | Identifying community trophic structures

To obtain global community trophic structures for birds, we considered the native species present in each $1^\circ \times 1^\circ$ grid cell as a 'community'. The assumption of homogeneity within cells is disputable (see 'Spatial scale' section in Appendix S1) but necessary in regionalisation exercises at both global (e.g. Holt et al., 2013; Mendoza & Araújo, 2019, 2022) and regional levels (e.g. Rodrigues et al., 2015). We used the nine trophic guild categories previously identify by Mendoza and Araújo (2022): carnivores, frug-invertivores, frugivores, generalist-invertivores, granivores, nectarivores, plant-invertivores (group whose food source is represented by plants, seeds, fruit and invertebrates), plantivores and specialist-invertivores. Next, we counted the number of species per guild within each cell, resulting in a matrix with 18,418 communities as rows, the nine trophic guilds as columns, and values representing numbers of species. The trophic profile of every community is thus a point in a 9-dimensional 'community-level trophic space' defined by the number of species from each trophic guild (a vector of dimension 9). To test for the existence of well-defined clusters (interpreted as distinct trophic structures), we applied the AMDi analysis (index of average membership degree) developed by Mendoza and Araújo (2019) and implemented by Mendoza and Araújo (2022), which uses fuzzy c-means clustering, on the basis of the Euclidean distance between

the communities in this community-level trophic space. This analysis revealed six trophic structures around the world.

2.4 | Alien species spatial data

To obtain the alien range of species, we used the global database on alien species distributions for birds (Dyer et al., 2017), which includes 355 established non-marine bird species. We obtained their alien distribution through literature search using the Global Biodiversity Information Facility database (GBIF, 2020), and the International Union for the Conservation of Nature range maps (IUCN, 2020) (see 'Alien species spatial data' section in Appendix S1).

More than half of the 355 alien species considered belong to two trophic groups: plant-invertivores (98 species) and granivores (101 species). Subsequent analyses focused on these two trophic guilds as they represent the only groups whose number of alien species represent more than 10% of the total number of native species from the same guild and also have a minimum of 10 species distributed in each of the regions considered in this study (Table S1). We plotted their geographical distributions into the 1°×1° global grid system with a WGS84 coordinate system and the distribution of each alien bird was associated with the grid cell they overlapped with, creating a presence-absence matrix of alien bird species as columns and grid cells as rows (see 'Alien species spatial data' section in Appendix S1 regarding our decision to use presence-absence data). While bird alien species are distributed across all six community trophic structures detected worldwide, data quality is unevenly distributed across trophic structures (Figure S1). Consequently, we restricted testing of the relationship between niche vacancy and the presence of alien species to the two geographical regions with greater data quality and quantity on alien species: European region (620 grid cells; see 'Alien species spatial data' section in Appendix S1 for a list of countries included) and North America region (encompassing Canada and United States; 2017 grid cells). These two regions comprise 44 and 30 species of plant-invertivores and granivores, respectively (Europe: 24 and 24; North America: 30 and 14 species of plant-invertivores and granivores, respectively) and encompassed four trophic structures (TS1–4; Tables S2 and S3). Two trophic structures were not included in the analyses as they did not overlap with the selected regions (TS5–6; Figure S2) and one trophic structure was further excluded due to its depauperated nature/configuration (TS1; Mendoza & Araújo, 2019), resulting in 2333 analysed communities (i.e. grid cells).

2.5 | Estimating vacant niche ratio

Each one of the 18,418 communities (i.e. terrestrial grid cells of the world) were classified into one of the six trophic structures. We recorded the maximum and minimum number of species per guild within each of the six trophic structures. We make the 'working assumption' (i.e. a simplification required for model building rather

than a rigorous assertion; Araújo & Peterson, 2012) that the maximum recorded number of species per guild found in each trophic structure is the maximum possible number (i.e. saturation point). If the number of species found in a given guild and trophic structure equals the maximum recorded anywhere in the world, in a similar guild and trophic structure, then the trophic community is classified as 'saturated' and is expected to offer few to no vacant niches. In contrast, if the number of species found is below the maximum recorded number for the guild and trophic structure, then the community would theoretically offer vacant niches and potentially house more species. Thus, the greater the distance from saturation, the greater the expected potential for invasion by non-native species. Furthermore, since climate determines the type of trophic structure of a community (Mendoza & Araújo, 2019), the saturation point of each guild is at least partially determined by the climate of the region in which the community is located.

The vacant niche metric was calculated as a ratio representing a relative deficit (i.e. the difference between observed and maximum recorded species richness within each guild). We estimated the vacant niche ratio as follows:

$$\text{Vacant niche ratio} = 1 - \left[\frac{S - \min(S)}{\max(S) - \min(S)} \right], \quad (1)$$

where S is the number of species from a specific guild found in a community (i.e. within a grid cell) belonging to a specific trophic structure, \min is the minimum number of species from all the possibilities of S and \max is the maximum richness from all the possibilities of S .

Following Equation (1), the vacant niche ratio goes from 0 (the community has the maximum recorded number of species in that trophic structure, thus being qualified as saturated and with the lowest potential number of available vacant niches) to 1 (the community has the minimum recorded number of species and the highest potential number of available vacant niches) (Figure 1). We calculated a vacant niche ratio for each guild and community, which resulted in nine different vacant niche ratios per community (Figure S3).

2.6 | Propagule pressure and human impact

We obtained two additional metrics related to invasion success: propagule pressure (number of individuals introduced; Lockwood et al., 2005) and human impact (Sanderson et al., 2002). As a proxy for propagule pressure, we calculated the number of living wild bird individuals imported per country from 1975 to 2000 from CITES (see 'Propagule pressure' section in Appendices S1 and S2). While CITES has known limitations (see 'Propagule pressure' section in Appendix S1; see also [Naimi et al., 2022]), it represents the only global, legally binding, structured convention addressing international trade in wildlife (Reino et al., 2017). We normalised the trade data and created a propagule pressure metric that goes from 0 (no imported individuals) to 1 (maximum number of imported bird individuals). For human impact, we extracted a global human footprint index for each community from the NASA socioeconomic data and

applications centre (Wildlife Conservation Society & Center for International Earth Science Information Network, 2005). This human footprint index is expressed as a percentage with values ranging from 0 (lowest human impact) to 100 (most impacted, least wild) and has been shown to relate with metrics describing the trophic organisation of communities worldwide (Mestre et al., 2022).

2.7 | Habitat type preference of alien species

We extracted the land-cover category linked with each community to determine whether the relationship between the presence of alien species and the number of vacant niches differed within habitat types. We used the European Space Agency (ESA) global land cover map, which spans the period from 2008 to 2012 (ESA, 2017). Given the geographical extension of each grid cell, more than one land cover is normally found in each grid cell. Thus, we obtained all the land-cover categories from the centroid of each grid cell to a buffer area of 50 km using the `extract` function from the `raster` package 3.6-14 (Hijmans & Van Etten, 2020) and used the mode to obtain the predominant land-cover per community. We then assessed the vacant niche ratio of grid cells within the two habitat types where most alien species (84% and 67% for Europe and North America, respectively) were found: forests and croplands. To evaluate whether significant differences existed in the incidence of alien species and vacant niche ratio across the different regions and habitats we performed a Kruskal–Wallis test, which is robust to non-normality in the data (see Figure S4 for all habitats).

2.8 | Random forest model approach and evaluation

We used random forests (Breiman et al., 1984) to detect the role of vacant niches in determining the distribution of alien species. We used the presence–absence of alien species as a response variable. To determine the importance of the vacant niche ratio as predictor variable, we fitted models with the following four predictor variable combinations: (a) vacant niche ratio (see 'Supplementary analysis' in Appendix S1 regarding random forests with one predictor); (b) vacant niche ratio + propagule pressure (number of individuals introduced; Lockwood et al., 2005); (c) vacant niche ratio + human footprint index (Wildlife Conservation Society & Center for International Earth Science Information Network, 2005); and (d) vacant niche ratio + propagule pressure + human footprint index.

Spatial data encompassed the two regions selected in Section 2.4: Europe and North America. The models were evaluated on regions excluded during the model fitting process to decrease the effects of spatial autocorrelation and the regional bias of bird distribution data on predictions (e.g. Dormann et al., 2007; Segurado et al., 2006). As we evaluated the models on excluded regions, three regional combinations were executed during the evaluation analyses: (a) fit model in Europe and evaluate in North America (i.e. create a random

forests model with spatial data from Europe. Subsequently, evaluate the model by predicting the presence-absence of alien species in North America and assess the accuracy of the predictions); (b) fit in North America and evaluate in Europe; and (c) fit the model with 60% of data from both regions and evaluate the model in the 40% remaining data.

Overall, four predictor combinations and three regional combinations were obtained, totalling 12 models representing the predictor-regional combinations. Each of these models were fitted using equal-sampling (Barbet-Massin et al., 2012), meaning that we balanced the training data (following Valavi et al., 2021). Each model was replicated 100 times across two replication methods (50 for bootstrapping and 50 for subsampling performed in 30% of data), totalling 1200 models, implemented via the `'sdm'` package 1.1-8 (Naimi & Araújo, 2016) in the R 3.6.3 statistical programming language (R, 2020). To determine how accurately each model correctly predicted the binary classification of presence of alien bird species, we measured the accuracy of the predictions from the validation analysis as follows:

$$\text{Accuracy} = \frac{(\text{true presences} + \text{true absences}) * 100}{(\text{true presences} + \text{true absences} + \text{false presences} + \text{false absences})}$$

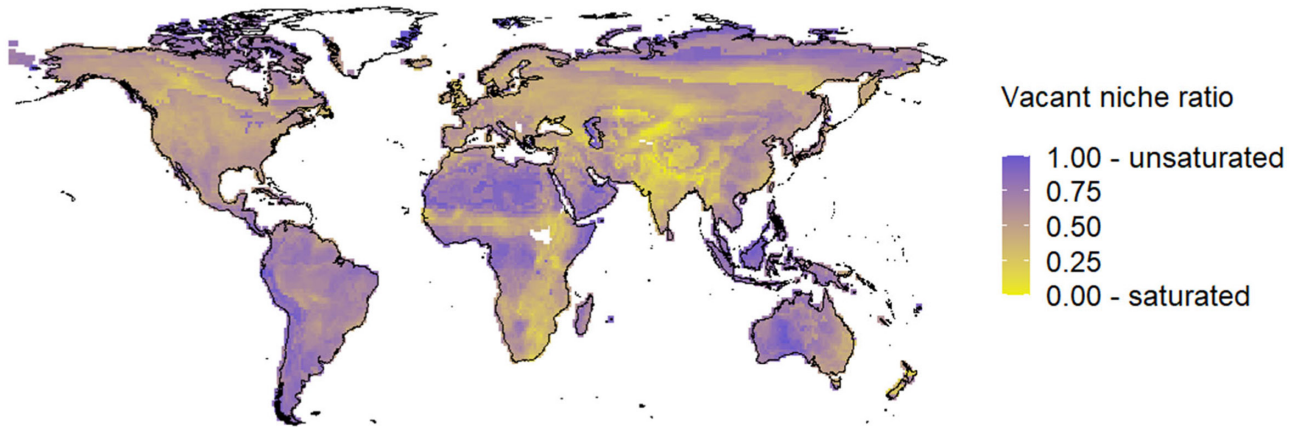
We calculated accuracy for each of the 1200 models and obtained the mean accuracy for each of the 12 unique predictor-regional combinations models. We also obtained two indices for discrimination ability: area under the curve (AUC; values close to 1 represent models with good predictive performance), and true skill statistic (TSS; values below zero represent a poor model, and values higher than 0.20, 0.40 and 0.60 represent fair, moderate and substantial discriminatory ability, respectively; Landis & Koch, 1977). The same method was replicated both for plant-invertivores and granivores, totalling 2400 models, and thus 24 mean accuracy, AUC and TSS outputs (see 'Supplementary analysis' in Appendix S1 for a predictor-regional combination list).

3 | RESULTS

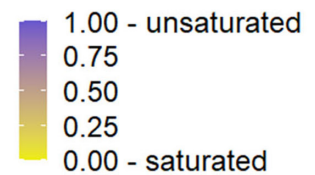
The level of community saturation differs across trophic guilds and regions, with hot deserts and polar regions being primarily characterised by unsaturated communities (Figure 2; Figure S3). Communities, overall, are more likely to show a low level of saturation, that is with the vacant niche ratio closer to 1 than 0. Indeed, 75% of the communities have a vacant niche ratio >0.5 (first quantile range across all guilds = 0.33–0.94), 50% of communities have a vacant niche ratio >0.70 (second quantile or median across all guilds = 0.51–1) and for 25% of the communities their vacant niche ratio was >0.89 (third quantile range across all guilds = 0.81–1).

Consistent with our original prediction, greater numbers of alien plant-invertivore and granivore species in Europe were found in communities that offered greater numbers of vacant niches overall (Figure 3); a pattern also repeated when analysing communities in forests and croplands separately (Figure 3b,c,e,f). In North America, plant-invertivores showed no discrimination toward vacant

Plant-invertivores



Vacant niche ratio



Granivores

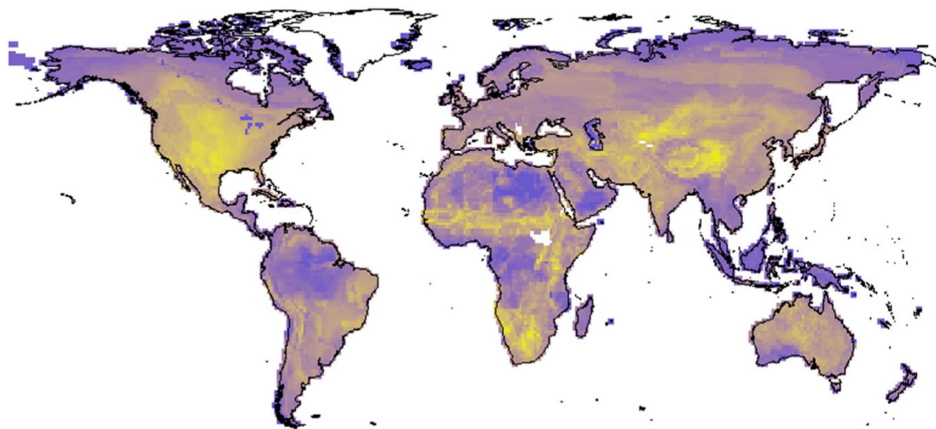


FIGURE 2 Geographic distribution of vacant niche ratio. Vacant niche ratio for plant-invertivore (upper panel) and granivore (lower panel) alien bird species globally. Vacant niche ratio ranges from 0 (saturated community with no vacant niches) to 1 (unsaturated community with great degree of niche vacancy). Maps are based on the geographical projection and WGS84 coordinate system.

niches overall and across all habitats. Contrary to our initial prediction, greater numbers of granivores were found in communities with a lower number of vacant niches in North America (Figure 3d). Interestingly, this negative relationship was significant in forests, but was not significant in croplands (Figure 3e,f).

During the fitting process, random forest models using vacant niche ratio alone performed well in discerning the presence of alien species across all three regional combinations (1: Europe, 2: North America, 3: Europe and North America combined; \bar{x} AUC=0.76; Table S4). Although, models fitted with more than one predictor variable can improve the models' performance compared to models with one predictor (Figure 4), the increase in performance of models with three predictors in both regions combined was not great (AUC increased 0.08–0.13; TSS increased 0.15–0.19; Table S4) compared to models using vacant niches alone due to the suitable performance of the latter.

When we evaluated predictive performance of the Random Forest models we found that using the vacant niche metric helped improve the models' ability to predict the incidence of alien

species. Models incorporating only vacant niches showed high accuracy when predicting the occurrence of alien species across both regions combined (\bar{x} accuracy=69%), while model discriminatory ability was slightly higher for granivores (AUC=0.67 and 0.77 for plant-invertivores and granivores, respectively). However, model performance was poor when using spatially independent test data (i.e. when models were fitted in regions different than evaluated ones; \bar{x} accuracy=47.4%, \bar{x} AUC=0.50; Table S5). This was true across all predictor combinations (\bar{x} AUC=0.51), emphasising the large dissimilarities between both regions. Moreover, when examining additional well-established predictors of invasion, on equal footing, niche vacancy still features prominently (models using human impact and propagule pressure alone were 2.6%–8.5% more accurate and had an increase of 0–0.06 on AUC, respectively, compared to models using vacant niches alone averaged across both trophic guilds and combining both regions). For plant-invertivores, model accuracy across both regions was highest when vacant niches and human footprint index were included

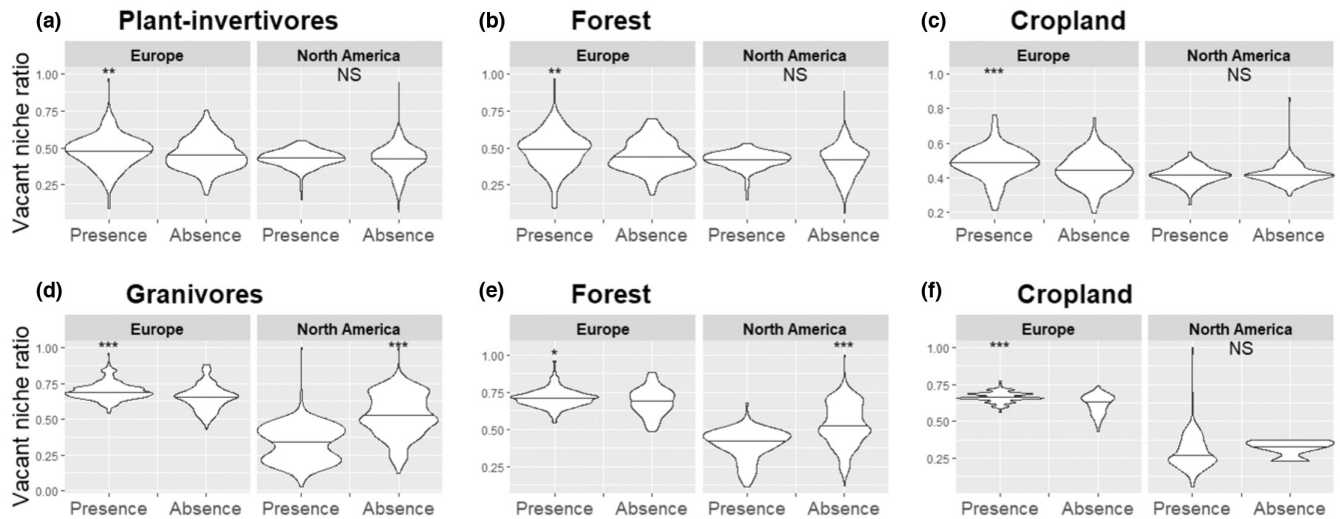


FIGURE 3 Presence–absence of alien bird species and vacant niche ratio. Distribution of presence–absence of plant-invertivore (a–c) and granivore (d–f) alien bird species according to vacant niche ratio per community in Europe and North America and across forests (b and e) or croplands (c and f). The line represents the median. NS, no significant differences between groups. Asterisks denoting significant differences are placed on top of the group with the higher vacant niche ratio and represent p values. * <0.05 ; ** <0.01 ; and *** <0.001 .

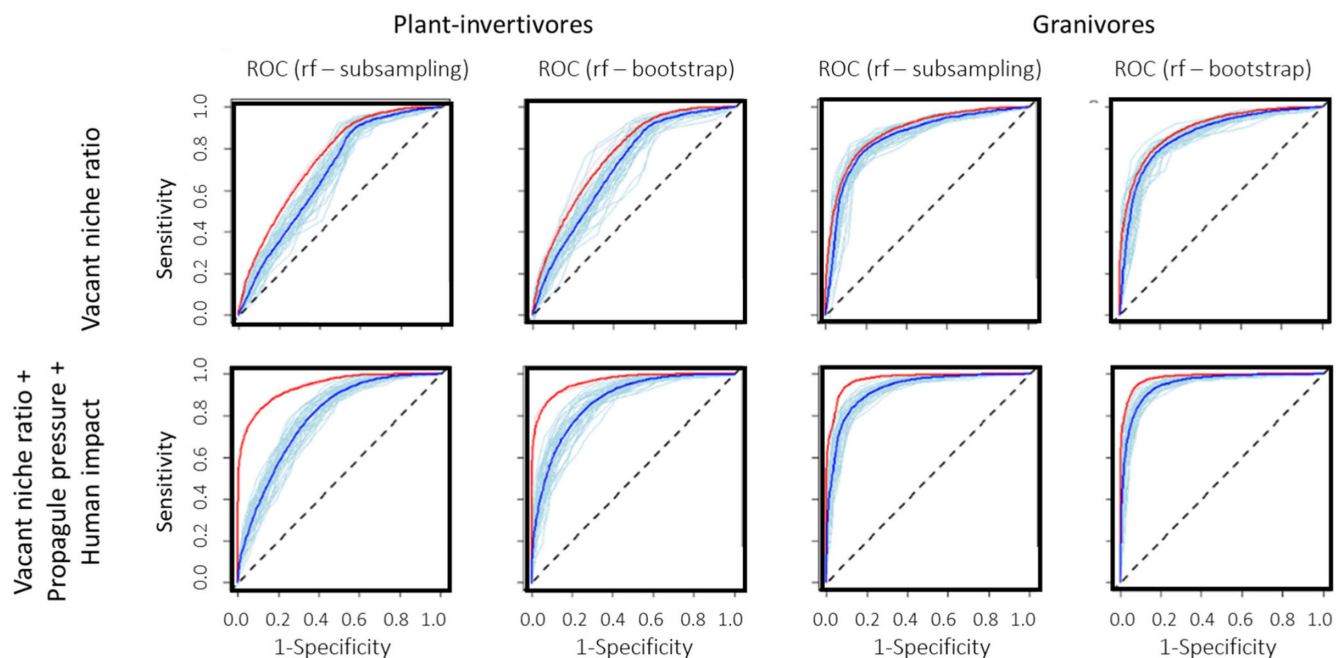


FIGURE 4 Random forests models' outcomes. ROC curves showing the relationship between true positive (sensitivity; y axis) and false positive (1 minus specificity; x axis) rates from the random forests model outcomes when using one predictor (upper panels) and three predictors (lower panels) for Europe and North America regions combined, for plant-invertivore and granivore alien bird species. The diagonal dash-line going from 0, 0 to 1, 1 represents the expected pattern if the predictions were no better than random at discriminating presence of species. The area under the curve (AUC), which varies between 0 and 1, is a measure of the model's ability to adequately characterise the fitting dataset, including the training (red) and out of bag dataset (blue line).

(increasing 10.7% in accuracy, on average, compared to models using only vacant niches). In contrast, for granivores, the highest accuracy was obtained using three predictors (accuracy was 4.9% higher, on average, than the accuracy obtained using only vacant niches). Unsurprisingly, the highest ability to predict the distribution of alien species was obtained when combining both

regions and all three predictors as model fitting is undertaken across all possible ranges of predictor values (\bar{x} accuracy = 78.6%, \bar{x} AUC = 0.79, \bar{x} TSS = 0.60; Table S5). These results were similar when performing the same analyses at sub-trophic level (see 'Supplementary analysis' and Table S6 and S7 in Appendix S1 for sub-level trophic structure analyses).

4 | DISCUSSION

Our study underscores the pivotal role vacant niches have in biological invasions. Empirical evidence has supported the view that alien species fill vacant niches in plant communities at local (Brym et al., 2011) and regional scales (Dong et al., 2020), and simulated communities at regional scale have also provided results consistent with such view (Gauzere et al., 2020). Our study is the first examining the link between alien species and community saturation at global scale and the results are partially consistent with the theoretical expectation that greater numbers of alien species should be found where more vacant niches are available (Johnstone, 1986; Moles et al., 2008). For example, in Europe, estimated vacant niches were positively related to avian invasions, suggesting that our metric of community saturation possibly captured a main driver of avian invasion across the continent. This result is consistent with the knowledge that Europe harbours strongly defaunated communities (e.g. Mendoza & Araújo, 2019) owing to a long history of land use, which has led to intensive modification and destruction of natural habitats (EEA, 2020). Our results are also consistent with the expectation that invasions are preferentially occurring where vacant niches abound. In contrast with the patterns observed across Europe, the relationship between alien species and vacant niches was negative or null across North America. Such a relationship could indicate that the distributional patterns of alien bird species are driven by other factors, or that lack of meaningful relationship between richness of alien species and vacant niches is, in effect, the outcome of confounding effects emerging from multiple drivers acting in combination. Alternatively, given that data on alien species distributions are not systematically collected, biases could emerge that confound assessments of relationships. Unfortunately, data on distributional ranges of alien species are largely absent from most parts of the world, and the comparison between estimated community saturation had to be restricted to two regions with data that are also far from perfect (Europe and North America), leaving aside most biodiversity-rich areas of the planet (e.g. tropical areas; Pillay et al., 2022).

More generally, as for most broad-scale ecological studies providing inferences of process from patterns, support for an expected relationship is no proof of a causal relationship. Likewise, lack of support for an expected relationship is not equal to disproving the existence of an expected underlying causal link. In other words, while the detected relationship between the numbers of alien species and our estimates of community saturation in Europe is promising and invites further scrutiny, we cannot firmly discard the existence of such a positive relationship between these two factors in North America. Indeed, there are just too many co-varying factors potentially causing variation in the incidence of alien species across geographical space (Brym et al., 2011; Dong et al., 2020) to expect a single bullet variable to explain it all. In spite of this, the vacant niche metric alone was largely successful in predicting 69% of the incidence of alien species in our targeted studied regions (across both trophic groups and combining both regions), which is encouraging.

In line with the co-varying factors and consistent with our expectations (e.g. Meier et al., 2010), accuracy on the predictions of the distribution of alien species increased 10% (combining both regions) when including other well-known drivers: human impact (Hobbs & Huenneke, 1992; Sanderson et al., 2002) and propagule pressure (Essl et al., 2020; Lockwood et al., 2005; Reino et al., 2017). This increase in accuracy was not surprising as human activities have been associated with biological invasions for over half a century (Bergamin et al., 2022; Elton, 1958) and continue to be one of the main drivers of alien invasions (Leprieur et al., 2008). On the other hand, propagule pressure has become more relevant with the increase in globalisation, transportation and trade (which increases the prevalence of alien species) (Humair et al., 2015; Pauchard et al., 2016; Reino et al., 2017) but it is not always a crucial driver of invasions at a global scale (Roura-Pascual et al., 2011). Furthermore, the constant interplay of biotic and abiotic determinants of biological invasions increases the difficulty of predicting future invasions (Roura-Pascual et al., 2011). For example, socio-political factors (Ribeiro et al., 2022) causing changes in the direction and intensity of propagule pressure (Reino et al., 2017; Thuiller et al., 2005), as well as projected climate change (e.g. Baquero et al., 2021; Peterson et al., 2008), land-use change (e.g. Cardador & Blackburn, 2019) and their interactions (e.g. Di Febbraro et al., 2019; Naimi et al., 2022; Vicente et al., 2019), are factors known to alter the patterns of invasion across taxonomic groups.

Despite our metric being estimated using a global approach, our results invite the interpretation that vacant niches are a partial determinant of the ease with which species become established in alien territory in some regions, thus revealing a potential driver of invasion that has rarely been considered in previous invasion risk assessments (e.g. ballast water, Casas-Monroy et al., 2014; pet trade, da Rosa et al., 2018; distance to roads and human population, Lanner et al., 2022). We suggest that the applicability of the vacant niche metric can be exploited to develop improved predictive models based on rigorous statistical inference. As our metric is not adequate for understanding all avian invasions, exemplified by the discrepancy of the relationship with vacant niches across regions, vacant niches should be more appropriately used as one of the explanatory variables, among others, to be included in a multi-model inference approaches to predict the incidence of alien species; an approach rarely used with alien species (Matos et al., 2022).

In this study, we demonstrate that although results are not consistent across regions, our metric of saturation was able to unravel a relationship between vacant niches and avian invasions in one of the targeted regions. Our study, thus, contributes to the pressing need to formulate scientifically sound methods and approaches in the growing field of invasion risk. As our results were only partially in line with our predictions, further understanding of the mechanisms regarding invasion will require approaches that incorporate further taxonomic groups (e.g. mammals, Mendoza & Araújo, 2022) and other global scales. Overall, our study underscores the potential importance that vacant niches may have in influencing the distribution of alien bird assemblages.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All datasets used in this paper are available via the citations identified in the Methods and in <https://datadryad.org/stash/landing/show?id=doi%3A10.5061%2Fdryad.nk98sf7st>.

CODE AVAILABILITY

R code for Random Forests models is available at <https://doi.org/10.5061/dryad.tdz08kq4r>.

ORCID

Pamela González-del-Pliego  <https://orcid.org/0000-0001-5390-3332>

Luís Reino  <https://orcid.org/0000-0002-9768-1097>

Miguel B. Araújo  <https://orcid.org/0000-0002-5107-7265>

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BIOSKETCHES

Our research team is an international network (including *Maraujo lab*) with a focus on the fields of biogeography, conservation biology, global change biology, macroecology and invasion biology. Our team integrates large climate and species distributions databases with descriptions of behavioural and physiological traits of species, molecular phylogenies and the fossil record. Most research in our team involves statistical analyses of ecological data, including data mining, bioclimatic modelling and mathematical simulations.

Author Contributions: P.G., M.M. and M.B.A. conceived the study. P.G. curated the data collection, built the models, and performed the analyses. P.G. and M.B.A. wrote the manuscript with contributions from all authors.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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