

Niche differences may reduce susceptibility to competition between native and non-native birds in oceanic islands

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Abstract

Aim: Few bird extinctions on oceanic island have been attributed to competition with non-native species, even though it might be an overlooked driver of biodiversity loss. We evaluate the potential competition between native and non-native island bird species, identifying species and island characteristics that enhance it and may promote future extinctions.

Location: Seventy-three (>100 km²) oceanic islands worldwide.

Methods: We compiled a species list for each island and used single-trait meta-analyses to assess differences between native and non-native species. Then, we used single-trait beta regression models to identify species traits linked to potential competition. Finally, we used a trait-based approach to calculate the potential competition between native and non-native species on each island and identify island characteristics linked to potential competition.

Results: Native bird species tended to be smaller forest dwellers, that were either carnivore, frugivore or insectivore, and that foraged in flight, in the canopy or at mid-height. In contrast, non-native birds tended to be open habitat granivores, that were either ground or unspecialized foragers. Potential competition tended to be higher for native species with typical non-native traits and forest-dwelling unspecialized non-native species. Potential competition between native and non-native birds was consistently higher in islands that were larger, had more non-native birds or were drier.

Main conclusions: Niche differentiation of native and non-native species may explain the scarcity of reported competition-driven extinctions since non-natives clearly tend to favour and are better adapted to anthropogenic environments. However, the few non-native birds that occur in native ecosystems may be problematic. The loss of native ecosystems coupled with the introduction of species that might outcompete native species may enhance the relevance of competition in future island extinctions.

KEYWORDS

competition, extinction, Functional Nearest Neighbour Index, introduced species, island biogeography, oceanic islands, recently established species, species interactions, species traits

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1 | INTRODUCTION

Across the globe, many species have been introduced outside their natural geographic range by human actions, either intentionally or accidentally. Despite international agreements aiming to control species introductions, globalization is expected to continue increasing the numbers of non-native species worldwide (Seebens et al., 2017). This is a major conservation problem because non-native species are one of the main direct drivers of biodiversity loss at the global scale (Bellard et al., 2016; Spatz et al., 2017).

Non-native species have long been recognized as a leading cause of biodiversity decline on islands (Bellard et al., 2016; Blackburn et al., 2004; Clavero et al., 2009; Sax & Brown, 2000). Island native species tend to have small population sizes, low reproductive rates, reduced defences against predators and restricted distributions, all of which make them particularly susceptible to the impacts of non-native species. Moreover, islands tend to suffer more species introductions and more extensive anthropogenic land use changes (Russel & Kueffer, 2019; Spatz et al., 2017).

The impacts of non-native species on island native biodiversity are widely acknowledged (Evans et al., 2018; Medina et al., 2011). Among vertebrate species, birds have been one of the most affected across oceanic islands worldwide (Blackburn et al., 2004; Spatz et al., 2017). For example, predation by introduced mammal predators has caused the extinction of many native island species, especially island endemic birds (Blackburn et al., 2004; Davis, 2003; Sax et al., 2007). In contrast, competition between native and non-native species appears to have caused few known bird extinctions (Davis, 2003; Sax et al., 2007), and most bird introductions on oceanic islands occur after extinctions (Sax & Gaines, 2003). However, competition can still affect native populations (Blackburn et al., 2009), as in the case of the introduction of the Japanese white-eye (*Zosterops japonicus*) in Hawai'i. This species caused a decrease in juvenile size and survival in several native bird species through competition for food resources and was responsible for the extirpation of a major population of Hawai'i 'akepa (*Loxops coccineus coccineus*) (Freed & Cann, 2009). Interspecific competition is known to be a major driver of the composition of species assemblages (McGill et al., 2006), so it is somewhat surprising that it has not caused as many extinctions of island birds as other types of species interactions, like predation by non-native species (Boyer, 2008; Sax et al., 2007). A small overlap between the niches of native and non-native birds could explain this lower impact of competition, but to our knowledge, this possibility has not been evaluated.

Competition can be observed directly or demonstrated indirectly (Ricciardi et al., 2013). Indirect niche-based approaches infer competition by quantifying species ecological niche overlap. Traits that relate to resource acquisition along the niche dimensions, such as diet, habitat use and body mass, are used to estimate the similarity between species ecological niches (Dhondt, 2012; McGill et al., 2006). These approaches do not quantify the availability of limiting resources and assume that coexisting species are more likely to compete if they have greater trait similarity, that is higher niche overlap (Ricciardi et al., 2013). Trait-based quantification of ecological niches has been

used to assess the potential competition between native and non-native fish species in the Mediterranean (Elleouet et al., 2014).

Native species extinctions resulting from competition with non-native species might indeed be rare events, namely due to their distinct ecological niches. However, limited evidence of such extinctions may also be a consequence of their subtlety, since competitive pressure might lead to slow extinction processes (Davis, 2003; Sax et al., 2007). Nowadays, competition between native and non-native species may be overlooked, but in the long run, it can exacerbate species extinction debts (Sax & Gaines, 2003; Sax et al., 2007). To address this potential threat, it is vital to identify which native species are more vulnerable to non-native species competition and which non-native species are more competitive. This information will allow defining priorities for conservation research and action at the species level, but efforts should also be made to understand why some islands appear to be more at risk. To delineate a more comprehensive conservation strategy and protect the native avifauna across oceanic islands worldwide, we also need to understand which characteristics make an island more susceptible to non-native bird competition. Even so, no study has yet focused on this topic (but see: Bellard et al., 2017; Patiño et al., 2017; Walsh et al., 2012).

Our study aims to evaluate the potential competition between native and non-native bird species across oceanic islands. We use birds as a model because they are one of the best-studied animal groups worldwide and are well represented on oceanic islands. More specifically, we will (1) assess the differences between the traits of native and non-native species, (2) identify which traits are more likely to be linked to competition between native and non-native species and (3) explore which island characteristics promote this competition. Most bird species introduced to oceanic islands appear to thrive in humanized environments (Sol et al., 2012); therefore, we expect that native birds with similar traits that can occupy these more humanized environments will be more vulnerable to competition by non-native birds. In the same way, apart from island area which is positively related to the number of non-native bird species (Blackburn et al., 2016), islands dominated by human-altered habitats, or habitats ecologically similar to those (e.g. dry islands with natural grasslands and savannas), might be more susceptible to competition between native and non-native birds. Lastly, we will consider the implications of our findings for the conservation of native bird species on oceanic islands.

2 | METHODS

2.1 | Island selection and characterization

We selected only oceanic islands, as their biotas are particularly sensitive to non-native species, and focused on 87 tropical, subtropical and temperate oceanic islands larger than 100 km² because smaller islands usually do not hold enough terrestrial bird species to support meaningful analyses. For each of these islands, we identified if they were part of an archipelago, and compiled information on several island characteristics, that are known to influence non-native bird

species richness (Blackburn et al., 2016) and thus their potential to compete with native birds: island area, isolation to surrounding land-mass (island and/or continent), environmental heterogeneity (elevation range used as a proxy), present climate (including mean annual temperature, annual precipitation, temperature seasonality and precipitation seasonality) and aridity (including global aridity index and global reference evapotranspiration) (Table S2.1; Olson et al., 2001; Trabucco & Zomer, 2018; Weigelt et al., 2015).

2.2 | Bird species database

To compile a list of resident native bird species and established non-native species for each oceanic island, we gathered information from “Avibase” (Lepage, 2018), following the “Handbook of the Birds of the World” (HBW) and “Birdlife International” taxonomy (Handbook of the Birds of the World & BirdLife International, 2018). We removed all species belonging to aquatic bird families due to their distinct ecological niches compared to terrestrial birds (12 marine and 19 aquatic families; see step 2 in Figure S2.1 and Table S2.2), and species considered to be “extirpated,” “extinct,” “extinct in the wild” or “rare/accidental” (Lepage, 2018; see step 3 in Figure S2.1). Competition with non-native bird species was not identified as a cause for the decline of any species considered “extinct” and “extinct in the wild” ($n = 56$; IUCN, 2019; Table S2.3).

The lists compiled from “Avibase” included some vagrant and migrant species, which would cause noise in the analysis. To remove these species, we deleted all species entries on islands if they were not listed for that island on both “IUCN Red List of Threatened Species” (IUCN, 2019) and “HBW Alive” (Hoyo et al., 2014). Out of the 740 species investigated, 341 species were removed from the database (see step 5 in Figure S2.1).

We analysed inconsistencies in species non-native status between source databases and identified 43 native species that were considered non-native on either the “IUCN Red List of Threatened Species” ($n = 17$) or “HBW Alive” ($n = 26$). After a comprehensive bibliographic search (Table S2.4), we confirmed that 17 of these species were wrongly classified as native ($n = 8$ species on “IUCN” and $n = 9$ species on “HBW Alive”) and corrected their status on our database.

We considered a species to be non-native if it was classified as “introduced species” on “Avibase” and/or “established” on the “Global Avian Invasions Atlas” (GAVIA) (Dyer, et al., 2017; see step 4 in Figure S2.1). For example, we changed the status of Mauritius fody (*Foudia rubra*) in Mauritius since we realized it was wrongly classified as non-native on “GAVIA” (IUCN, 2019; Lepage, 2018).

Fourteen islands were removed from the database because they were not listed in “Avibase” ($n = 7$; see step 1 in Figure S2.1), only hosted aquatic bird species or species considered “rare/accidental” ($n = 5$; see step 2 and 3 in Figure S2.1), or had avifaunas composed exclusively of native (Socorro: Wehtje et al., 1993) or non-native terrestrial bird species (Saint Helena: Prater, 2012; see step 6 in Figure S2.1).

Total species richness, native species richness, non-native species richness and proportion of non-native species were estimated for each island from our bird species database (Table S2.5).

2.3 | Bird species traits

To evaluate the potential competition between native and non-native bird species, we gathered information on five species traits, that are known to influence the ability of birds to obtain limiting resources: diet, foraging strata, foraging time, body mass and habitat (Dhondt, 2012).

Information about diet, foraging strata, foraging time and body mass was taken from “EltonTraits” (Wilman et al., 2014). Only 40 out of 533 species were missing from this database, for which we used information from the closest species in the same genus (Table S2.6). Diet was obtained from the relevant five categories on “EltonTraits”: granivore (at least 50% “PlantSeed”: plants and/or seeds), frugivore (at least 50% “FruNect”: fruits and/or nectar), insectivore (at least 50% “Invertebrate”: invertebrates), carnivore (at least 50% “VertFishScav”: vertebrates, fish and/or carrion) and omnivore (“Omnivore”: less than 50% in any of the other 4 categories). Foraging strata was created from five of the relevant seven categories on “EltonTraits”: “ground,” “understorey,” “mid-high,” “canopy” and “aerial.” The two categories corresponding to aquatic foraging strategies (foraging below or on the water surface) were not included since we are focusing on terrestrial species. Species were assigned to a foraging strata category when they had a prevalence above 50. Otherwise, the species was categorized as “unspecialized.” Foraging time and body mass were extracted directly from “EltonTraits.”

Information about the habitat of each species was taken from the first level of classification of the IUCN Habitats Classification Scheme (IUCN, 2019). This trait was composed of seven asymmetric binary classes, meaning that each species could belong simultaneously to several categories: forest, savanna, shrubland, grassland, desert, artificial terrestrial habitats and rocky areas, caves and subterranean habitats. Artificial terrestrial habitats are a combination of artificial terrestrial habitats—which include arable lands, pasturelands, plantations, rural gardens, urban areas and subtropical/tropical heavily degraded former forest—plus introduced vegetation, whereas rocky areas, caves and subterranean habitats are a combination of rocky areas plus caves and subterranean habitats. These habitat classes were combined because they had few species that were ecologically similar and presented similar responses to environmental variables.

2.4 | Data analysis

All statistical analyses were made in R (v.3.5.3; R Core Team, 2019—see Appendix S1 for a detailed description of the R packages that were used). Multicollinearity of island characteristics was tested with Spearman's rank correlation coefficient. To maintain correlation coefficients below 0.7, we excluded temperature seasonality, precipitation, native species richness and proportion of non-native species

(Figure S2.2). Multicollinearity of species traits was tested between continuous and categorical traits with polyserial correlation and between categorical traits with polychoric correlation (Table S2.7). Furthermore, we checked for outliers using boxplots across all island characteristics and removed Iceland ($n = 16$ species) from the analysis for being an island area outlier (9.7 times larger than the second largest island; Figure S2.3).

2.4.1 | Comparing traits of native and non-native species

To assess the differences between native and non-native species traits, we performed a meta-analysis for each species trait (foraging time, body mass, diet, foraging strata and habitat) using each island as a case study.

Binary traits (diet, foraging time, foraging strata, habitat) were assessed using two-way contingency tables describing native and non-native species traits in each island. The effect size was calculated as the ratio between the proportion of non-native species and the proportion of native species that belong to a trait, or trait class in the case of categorical variables, and using risk ratio as a measure of effect size. We chose the Mantel–Haenszel method to pool effect sizes because it can tolerate islands with species proportion equal to zero (Borenstein et al., 2009), and we added the treatment arm continuity correction to estimate risk ratio (Sweeting et al., 2004).

For body mass, the only continuous trait, the effect size was calculated using the average value and standard error obtained for native and non-native species in each island, and the response ratio was used as a measure. The Inverse variance method was used to pool effect sizes (Borenstein et al., 2009).

We used a random-effects meta-analysis with Sidik–Jonkman approach to calculate summary effect sizes and corresponding 95% confidence intervals (Sidik & Jonkman, 2007) and Hartung–Knapp adjustment for the random-effects model to ensure robust estimates of the variance of the pooled effect (Borenstein et al., 2009; Hartung & Knapp, 2001).

To ensure that the lack of independence between islands of the same archipelago was not affecting summary effect sizes, we performed a mixed-effects model for each trait, or class of categorical traits, having “island group” as a random factor (9 single islands and 11 archipelagos). Since some archipelagos have few islands (5 or less), we followed the recommendation to pool the estimates of the 12 within-group variances to yield a combined estimate, therefore assuming a common between-island variance for all archipelagos and single islands (Borenstein et al., 2009).

2.4.2 | Estimating potential competition between native and non-native species

To quantify the potential competition between native and non-native bird species on each island, we used a trait-based approach

as a proxy, the relative Functional Nearest Neighbour Index (FNN_r ; Elleouet et al., 2014). This index computes the functional similarity (or niche overlap) between native and non-native species as a proportion of the total number of native species. We started by calculating a functional dissimilarity matrix for each island based on Gower's distance and five species traits (equal weight was given to each trait: diet, foraging strata, foraging time, body mass, habitat). In four islands, there was a pair of functionally equal species (Gower's distance = 0), and 0.01 was added to the body mass of one species in each pair, just to allow calculations. The functional dissimilarity matrix of each island was transformed into a Euclidean similarity matrix, ranging from 0 (lowest functional similarity) to 1 (perfect functional similarity). Then, for each island independently, we considered all functional similarity values between native and non-native species and only retained the maximal similarity value between each native species and all the co-occurring non-natives (Figure S2.4). This maximal similarity value corresponds to the highest value (i.e. maximum distance) found between a pair of species (one native and one non-native) in the Euclidean similarity matrix of each island. Lastly, all the retained maximal similarity values of all native species of each island are summed up and, subsequently, divided by the number of native species occurring in the island to obtain a standardized index (FNN_r ; $n = 73$ islands). Thus, FNN_r allows the identification of the islands where the niche of native species has a higher overlap with that of non-natives and therefore where competition between these two groups of species is potentially more likely to occur. It is important to note that the similarity between omnivores and the other more specialized species is zero; however, this has low to none implications to our results because we always retain the pair of species with the highest similarity, which will naturally be between the specialized species that share the same diet.

Identifying traits of native and non-native species linked to competition

To identify species traits associated with competition, we used the average maximal similarity as a proxy for species proneness to competition. We started by calculating the similarity value between each native species and all co-occurring non-native species in each island, as well as between each non-native and all co-occurring natives. From these, we identified the highest value for each species in each island as the maximal similarity value (Figure S2.4), and computed the average maximal similarity for each species as the arithmetic mean of its maximal similarity values, one for each island where it occurred. An average maximal similarity ranges from 0, when there is no niche overlap and thus no potential competition, to 1, when niche overlap and thus potential competition is highest. Therefore, high values for native species indicate a high vulnerability to potential competition by non-natives, whereas for non-natives, they indicate a high potential to threaten natives by competition.

To explore how species traits are linked to potential competition, we performed beta regression models with logit link function for body mass, foraging time, diet, foraging strata and each habitat

class (forest, savanna, shrubland, grassland, rocky areas and caves, desert, artificial terrestrial habitats). We built separate models for native ($n = 417$ species) and non-native species ($n = 151$ species), in both cases using species average maximal similarity as the response variable. Therefore, four single-trait models and seven single-class models were obtained for native and non-native species. In the single-trait models for diet, foraging time and foraging strata, a single factor with different levels was considered, whereas for habitat, a single model was performed for each class. Sample size varied in habitat, because some species were associated with more than one habitat category.

In all ten models with categorical traits (diet, foraging time, foraging strata and seven habitat classes), there is an unbalanced distribution of sample sizes across the levels of the independent categorical trait. Since this will result in lower precision of the estimated regression coefficient of the less-frequent levels, we will only interpret the levels whose estimated regression coefficients were statistically different from zero (p -value $< .05$).

The potentially more vulnerable native species and the potentially more threatening non-native species of each oceanic island were identified by ranking the species according to average maximal similarity values.

Identifying island characteristics linked to competition between native and non-native species

To identify how island characteristics affect potential competition between native and non-native bird species, we built a generalized linear mixed model (GLMM) with beta distribution, logit link function and FNN_r as the response variable ($n = 72$; Table S2.5). As fixed effects, we included log-transformed island area, isolation, elevation range, mean annual temperature, precipitation seasonality, aridity index, evapotranspiration index, total species richness and non-native species richness (Table S2.1), all of which were standardized

before modelling. As a random effect, we used "island group" (8 single islands and 11 archipelagos; Table S2.5).

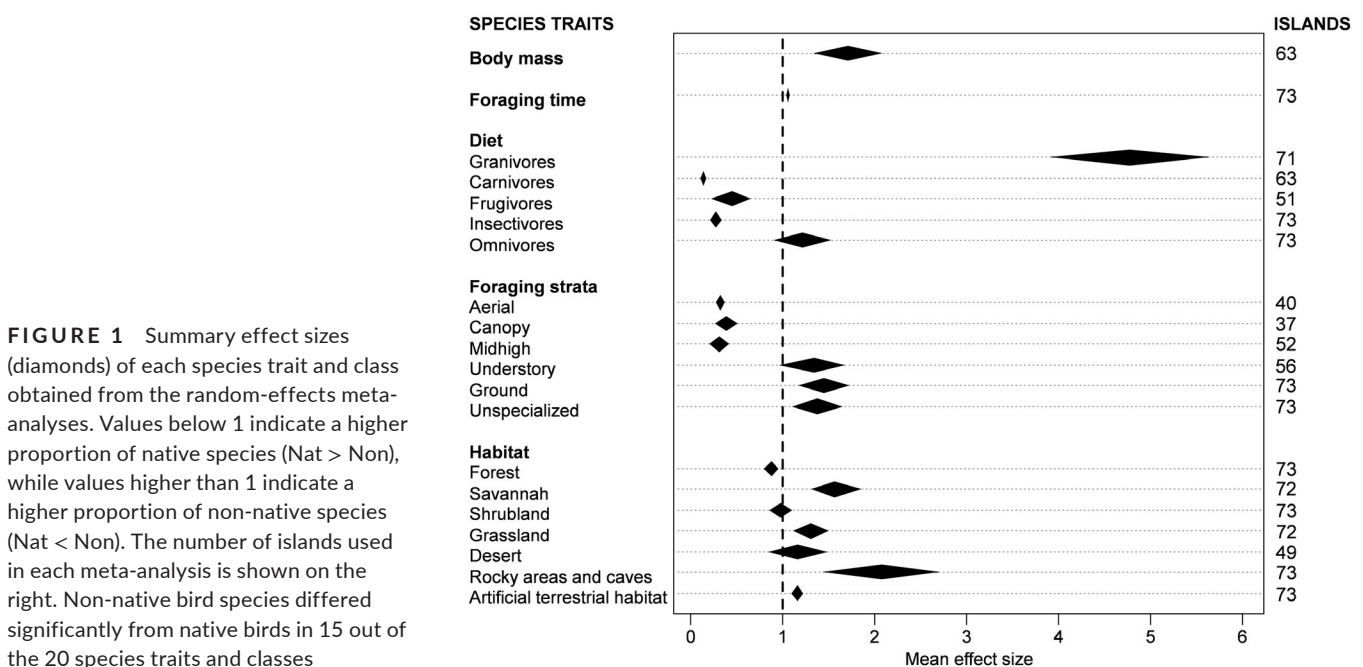
To select the best model to describe FNN_r variation, we used maximum likelihood (ML) methods and model selection based on Akaike's information criterion corrected for small sample size (AICc). We ran a complete set of models with all possible combinations of fixed effects and considered "best models" those that had $\Delta AICc < 2$ (Burnham & Anderson, 2002). Relative variable importance (RVI) was estimated by summing the Akaike weights ($wAICc$) of models in which each variable was included, both for the full subset and for the subset of "best models." Biplots were used to explore the relationship between FNN_r and the most important variables and between FNN_r and non-native species richness, as this is the only conservation-reliant variable. To assess model fit, we analysed residual deviance, and to assess normality, we explored residuals using quantile-quantile plots.

3 | RESULTS

The final species database included 533 bird species on 73 oceanic islands (average number of species per island = 30 ± 16 ; Table S2.5).

3.1 | How similar are the trait-based niches of native and non-native species?

The functional trait analysis suggests that the ecological spaces occupied by native and non-native bird species on oceanic islands are in general very distinct. The meta-analyses showed that native bird species differed significantly from non-native birds in 15 out of 20 species traits (Figure 1 and Table S2.8). The combined summary



effect sizes obtained from the mixed-effects models did not differ from those calculated with the random-effects meta-analyses (Table S2.9), suggesting that archipelagos did not have a significant influence on the main effect of traits (Figure S2.5).

Compared to native bird species, non-natives tended to be heavier and to include more diurnal species. Native species had a higher proportion of carnivores, frugivores and insectivores, while non-natives had a higher proportion of granivores. Native birds also had a higher proportion of aerial, canopy and mid-high foragers, while non-natives had a higher proportion of ground and unspecialized foragers. There was a higher proportion of native species in forests and of non-natives in savannas, grasslands, rocky areas and caves, and artificial terrestrial habitats.

3.2 | Traits that make natives potentially vulnerable to non-native competition

All analysed species traits were relevant to explain the high niche overlap between native and non-native species, which potentially reflects a high vulnerability of native species to competition by non-natives (p -value $<.05$; Table 1 and S2.10, and Figure S2.6). Smaller and diurnal native species had a higher niche overlap with non-native species. Considering diet, granivore native species had the highest niche overlap with non-natives, followed by omnivores, frugivores and insectivores. Regarding foraging strata, ground forager native species had a higher niche overlap compared to unspecialized foragers. Concerning habitat, native species that occur in savannas had

Traits	Native species		Non-native species	
	Coefficient (p -value)	No. of species	Coefficient (p -value)	No. of species
Body mass	-0.0003 (.032)	415 ^a	0.00004 (.831)	149 ^b
Foraging time				
Diurnal	0.560 (2e-16)	403	^c	
Nocturnal	0.460 (.278)	14		
Diet				
Carnivore	0.522 (.321)	33	0.438 (.525)	2
Frugivore	0.535 (.027)	65	0.560 (.286)	6
Granivore	0.651 (2e-16)	55	0.558 (5.64e-05)	93
Insectivore	0.524 (.015)	171	0.563 (.048)	19
Omnivore	0.585 (2.32e-10)	93	0.617 (2.78e-06)	31
Foraging strata				
Aerial	0.461 (.175)	21	0.536 (.718)	2
Canopy	0.508 (.698)	36	0.593 (.182)	4
Ground	0.597 (2e-16)	143	0.573 (7.4e-07)	90
Mid-high	0.518 (.308)	53	0.504 (.950)	6
Unspecialized	0.576 (3.85e-11)	130	0.586 (1.0e-04)	40
Understorey	0.511 (.637)	34	0.500 (.996)	9
Habitat				
Forest	0.556 (1.57e-14)	354	0.607 (2e-16)	103
Savanna	0.585 (1.73e-08)	89	0.554 (.011)	51
Shrubland	0.583 (2e-16)	236	0.568 (1.43e-06)	107
Grassland	0.575 (8e-08)	105	0.549 (.011)	64
Rocky areas and caves	0.504 (.874)	32	0.527 (.641)	7
Desert	0.563 (.056)	20	0.547 (.392)	8
Artificial terrestrial habitats	0.572 (2e-16)	297	0.581 (5.45e-11)	128

TABLE 1 Coefficient values on probability scale and corresponding p -values are shown for each beta regression model

Note: Except for the continuous trait body mass, all coefficients are equal to the mean of average maximal similarity values for that trait class. The t tests are testing whether the coefficients are different than zero. The number of species belonging to each trait class is also shown.

^aTwo species (*Meleagris gallopavo* and *Pavo cristatus*) were excluded for being outliers.

^bTwo species (*Haliaeetus albicilla* and *Neophron percnopterus*) were excluded for being outliers.

^cNot comparable because there was only one nocturnal species (*Tyto alba*).

the highest niche overlap, followed by those occurring in shrublands, grasslands, artificial terrestrial habitats and forests.

The potentially more vulnerable native species were often shared between islands belonging to the same archipelago (Table S2.11). For example, the Cape Verde sparrow (*Passer iagoensis*) was the most potentially vulnerable native species in six out of eight Cape Verde Islands.

3.3 | Traits that make non-native species more likely competitors

Only three species traits were important to explain the high niche overlap between native and non-native species, which reflects the potential of non-native species to threaten native species by competition (p -value $< .05$; Table 1 and S2.12, and Figure S2.7). Body mass was not significant and foraging time had insufficient data since the barn-owl (*Tyto alba*) was the only nocturnal non-native species. Regarding diet, omnivore non-native species had a higher niche overlap with native species, followed by insectivores and granivores. Concerning foraging strata, unspecialized foragers had a higher niche overlap than ground forager species. In relation to habitat, non-native species that occurred in forests had the highest niche overlap, followed by those occurring in artificial terrestrial habitats, shrublands, savannas and grasslands.

Non-native species that potentially posed the biggest competition threat were often shared between islands belonging to the same archipelago (Table S2.11). For example, the helmeted guineafowl (*Numida meleagris*) was the most potentially threatening non-native species in seven out of eight Cape Verde Islands.

3.4 | Island characteristics that promote competition by non-native species

Islands had an average FNN_r of 0.563 (std = 0.068), ranging from the lowest FNN_r with 0.373 in Saint Vincent to the highest with 0.685 in Guadalupe (Table S2.11). Island area was the most important variable to explain FNN_r variation across islands ($RVI = 0.86$; Figure S2.8, Tables S2.13 and S2.14). FNN_r was consistently high in larger islands, but variable in smaller ones (Figure 2a and Table S2.15). Among smaller islands (area $< 500 \text{ km}^2$), single islands tended to have higher FNN_r than those smaller islands belonging to an archipelago ($0.578 > 0.539$). These small single islands included Guadalupe, the island with the highest FNN_r .

Islands with more non-native species tended to have higher FNN_r ($\rho = 0.430$, p -value = .0001— ρ represents the Spearman's rank correlation coefficient between FNN_r and non-native species richness; Figure 2b,c). Among the 72 islands considered, the Hawaiian Islands had the greatest number of non-native bird species (25 to 70). Many islands that have arid to semi-arid climates (Middleton & Thomas, 1997), such as the Canary, Cape Verde and the Galápagos Islands, have a remarkably high FNN_r considering their small number of non-natives (Figure 2c).

4 | DISCUSSION

We found that, on oceanic islands, native bird species tended to be smaller than non-native birds, and to include more nocturnal, carnivore, frugivore and insectivore species that were preferably aerial, canopy and mid-high foragers, and tending to occur in forests. Conversely, non-native birds tended to be ground or unspecialized granivores that occurred mostly in savannas, grasslands, rocky areas and caves, or artificial terrestrial habitats. Native species that had traits prevalent in non-native birds were more likely to suffer competition from them. Unspecialized non-native species that occurred in forests had the highest niche overlap with native species, suggesting their greatest potential to compete. Potential competition between native and non-native bird species across islands was best explained by island area; it was highly variable in smaller islands but consistently high in larger ones. It was also consistently high in islands that had more non-native species and in drier islands even if they had few non-native species.

4.1 | Non-native species traits reflect the history of introduction and adaptability to anthropogenic environments

Non-native bird species tended to be heavier, diurnal, ground or unspecialized granivores that prefer open habitats, which are traits that make them easier to keep in captivity (Duncan et al., 2003; Dyer, Cassey, et al., 2017; Soares et al., 2020). They are also typical of many temperate game birds (Anatidae and Phasianidae) or cage birds (Psittacidae, Fringillidae and Passeridae), which were often introduced during European colonization to increase hunting opportunities or to satisfy aesthetic preferences (Blackburn et al., 2009; Duncan et al., 2003). Nowadays, bird introductions result mostly from accidental or intentional releases of caged pet birds (Abellán et al., 2016; Blackburn et al., 2009; Dyer, Cassey, et al., 2017).

Besides favouring introduction, non-native bird species traits may also favour their establishment. Higher body mass is advantageous for establishment in novel environments (Blackburn et al., 2009; Duncan et al., 2003). It is also easier for unspecialized granivores to colonize new environments since these species are less dependent on complex ecological interactions (Duncan et al., 2003; Murgui & Hedblom, 2017). Finally, open areas on oceanic islands are frequently associated with anthropogenic disturbances (Murgui & Hedblom, 2017; Sax & Brown, 2000; Sol et al., 2012). Thus, human changes in vegetation (e.g. deforestation), climate (e.g. heat island effect), resources (e.g. food and shelter) and bird assemblages (e.g. extirpation of native competitor species) create conditions for non-native birds to thrive (Blackburn et al., 2009; Murgui & Hedblom, 2017; Walsh et al., 2012). They also indicate that the success of non-native species on islands depends not only on their traits but also on how these allow them to take advantage of conditions created by humans in their introduced range (Blackburn et al., 2009; Cardador & Blackburn, 2019; Sol et al., 2012).

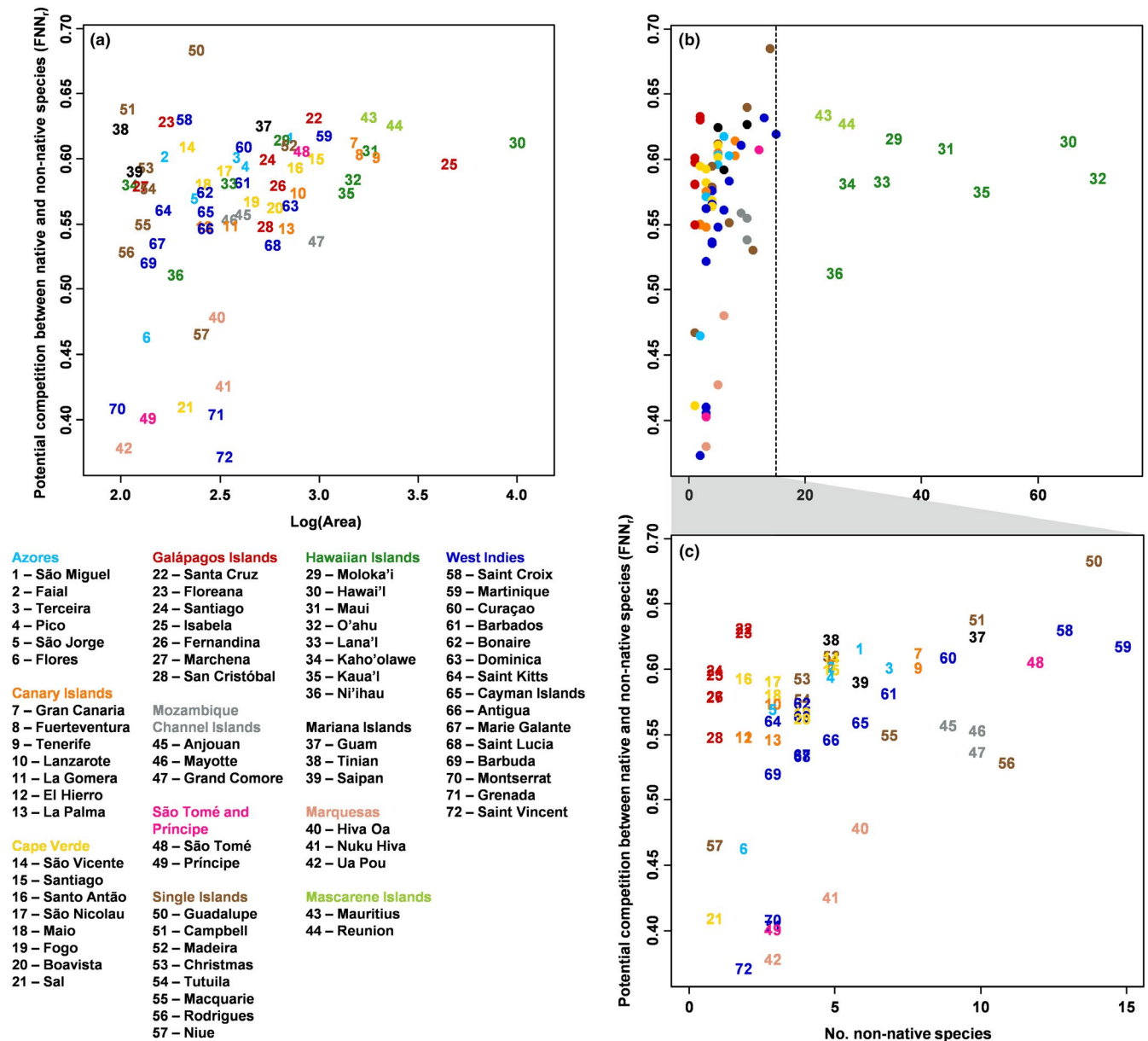


FIGURE 2 Relationship between potential competition between native and non-native species (FNN_r) and log-transformed island area (a) and non-native species richness (b and c). In (b), all islands are represented but only those with more than 15 non-native species are labelled, whereas in (c) only islands with less than 15 non-native species are shown ($n = 62$). The 72 islands (circles or numbers—see legend) are coloured by archipelago ($n = 11$), and single islands are represented in brown ($n = 8$; islands that do not belong to any archipelago). Potential competition (FNN_r) was consistently high in larger islands, but variable in smaller ones (a). Islands with a great number of non-native species tended to have higher FNN_r (b and c)

4.2 | Differences between niches of native and non-native birds may explain why competition-driven extinctions are rare

In contrast to non-natives, native bird species tended to prefer forests and to have traits that enabled them to explore forest resources, such as being frugivores and insectivores that rather feed at mid-high or on the canopy. Since 76.7% of the oceanic islands we studied are dominated by forests (Table S2.5; Olson et al., 2001), native species are expected to rely on

complex ecological interactions typical of these habitats (Russel & Kueffer, 2019).

The mismatch between the ecological niches of native and non-native birds suggests that potential competition between these species is low on oceanic islands, which could help justify why there are almost no extinctions that resulted solely from competition with non-native species (Davis, 2003; Sax et al., 2007). However, some native bird species have traits that are common in non-natives and may thus be more vulnerable to competition from them, while unspecialized non-native species that occur in

forests might pose a bigger threat for competition with the natives (Table 1).

Contrary to habitat loss, which threatens native bird species that are unable to adapt to novel human-altered ecosystems (Newbold et al., 2013), competition with non-native species mostly occurs between these and the native species that can occupy anthropogenic environments. However, competition from non-natives that can occupy typical ecological niches of native species can become particularly problematic (e.g. Freed & Cann, 2009), as this factor compounds that of habitat loss (Myers et al., 2000; Newbold et al., 2013; Pimm et al., 2014). Worryingly, the number of non-native species that can use native forest habitats is expected to grow due to the appearance of new sources of non-native species, which include highly marketable species from the New World (e.g. Jandaya parakeet, *Aratinga jandaya*), but also to the increasing demand for cage birds in the Neotropical regions (Dyer, Cassey, et al., 2017). As such, we emphasize that particular efforts should be invested to control the international trade of forest species that may get established on islands and affect native birds, especially insectivore species which abound.

4.3 | Island size, non-native species richness and competition

The higher potential competition between native and non-native birds observed on larger islands can be explained by the increasing number of non-native species with island area (Figure 2a; Blackburn et al., 2016), which in turn is explained by the anthropogenic enhancement of non-native species colonization rates and habitat heterogeneity (Blackburn et al., 2009; Russel & Kueffer, 2019).

Among smaller islands, which showed high variability in potential competition, single islands were particularly susceptible (Figure 2c). For example, the small isolated island of Guadalupe, known for the devastating impacts of forest loss and non-native species (Medina et al., 2011), had the highest potential competition of all islands. This can be explained by their high proportion of non-native species (e.g. more than 50% in Rodrigues, Macquarie, Campbell and Guadalupe) and great similarity between some pairs of native and non-native species (e.g. 0.81 between the native European goldfinch—*Carduelis carduelis*—and the non-native Spanish sparrow—*Passer hispaniolensis*—in Madeira Island). However, we did not find any apparent justification for both the greater number of non-native species and their greater similarity with the extant native species of single more isolated islands; hence, future studies are urgently needed.

In many islands belonging to the same archipelago, the same non-native bird species was considered the most threatening to native species. This is likely due to a shared non-native species pool and within-archipelago translocations, both a result of colonization history and geographic location, but also due to similar abiotic and biotic characteristics (Clavero et al., 2009).

The Hawaiian Islands are a hotspot for bird extinctions and non-native bird introductions (Freed & Cann, 2009; Moulton & Pimm, 1983). A combination of direct and indirect human impacts, such as direct hunting, habitat loss (e.g. deforestation and urbanization), non-native species (e.g. introduced predators) and disease (e.g. avian malaria), drove more than 50 native passerines to extinction since the arrival of early Polynesian settlers (Boyer, 2008), and currently, non-native bird species represent 80 to 96% of the terrestrial avifauna of each island. Many Hawaiian Islands are unusually large for oceanic islands, allowing for multiple ecological niches: most non-native birds occupying the highly disturbed lowlands, while natives are restricted to the better-preserved highlands (Moulton & Pimm, 1983). This might help explain why potential competition in these islands is not proportional to the dominance of non-native bird species when compared to smaller islands (Figure 2a).

Arid and semi-arid islands, such as Canary, Cape Verde and the Galápagos Islands, had surprisingly high potential competition considering their low number of non-native birds (Figure 2b and c). Native ecosystems in these dry islands are somewhat similar to anthropogenic environments. Therefore, bird species native to these islands have adaptations to dry open environments, which immediately increase their potential competition with non-natives, even when there are only a few of these species.

4.4 | Concluding remarks

Preventing species introductions is a priority to protect native island biodiversity (Walsh et al., 2012). Our results provide cues on how to integrate potential competition with non-native species in conservation strategies. Protecting native ecosystems remains the best single measure to avoid extinction, but we believe that the success of this measure depends on reducing the risk of introduction of species that can inhabit native ecosystems, including those that share important components of the niche with native species. Furthermore, we suggest that our results should be used to provide clues on which species to prioritize in future studies. The Maui alauahio (*Paroreomyza montana newtoni*) was ranked as the 76 potentially most vulnerable native species out of 417 (Table S2.10). We showed that this insectivore native bird had the highest niche overlap with a well-known competitor, the non-native red-billed leiothrix (*Leiothrix lutea*), which was ranked as the 41 potentially biggest competition threat out of 151 non-native species (Table S2.12; Foster, 2005). Although habitat degradation seems to be driving the population decline of this endemic bird, attention should also be given to competition with non-native birds as these two drivers can act synergistically. Therefore, we reinforce that particular efforts should be made to control the international trade of forest species, that like natives rely mostly on fruits and insects. Complementarily, larger islands and native birds with typical non-native traits, that is ground or unspecialized granivores that mostly occur in drier open habitats, might warrant

special attention since they are more vulnerable to potential competition with non-native birds. The same applies to arid and semi-arid islands, especially since conventional conservation actions, like the implementation of protected areas, might be less efficient in these cases (Pimm et al., 2014).

Open-source global databases are crucial for evidence-based conservation strategies. Unfortunately, those focusing on non-native and invasive species are often incomplete or lack detail (Spatz et al., 2017), even among the best-known taxonomic groups (e.g. birds: Dyer, Redding, et al., 2017). Improving high-quality and global-scale species and ecosystems distribution data with species-level functional and phylogenetic information would greatly increase our understanding of biological invasions and help to refine global conservation priorities (Myers et al., 2000; Pimm et al., 2014). We suggest that databases should include data variability of species traits to capture the plasticity of non-native species to environmental pressures in the introduced range, especially in islands which are known for their singular extreme conditions (Russel & Kueffer, 2019). Although information on species habitat selection and suitability is available for a greater number of species worldwide (e.g. del Hoyo et al., 2014; IUCN, 2019), it is still in many cases not sufficiently robust, especially for insular species whose habitat preferences are usually not well known. In our analyses, this type of information would allow us to build a more complex and realistic ecological niche for each species, which would result in more accurate estimates of the niche overlap between native and non-native species. However, even just by including information about the habitats where the species occurs, our findings suggest that the substantial mismatch between the ecological niches of native and non-native species, due to differences in key traits such as habitat, foraging strata and diet, might help explain why there are so few known competition-driven bird extinctions on oceanic islands. The combination of the ongoing loss of native ecosystems, the continued introduction of bird species on oceanic islands, especially of forest-dwelling birds, and the fact that competitive pressure could lead to slow extinction processes can, in the long term, exacerbate the threat of competition with non-native species and, ultimately, species extinction debts (Davis, 2003; Sax & Gaines, 2003; Sax et al., 2007). It is therefore vital to keep working towards a better understanding of the drivers and consequences of competition between native and non-native species.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data used in this manuscript were drawn from published sources cited in the main text (Dyer, Redding, et al., 2017; Handbook of the Birds of the World & BirdLife International, 2018; del Hoyo et al., 2014; IUCN, 2019; Lepage, 2018; Olson et al., 2001; Trabucco & Zomer, 2018; Weigelt et al., 2015; Wilman et al., 2014).

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BIOSKETCH

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SUPPORTING INFORMATION

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

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