









# Trait-environment associations diverge between native and alien breeding bird assemblages on the world's oceanic islands

Charlotte Rault<sup>1</sup> | Fabien Leprieur<sup>2,3</sup>  | Luc Barbaro<sup>4,5</sup>  | Holger Kreft<sup>6,7</sup>  |  
Nicolas Mouquet<sup>2,8</sup>  | Julien Papaix<sup>9</sup>  | Çağan H. Şekercioğlu<sup>10,11</sup>  | Cyrille Violle<sup>1</sup>  |  
Jean-Yves Barnagaud<sup>1</sup> 

<sup>1</sup>CEFE, Univ Montpellier, CNRS, EPHE-PSL University, IRD, Montpellier, France

<sup>2</sup>MARBECC, University of Montpellier, CNRS, Ifremer, IRD, Montpellier, France

<sup>3</sup>Institut Universitaire de France, Paris, France

<sup>4</sup>DYNAFOR, University of Toulouse, INRAE, Castanet-Tolosan, France

<sup>5</sup>CESCO, Muséum national d'Histoire naturelle, CNRS, Sorbonne University, Paris, France

<sup>6</sup>Biodiversity, Macroecology & Biogeography, University of Goettingen, Göttingen, Germany

<sup>7</sup>Centre of Biodiversity and Sustainable Land Use (CBL), University of Goettingen, Göttingen, Germany

<sup>8</sup>CESAB FRB, Montpellier, France

<sup>9</sup>INRAE – UR Biostatistiques et Processus Spatiaux (BioSp), Avignon, France

<sup>10</sup>School of Biological Sciences, University of Utah, Salt Lake City, Utah, USA

<sup>11</sup>Department of Molecular Biology and Genetics, Koç University, Istanbul, Turkey

## Correspondence

Jean-Yves Barnagaud, CEFE, Univ Montpellier, CNRS, EPHE-PSL University, IRD, Montpellier, France.

Email: [jean-yves.barnagaud@ephe.psl.eu](mailto:jean-yves.barnagaud@ephe.psl.eu)

## Funding information

Centre Méditerranéen de l'Environnement et de la Biodiversité, Grant/Award Number: BIOTA; German Science Foundation, Grant/Award Number: DynaCom project (Research Unit number FOR 2716)

**Handling Editor:** Volker Bahn

## Abstract

**Aim:** To investigate spatial variations in the ecological trait structure of breeding bird assemblages on oceanic islands. To test the hypothesis that native and naturalized alien bird species are filtered by different processes, leading to diverging associations between traits and insular environmental gradients.

**Location:** Oceanic islands worldwide.

**Time Period:** Current.

**Major Taxa Studied:** Terrestrial breeding birds.

**Methods:** We assessed the composition of breeding terrestrial bird assemblages from the extent-of-occurrence maps of 3170 native and 169 naturalized alien species on 4660 oceanic islands. We quantified their ecological trait structures with respect to diet, mobility and body mass as the standardized distance between a mean pairwise trait distance index and its expectation from a null model. We used spatial generalized additive models to relate trait structures to proxies of environmental conditions and human impact on land, accounting for all species, native species only and alien species only.

**Results:** Diet and mobility traits tended to be more diverse than expected by a null model, while body mass tended towards clustering. Trait-environment associations were idiosyncratic, but environmental variables tended to explain trait structures better than human impacts on habitats. Islands invaded by alien species had similar trait structures as noninvaded ones, although they hosted assemblages with more clustered body masses. However, trait-environment relationships diverged when considering all islands and all species, invaded islands only or alien species only.

**Main Conclusions:** Despite their ecosystem-level influences, alien species have a limited effect on the global patterns of trait structures in the breeding bird assemblages of the world's islands, either because they account for a low proportion of species or because successful invaders and native species have similar trait suites. Trait-environment associations suggest that filters related to the conditions of alien species' introductions explain their distributions in island assemblages better than the constraints associated with isolated environments.

## KEYWORDS

ecological filters, ecological traits, human impact, INLA, island avifaunas, isolation, macroecological patterns, null models, species introductions

## 1 | INTRODUCTION

Oceanic islands are simplified, near-closed ecosystems hosting small populations with limited gene flow and simplified biotic interaction networks (Grant, 1997; Itescu et al., 2020; Kier et al., 2009; MacArthur & Wilson, 1963, 1967). Insular species assemblages thus bear the heritage of long-term isolation, marked by evolutionary processes operating in a context of more limited and less diverse habitats or resources as compared to the source continents. Low gene flow and high competition for resources over the long term in a limited space result in “island syndromes”, or associations of ecological traits typical of long-term isolation on islands. In vertebrates, island syndromes typically take the form of gigantism or dwarfism, or the complete or partial loss of flight ability (Grant, 1997; Lomolino, 2005; McNab, 1994).

Beyond these spectacular examples, insular species' ecological traits (in a broad sense, species' characteristics that determine their relationship with the biotic and abiotic environment) reflect contrasts in resource and habitat use as compared with their continental relatives. For instance, differences in morphological (Boyer et al., 2010; Case, 1978; Leisler & Winkler, 2015; Lomolino, 2005), life history (Blondel, 1985; Covas, 2012), phenomenological (Prodon et al., 2002) and behavioural (Stamps & Buechner, 1985) traits have been reported between insular and continental species belonging to a same genus or family, in various taxonomic groups. Some of these patterns now form textbook examples of the consequences of adaptive processes or competition in isolated ecosystems, such as in Darwin's finches (Grant, 1997) or Mediterranean faunas (Blondel, 1985). Ecological traits are used both to investigate the evolutionary processes shaping species assemblages and to elucidate species' roles in ecosystem processes and services (Cardador & Blackburn, 2019, 2020; Leclerc et al., 2020; Sobral et al., 2016). The distribution of species inside a hypervolume structured by ecological traits (the ecological trait space) is theoretically expected to reflect evolutionary strategies of resource use or allocation and allows inferring processes of species coexistence within assemblages (Díaz et al., 2016; Violle et al., 2007). For instance, geographical patterns in bird diets (Kissling et al., 2011), species' propensity to mobility (Kirchman, 2009; McNab, 1994) and life history strategies (Heaney, 1978; Lomolino, 1985) can be used to show the relative imprints of biogeographical heritage and environmental determinants on the composition of species assemblages over macroecological extents.

The distribution of ecological traits among species co-occurring on an island (hereafter referred to as the “ecological trait structure” of a species assemblage) stems from a combination of local, niche-related processes determining how species share a restricted amount and diversity of resources, and external processes having

filtered the set of colonizing species from continental sources. Under a null hypothesis based on the latter, the distribution of ecological traits among species within an assemblage would be a random draw of the regional species pool, predictable from local species richness and the structure of the regional trait space. Alternatively, ecological traits may either be less diverse (clustered) or more diverse (overdispersed) than expected under this null hypothesis. More or less diverse trait syndromes therefore depend on whether processes that pack similar species together, or inversely permit the co-occurrence of ecologically heterogeneous species and dominate on a given island (Ackerly et al., 2006; Cavender-Bares et al., 2004, 2006; Silvertown et al., 2006).

Because of niche-related processes (Pavlek & Mammola, 2021; Pellissier et al., 2018; Pianka, 1974), the disparity between the null expectation and the ecological trait structure of a given assemblage may vary with factors affecting the distribution and availability of resources on an island, such as its location, isolation, topographic and climatic conditions and primary productivity (Novosolov et al., 2013; Si et al., 2017; Taylor et al., 2021). For instance, dispersal ability is expected to exhibit a quadratic relationship with distance from the source continent for land birds, because of selection pressure for sedentariness on the most remote islands (although this prediction may not hold for passerines, Ferrer et al., 2011). Morphological shifts that sometimes led to dwarfism or gigantism also emerged on the most isolated islands as a consequence of a combination of isolation and responses to competition over resources, as was the case for well-known examples of extinct species such as the moas (*Dinornithiformes*), elephant birds (*Aepyornithidae*) or Haast's eagle (*Hieraetus moorei*) (Hansford & Turvey, 2018; van Heteren et al., 2021). By contrast, foraging strategies are less directly structured by isolation than they are related to local environmental features such as altitude (e.g. insectivores dominate at low altitudes, while frugivores dominate at high altitudes in Peruvian bird assemblages, Sam et al., 2017) or primary productivity (e.g. high primary productivity in the tropics favouring the diversity of frugivores and nectarivores; Barnagaud et al., 2019; Jetz et al., 2009; Kissling et al., 2007).

Island faunas have undergone major transformations since human arrival on islands, starting from over 100,000 years ago in some Pacific archipelagos to a few hundred years ago for remote oceanic islands such as the Mascarenes (Blackburn et al., 2008; Si et al., 2017; Whittaker, 1998). Extensive hunting of island endemic species, the introduction of mammalian predators since the earliest human colonizations (Blackburn et al., 2004; Courchamp et al., 2003; Simberloff et al., 2013) and novel competitors (Baker et al., 2014; Blackburn et al., 2011; Mandon-Dalger et al., 2004; Sayol et al., 2021; Soares et al., 2021) have exacerbated extensive alterations of native habitats for agriculture and urbanization as a

consequence of human colonization (Sanchez-Ortiz et al., 2019). This combination of anthropogenic processes has resulted in the taxonomic and functional homogenization of many insular species assemblages (Capinha et al., 2020; Otto et al., 2020; Soares et al., 2022), through the loss of ecological traits associated with island syndromes through nonrandom extinction filters. Inversely, traits associated with commensalism, ubiquism and ecological generalism have been added to islands through the naturalization of introduced alien species (hereafter “alien species”), usually introduced for hunting or ornament purposes (Mahoney et al., 2015; Olden et al., 2004; Otto et al., 2020; Si et al., 2017; Whittaker & Fernandez-Palacios, 2007).

Although species introductions increase species richness, the consequences of the long-term establishment of alien species on island assemblages vary among taxonomic groups (Sax et al., 2002). Predation of native faunas by alien mammals has contributed to the vanishing of island trait syndromes, narrowing the ecological trait space of insular species and erasing ecosystem functions that are not compensated by alien species (Anderson et al., 2011; Sayol et al., 2021; Si et al., 2016; Sobral et al., 2016). Among alien species, those that achieve naturalization (i.e. establish viable populations) on islands often display traits that favour survival to long journeys in captivity (Pipek et al., 2020), the ability to survive in novel environments and exploit resources associated with human activities and sedentariness (Blackburn et al., 2009; Whittaker et al., 2014). At a macroecological scale, native and alien species may thus exhibit opposite responses to human impact on island ecosystems, driving the ecological trait structure of insular assemblages towards null patterns or biotic homogenization. Alternatively, filters imposed by specific local environmental conditions could result in native and alien species with similar trait suites.

In this study, we aimed at inferring the roles of latitude, environmental variables (primary productivity, altitudinal range, island area) and human alterations of native habitats in explaining the current ecological trait structure of breeding terrestrial bird assemblages across oceanic islands worldwide. We further investigated whether the trait structures of species assemblages on invaded islands differ from those of noninvaded islands, and whether alien species modify the trait structure of invaded insular assemblages and associated environmental patterns. We expected that invaded islands would be larger, predominantly located at low latitudes, and with higher human impact on land and habitats than noninvaded ones. We also predicted that alien species would add novel trait combinations that do not correspond to any island syndrome, driving island-level trait structures towards their null expectation (Olden et al., 2004; Otto et al., 2020; Rosenzweig, 2001). Because the establishment success of alien birds in islands is generally explained by introduction effort as much as local environmental features (Cassey et al., 2004; Mahoney et al., 2015), we expected that the spatial variation in their trait structure would mainly be explained by predictors reflecting isolation, island area and human impact on land, but less so by macroecological environmental proxies such as climate, latitude or primary productivity.

## 2 | METHODS

### 2.1 | Data

#### 2.1.1 | Ecological traits

We retrieved the ecological traits of the world's 11,117 extant bird species from Šekercioğlu et al. (2004, 2016), complemented on a case-by-case basis by additional sources (mostly Del Hoyo et al., 2013). We excluded pelagic species (270 species) to focus on terrestrial bird assemblages only (10,877 species) and 150 extinct species for which trait data were too incomplete and which were not relevant to our research questions focussed on the geographical patterns of extant species assemblages. Excluding extinct species is justified by the fact that we did not attempt to identify the processes leading to the emergence of trait structures in insular assemblages, but rather to understand how the current trait structures are distributed along environmental gradients and are affected by alien species (most of which were introduced after the main extinction waves). With respect to pelagic species, seabirds form a substantial part of island avifaunas, but their use of marine resources and their high dispersal capacity imply that isolation and environmental/anthropogenic conditions on islands may not be relevant for them. The resulting species set thus encompassed 10,717 extant species, encompassing both insular and noninsular species.

As in any trait-based study, species' trait records in our database were heterogenous and incomplete (Hortal et al., 2015). We thus selected ecological traits according to four selection criteria: (i) biological significance (a trait must be associated with a specific hypothesis with respect to the structure of bird assemblages in order to be included, Table 1); (ii) at least 20% of species with a record for a given trait had to be strictly insular, in order to approximate the actual proportion of strictly insular species at the world scale (25% among 11,147 bird species, BirdLife International & Nature Serve, 2012); (iii) each trait had to be represented in all biogeographical realms as defined by Olson et al. (2001; that is, 8 distinct biogeographical realms) and in both hemispheres. As a result of this selection, we retained three categories of ecological traits: diet (expressed in scores for eight food items, summing to 10 per species), mobility (latitudinal and altitudinal migration, erratism, postfledging nomadism) and log-transformed body mass (descriptions of ecological traits in Table 1).

#### 2.1.2 | Bird distributions

We extracted oceanic islands from Weigelt et al. (2013)'s polygon map of the world's 17,883 islands. Oceanic islands are defined in this database as islands without mainland connections during glacial periods. We then established the list of extant breeding species on each island by intersecting the polygons of the 4660 oceanic islands with BirdLife International and Nature Serve (2012)'s extent-of-occurrence database (uploaded from <http://datazone.birdlife.org/home> in 2021), which contains vector extent-of-occurrence

Trait group	Ecological traits	Type of variables	Prediction for strictly insular species
Number of bird species with data (number of strictly insular species)			
Diet 10,582 (2573)	Use of 8 types of prey: seeds, plants, fruits, nectar, insects, fishes, vertebrates, carrions	Scores summing to 10 per species for the 8 traits, from 0 (diet not used) to 10 (exclusive diet)	Overrepresentation of generalist, piscivorous and granivorous species
Mobility 10,717 (2736)	4 types of movement: seasonal latitudinal migration, seasonal altitudinal migration, irregular dispersal, postfledgling nomadism	Categorical with 3 modalities: 0, sedentary; 1, strict migrant; 2, partial migrant	Tendency to sedentariness, at least for nonpasserines
Body mass 9271 (1775)	1 trait: average body mass over males and females, in grams	Continuous quantitative (log-transformed in data analyses)	Tendency to extreme body masses

TABLE 1 Definition, structure and sample size for the ecological traits considered.

Variables	Acronym	Mean $\pm$ standard deviation [min, max]
Latitude (WGS84, °)	Lat	21.62 $\pm$ 36.71 [-59.46, 83.45]
Distance (km)	Dist	1300.87 $\pm$ 1134.46 [2.48, 6067.08]
Altitudinal range (m)	Alt	157.80 $\pm$ 358.63 [0, 4176]
Area (km <sup>2</sup> )	Area	584.60 $\pm$ 10,508.35 [1, 590,547.40]
Net primary production <sup>a</sup> (g carbon/year)	NPP	1.32e+11 $\pm$ 2.16e+11 [1.42e+09, 1.12e+12] (1807 missing values)
Human impact (HMc) <sup>b</sup>	Human	0.14 $\pm$ 0.14 [0, 0.88] (87 missing values)
Species richness	SP	30.25 $\pm$ 29.63 [1, 256]

TABLE 2 Environmental variables considered in our analyses.

Note: All variables are quantified for 4660 oceanic islands unless otherwise stated.

<sup>a</sup>Net primary production is a median per island.

<sup>b</sup>HMc = cumulative degree of human modification of land.

maps for the world's birds. We only considered species' breeding and resident ranges, since data on terrestrial species wintering on islands are fragmentary. Consistent with the filters imposed on our trait database, we also excluded extinct species. Hence, our study only encompassed extant breeding bird assemblages, irrespective of their historical composition prior to selective extinctions due to human invasions (Pimm et al., 2006). Eventually, we distinguished native and endemic species (hereafter "native species", 3170 species with origin = "native" in BirdLife's polygons) from alien species introduced by humans and have established feral populations (169 species with origin = "introduced" in BirdLife's polygons). We used these data to assess the composition of insular bird assemblages, from which we calculated species richness on each island (Table 2). BirdLife extent-of-occurrence data are not exempt from criticisms due to their proneness to sampling bias, geographical uncertainty and coarse resolution (Herkt et al., 2017). Nevertheless, comparisons of the species lists of several islands between BirdLife data and local ornithological inventories revealed no major inconsistencies likely to affect our study given its spatial extent and grain (a more

in-depth investigation would be necessary for finer-grained analyses, however). BirdLife International's Red List officer (*pers. comm.*) further confirmed that small-ranged and endangered species are given specific attention when compiling these maps, which implies that most island species' distributions included in our sample should be, as much as current knowledge allows, relatively exempt from major geographical errors.

### 2.1.3 | Environmental variables and human impact

We retrieved the centroid latitude, distance to the nearest continent (calculated from the centroid of each island), altitudinal range (maximum-minimum) and area for the 4660 islands from Weigelt et al. (2013; Table 2 and Appendix S1 for realm-level summaries). We extracted the median net primary production (NPP) from a 28 km resolution raster overlaying the shapefile of the oceanic islands (data available at <https://doi.org/10.7927/H40Z715X>; Imhoff & Bounoua, 2006; Table 2), and the median human impact on island

habitats from a 1 km resolution raster developed from a cumulative measure of human land modifications worldwide (hereafter “human impact”, data at <https://doi.org/10.7927/edbc-3z60>; Kennedy et al., 2019; Table 2). These two medians were obtained from the values for each island by overlaying the respective raster and the shapefile of the islands. The resulting dataset included all covariates for the 4660 islands, except for human impact (4573 islands) and NPP (2853 islands). These missing observations did not impact the total sample size for analysis since, in our modelling framework, they are ignored for the estimation of associated parameters without removing the full data row (Gomez-Rubio, 2020). Latitude, distance to the nearest continent and human impact were weakly correlated, as well as were area and altitude (all correlations close to a Pearson's correlation coefficient of  $-0.3$ ); other variables were uncorrelated.

## 2.1.4 | Null models

We quantified the observed trait structure of each island bird assemblage by calculating the mean Gower's distance between species pairs for each trait category of Table 1 (mean pairwise trait distance, MTD, see Si et al., 2017; Swenson et al., 2012). Gower's distance allows dealing with nonindependent variables (e.g. fuzzy diet scores) and categorical variables with an appropriate weighting (Gower, 1966; Pavoine et al., 2009, as implemented in the `dist.ktab` function of the R package `ade4`, Thioulouse et al., 2018). We then constructed a null model to test whether the observed MTD could arise under the assumption that species are randomly sampled in the ecological trait space. Our null model redistributed randomly 999 times the columns of each trait dissimilarity matrix, restricted to species present on at least one oceanic island. This procedure randomizes the distribution of traits in species assemblages while preserving island-level species richness and relative species' frequencies (“`taxa.labels`” algorithm, Webb et al., 2008). We avoided unrealistic species compositions by forcing null dissimilarity matrices to be drawn from species present in the biogeographical realm corresponding to each island (native/alien species richness per realm: Australasia: 1090/63; Antarctic: 9/0; Afrotropic: 434/41; IndoMalay: 696/14; Nearctic: 263/12; Neotropic: 518/48; Oceania: 238/75; Palearctic: 429/17).

The deviation between the observed MTD ( $MTD_{obs}$ ) and the 999 null MTD ( $MTD_{null}$ ) on a given island indicates the extent to which species belonging to an assemblage have more or less similar ecological traits than expected by species richness only (Swenson et al., 2012). We quantified this deviation for each assemblage and each trait category with a standardized effect size (SES, Equation 1, Webb et al., 2008):

$$SES = \frac{MTD_{obs} - \overline{MTD_{null}}}{sd(MTD_{null})} \quad (1)$$

Positive SES values indicate that species assemblages are “overdispersed” (i.e. species are less closely related with respect to

their ecological traits than expected by the null model), while negative values indicate that species assemblages are “clustered” (i.e. species are more closely related with respect to their ecological traits than expected by the null model). We considered that SES was more extreme than expected under the null model when the rank of  $MTD_{obs}$  fell within the 5% highest (overdispersion) or lowest (clustering) values of  $MTD_{null}$  (following the computation used in the `ses.mpd` function in the R package `picante`, Webb et al., 2008).

## 2.1.5 | Trait structure—environment associations

We used spatial generalized additive models (GAM) to fit nonlinear relationships between the SES and environmental predictors while accounting for spatial autocorrelation. For each trait category  $k$  (diet, mobility or body mass), we related  $SES_k$  to latitude, distance to the nearest continent, total bird species richness, island area, altitudinal range, NPP and human impact through cubic splines with five degrees of freedom:

$$SES_k = \alpha + s(latitude) + s(distance) + s(species\ richness) + s(area) + s(altitudinal\ range) + s(NPP) + s(human\ impact) + \nu + \epsilon \quad (2)$$

Species richness, altitudinal range, NPP, distance to the nearest continent and area were log-transformed to limit the influence of very large values. In Equation 2,  $\alpha$  is an intercept,  $\epsilon$  is an independent and normally distributed error and  $\nu$  is a Gaussian random field with a Matérn correlation function defined over the sphere, aimed to account for spatial dependencies among islands. We estimated parameters with an Integrated Nested Laplace Approximation with Stochastic Partial Differential Equation (INLA-SPDE) approach (Lindgren et al., 2011; Rue et al., 2009), using the INLA package in R (Gomez-Rubio, 2020).

## 3 | RESULTS

### 3.1 | Standardized effect sizes

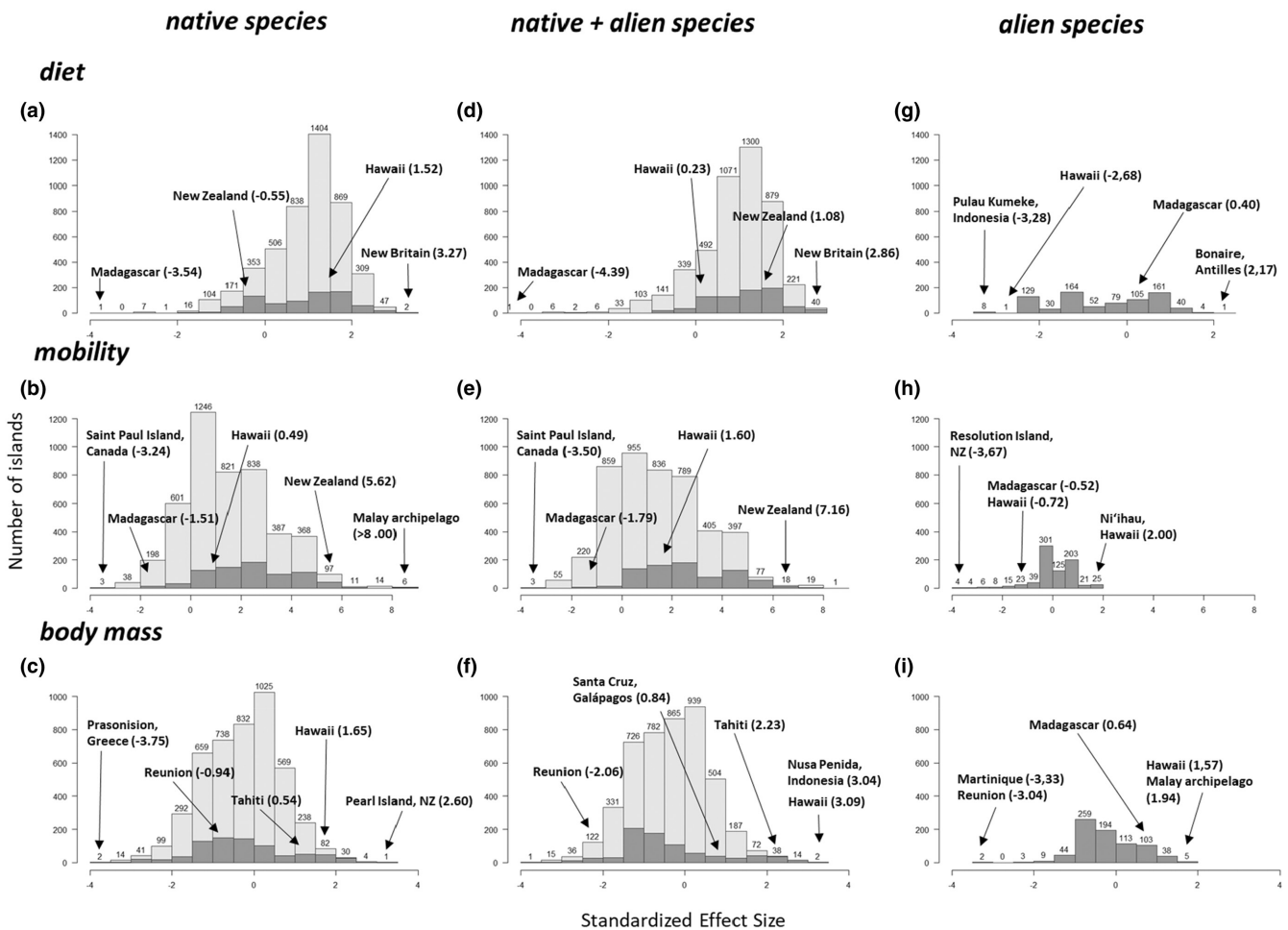
SES could only be computed for islands with at least two species with trait values (for native species: diet and mobility,  $n=4628$  islands, body mass  $n=4626$  islands; for alien species only: diet and mobility  $n=774$ , body mass  $n=770$ ; for alien and native species combined, all traits:  $n=4634$  islands). Spatial patterns of SES are shown in Appendix S2 and the associated  $p$ -values are in Appendix S3. Uncertainties are expressed in standard deviation (SD) units for raw variables and standard error (SE) units for model parameters, unless otherwise stated.

Diet was overdispersed in 1402 out of 4628 islands when accounting for native species only (30% of all islands, mostly in the Afrotropics and Nearctic realms, see Figure S3.4 in Appendix S3 for the distribution of SES per realm) and in 1276 out of 4634 assemblages

(27%) when accounting for all species. On these islands, species tended to exhibit more contrasting diets than expected in the null model. Consequently, the global distribution of  $SES_{\text{diet}}$  was shifted towards positive values (Figure 1a,b, mean  $SES_{\text{diet}} = 0.97 \pm 0.85$ , minimum and maximum  $[-3.54, 3.27]$ , see also maps in Appendix S2 and SES distributions with  $p$ -values in Appendix S3). Only 10/4628 (native species only) and 24/4634 (all species) islands had negative  $SES_{\text{diet}}$ , indicative of clustered diets (located in the Neotropic and Palearctic realms, Figure S3.4).

When accounting for all species, both the most clustered and the most overdispersed islands were located in the Southern Hemisphere, particularly in Madagascar (clustering,  $SES_{\text{diet}} = -3.54$ ), New Britain (overdispersion,  $SES_{\text{diet}} = 3.27$ ) and Umboi Island in the Bismarck Archipelago of Papua New Guinea (overdispersion,  $SES_{\text{diet}} = 3.01$ ). Conversely, alien species' diets were overdispersed in 19/774 islands only (2%, in the IndoMalay and Oceanian realms) but were clustered in 138/774 islands (18%, mostly in the Afrotropics).

SES for mobility-related traits were on average shifted towards positive values in native species assemblages (Figure 1b,  $SES_{\text{mob}} = 1.50 \pm 1.77$   $[-3.24, 8.83]$ ). Native species' mobility traits were significantly overdispersed in 2118/4628 islands (30%), 81% of positive  $SES_{\text{mob}}$  being located in the southern hemisphere (e.g.  $SES_{\text{mob}} > 8.00$  for Pulau Timor, Pulau Semau and the other islands of the Malay Archipelago, Figure 1b). By contrast, 840 islands had clustered mobility traits (negative  $SES_{\text{mob}}$ ), among which only 65 departed significantly from the null model. Most of these clustered islands were located in the northern hemisphere (e.g. Saint Paul Island, Canada,  $SES_{\text{mob}} = -3.24$  and Iceland,  $SES_{\text{mob}} = -3.04$ , Figure 1c), except Madagascar ( $SES_{\text{mob}} = -1.51$ , nonsignificantly different from the null model, Figures 1b and S3.4). We found similar figures when combining all species (2124/4634 overdispersed islands and 83/4634 clustered islands), but as in diet, most exotic species assemblages had null  $SES_{\text{mob}}$  (25 significantly overdispersed assemblages and 23 significantly clustered assemblages over 774 islands).



**FIGURE 1** Distributions of the trait structures of island bird assemblages with respect to diets (a, d, g), for mobility-related traits (b, e, h) and body mass (c, f, i). Trait structure is quantified as the standardized effect size (SES) of mean pairwise trait distances compared with a null model and is computed for islands with at least two species with trait data. Light grey: SES values for all oceanic islands with at least two species (diet  $n = 4628$ , migration  $n = 4628$ , body mass  $n = 4626$ ); dark grey: SES values for oceanic islands with at least two alien species (diet  $n = 774$ , migration  $n = 774$ , body mass  $n = 770$ ). SES are displayed for native bird species only (left column), alien bird species only (right column) and both combined (centre column).

Unlike the two other traits, SES for native species' body mass (Figure 1c) was mostly consistent with the null model (298 and 85 islands out of 4626 were significantly clustered and overdispersed, respectively, Figure S3.1b in Appendix S3). However, the native species'  $SES_{\text{body mass}}$  was slightly shifted towards negative values at the global scale ( $SES_{\text{body mass}} = -0.28 \pm 0.94$  [-3.75, 3.04], Figure S3.2b). The most clustered assemblages were located in the Mediterranean Sea (e.g. Prasonision, Greece,  $SES_{\text{body mass}} = -3.75$ , Figure 1e) and in the Andaman Sea (e.g. South Sentinel Island,  $SES_{\text{body mass}} = -3.57$ , Figure 1c). Conversely, 1949 islands had positive values (42%), especially in the Indo-Malayan region and Australia (e.g. Nusa Penida,  $SES_{\text{body mass}} = 3.04$ , Pear Island,  $SES_{\text{body mass}} = 2.60$ , Figure 1c and maps in Appendix S2 and S3).  $SES_{\text{body mass}}$  was dominated by nonsignificant negative values when accounting for all species or for alien species (see figures in Appendix S3).

### 3.2 | Effect of environment, geography and human impact on habitats

The effects of environmental variables on the SES of all traits were more idiosyncratic than expected, with marked nonlinear trends but without a consistent pattern among variables and traits (Figures 2–4, estimated parameters are provided in Appendix S4). Overdispersion of diets increased towards northern latitudes (Figure 2a) while clustering increased southwards for mobility and body mass (Figures 3a and 4a). Overdispersion increased along the species richness gradient for the three categories of traits. Diet overdispersion also increased with the distance from the nearest continent (Figure 2d). Curves for the effects of net primary productivity and human impact were essentially flat for all traits, except for a marked trend towards overdispersion in the diets and mobility of alien species (Figures 2u and 3u).

### 3.3 | Position of islands invaded by alien species

A total of 886 among the 1629 islands invaded by at least one alien species were located in the intertropical band, while 1933 of the 3031 islands exempt of alien species were in the temperate to boreal zones of the northern hemisphere (Figure 5). The average positions of invaded islands along environmental gradients were statistically different from those of noninvaded islands (Welch's *t*-tests, *p*-values  $< 10^{-11}$  with 1629 invaded islands and 3031 noninvaded islands for all variables except human impact: 1621 invaded and 2952 noninvaded islands, and NPP: 1169 invaded and 1684 noninvaded islands). However, these statistical differences are partly explained by our large sample sizes, and they came with large overlap for most variables (Figure 5).

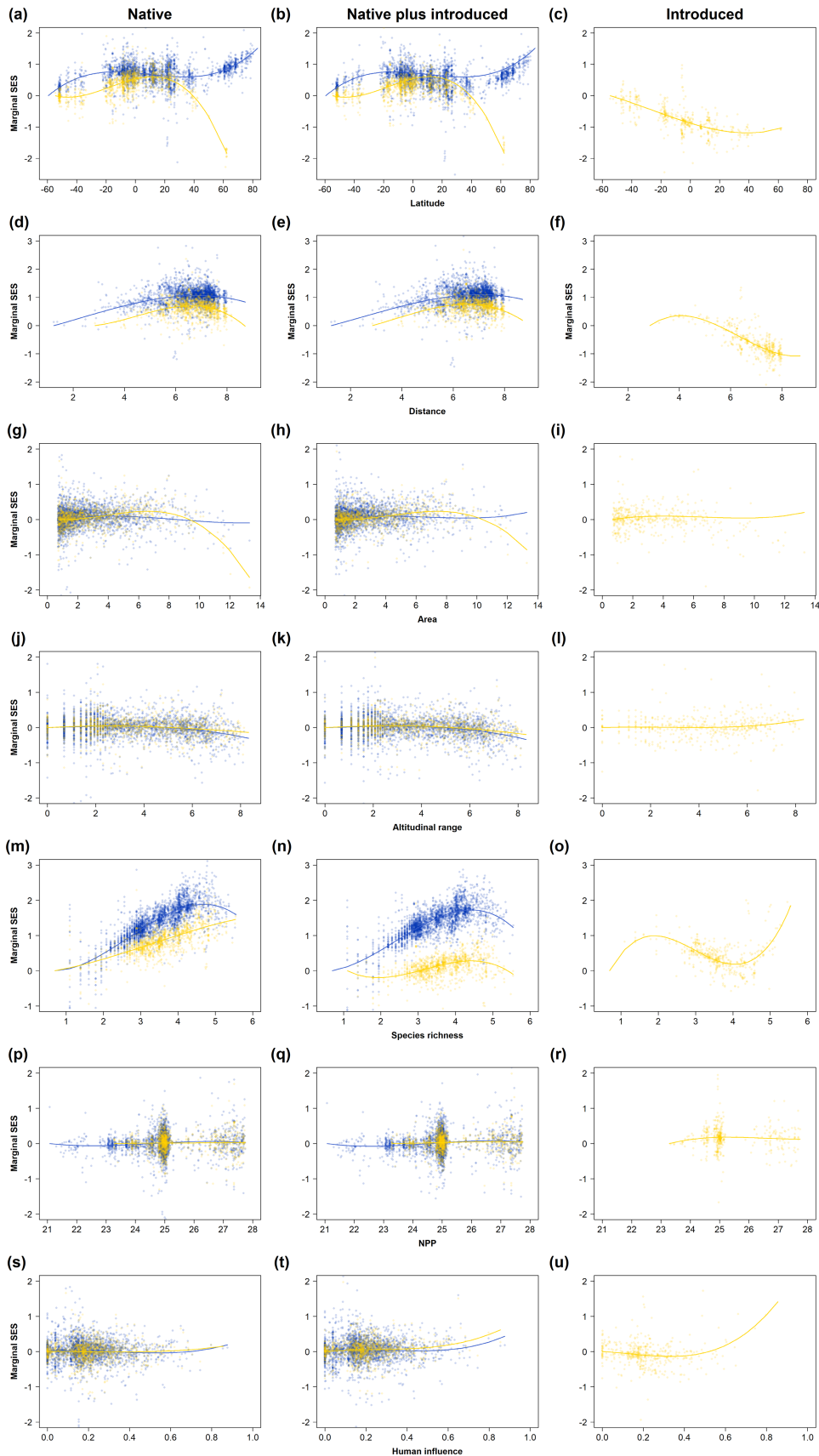
The relationships between SES and latitude, distance to the continent, area and species richness differed markedly from the general pattern when we restricted the dataset to islands invaded by alien

species (Figure 2a–i,m–o). The same discrepancy appeared for mobility traits and body mass at least for latitude and species richness (Figures 3 and 4), showing that islands hosting alien species form a nonrandom sample of the pool of oceanic islands along these environmental gradients. For instance,  $SES_{\text{diet}}$  decreased at high latitudes on invaded islands while it increased in the total set of islands (Figure 2a–c), but this was not attributable to the traits of the alien species themselves since native species also exhibited this pattern (Figure 2a). The drop in  $SES_{\text{diet}}$  at high distances from continents was also more marked in islands with alien species than in the whole set of islands (Figure 2d–f), but again, this was not attributable to alien species themselves (Figure 2d); similar patterns appeared for mobility and body mass (Figures 3 and 4, compare left and central panels).

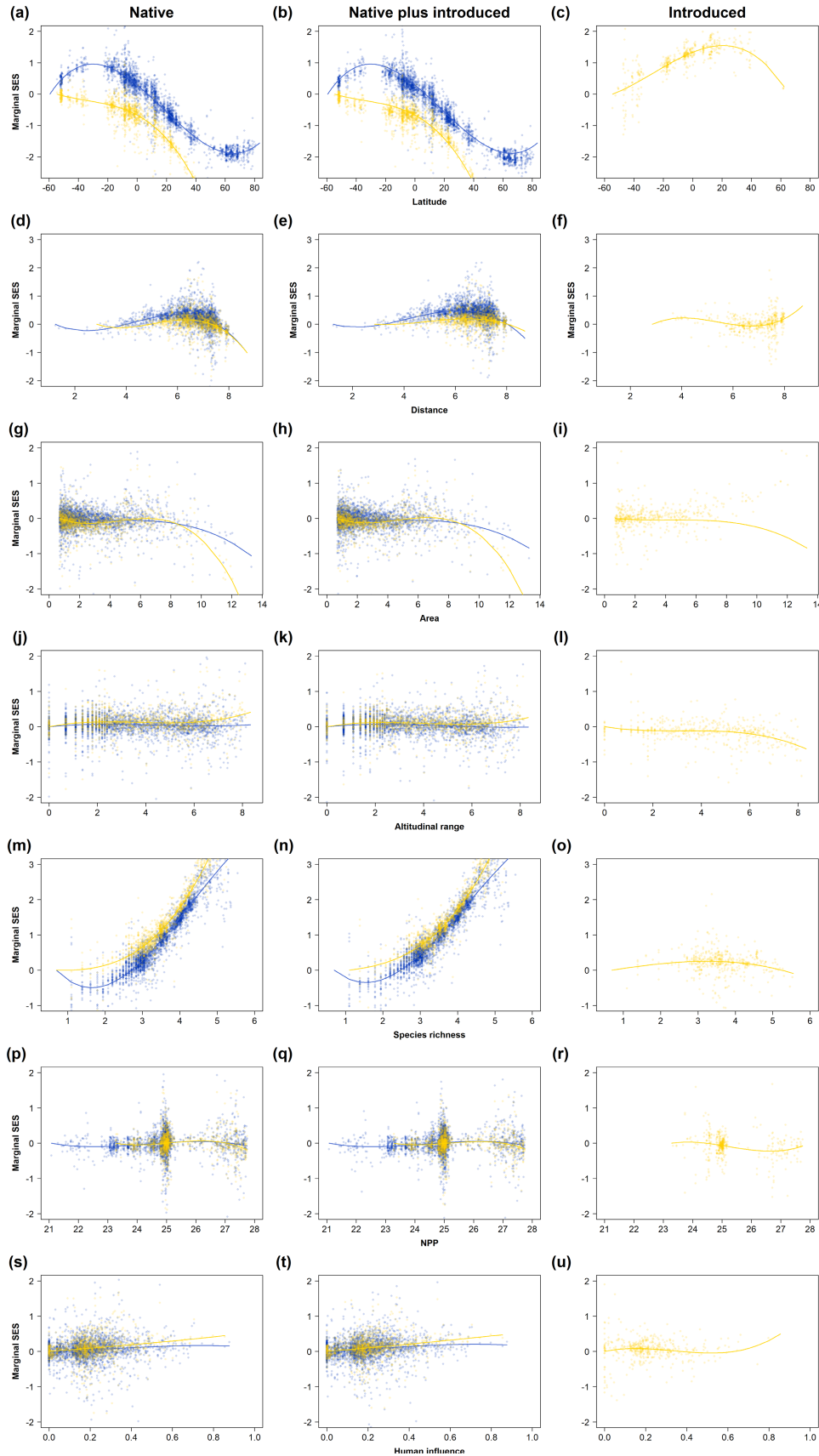
### 3.4 | Influence of alien species on the trait structures of invaded islands

On average, the 1629 invaded islands hosted  $2.59 \pm 3.71$  [1;36] alien species. When restricting the dataset to invaded islands with at least two species to compute a SES on all traits ( $n=770$ ), alien species overdispersed diets (difference between SES computed over native species only and SES computed over all species,  $\Delta = -0.24$ , 95% CI [-0.27, -0.20], paired *t*-test:  $t = -13.71$ ,  $df = 769$ ,  $p < 0.0001$ , Figure 5) and mobility traits ( $\Delta = -0.21$ , 95%CI [-0.24, -0.17],  $t = -11.97$ ,  $df = 769$ ,  $p < 0.0001$ ) but slightly increased the clustering in body mass ( $\Delta = 0.14$ , 95% CI [0.10, 0.17],  $t = 7.23$ ,  $df = 769$ ,  $p < 0.0001$ ). These patterns came with some spatial disparities. For instance, the effects of alien species on body mass varied from clustering in Tahiti (Society Islands, Polynesia:  $\Delta = 1.69$ , Figure 1c–f) to overdispersion in the other atolls of French Polynesia ( $\Delta = -1.24$ , Figure 1c–f). However, despite these shifts in the distributions of SES, the relationships between SES values and environmental variables were virtually not altered by alien species (Figures 3–5, compare “Native” and “Native plus alien” panels).

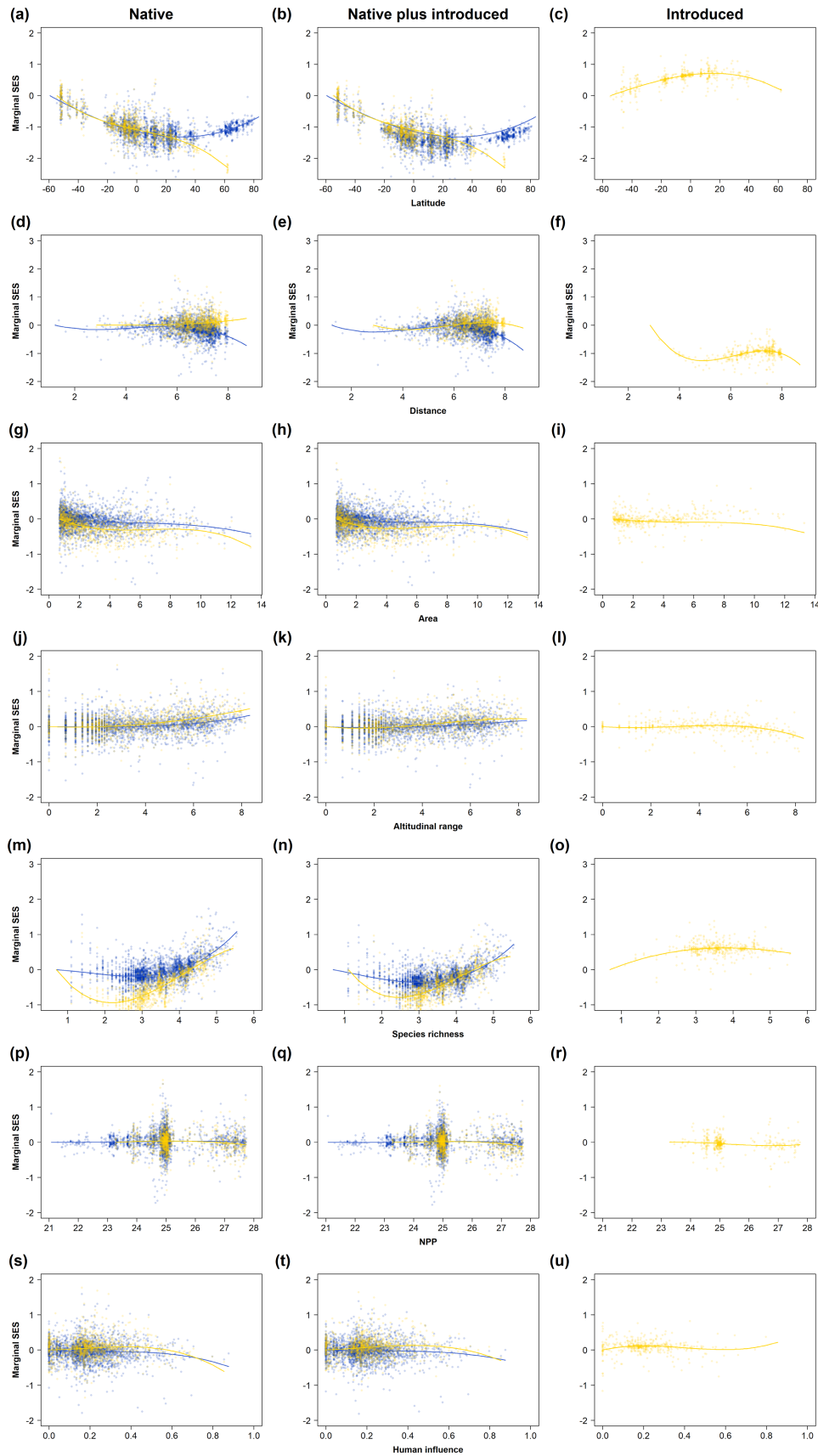
While environmental variations of SES changed little when considering only native species vs native and alien species together (Figures 2–4), variations of the  $SES_{\text{diet}}$  of alien species alone differed noticeably for latitude (more overdispersed at northern latitudes, compare Figure 2b,c, yellow curves), isolation (more clustered at large distances, Figure 2e,f, yellow curves) and species richness (strong overdispersion in the richest species assemblages, Figure 2n,o, yellow curves). Similar discrepancies occurred for  $SES_{\text{mobility}}$ . For instance, while mobility became more clustered from extreme south to extreme north latitudes when including both native and alien species, it peaked in tropical latitudes for alien species only (compare Figure 3a–c, yellow curves).  $SES_{\text{mobility}}$  was further unrelated to species richness in alien species, contrary to the pattern for all species (compare Figure 3n,o, yellow curves).  $SES_{\text{body mass}}$  showed comparable discrepancies, with a peak of overdispersion in tropical latitudes for alien species but a near-uniform decrease from south to north for all species (Figure 4b,c, yellow curves).



**FIGURE 2** Variations in the trait structure of bird assemblages along environmental gradients for traits related to diet (marginal standardized effect size in spatial additive models; 0 = null trait structure, positive values = overdispersion, negative values = clustering), with median curve (blue: all oceanic islands with at least two bird species ( $n = 4628$ ); yellow: only oceanic islands with at least two alien species ( $n = 774$ )). Credibility intervals are uninformative (too small due to high sample size) and are thus not displayed.

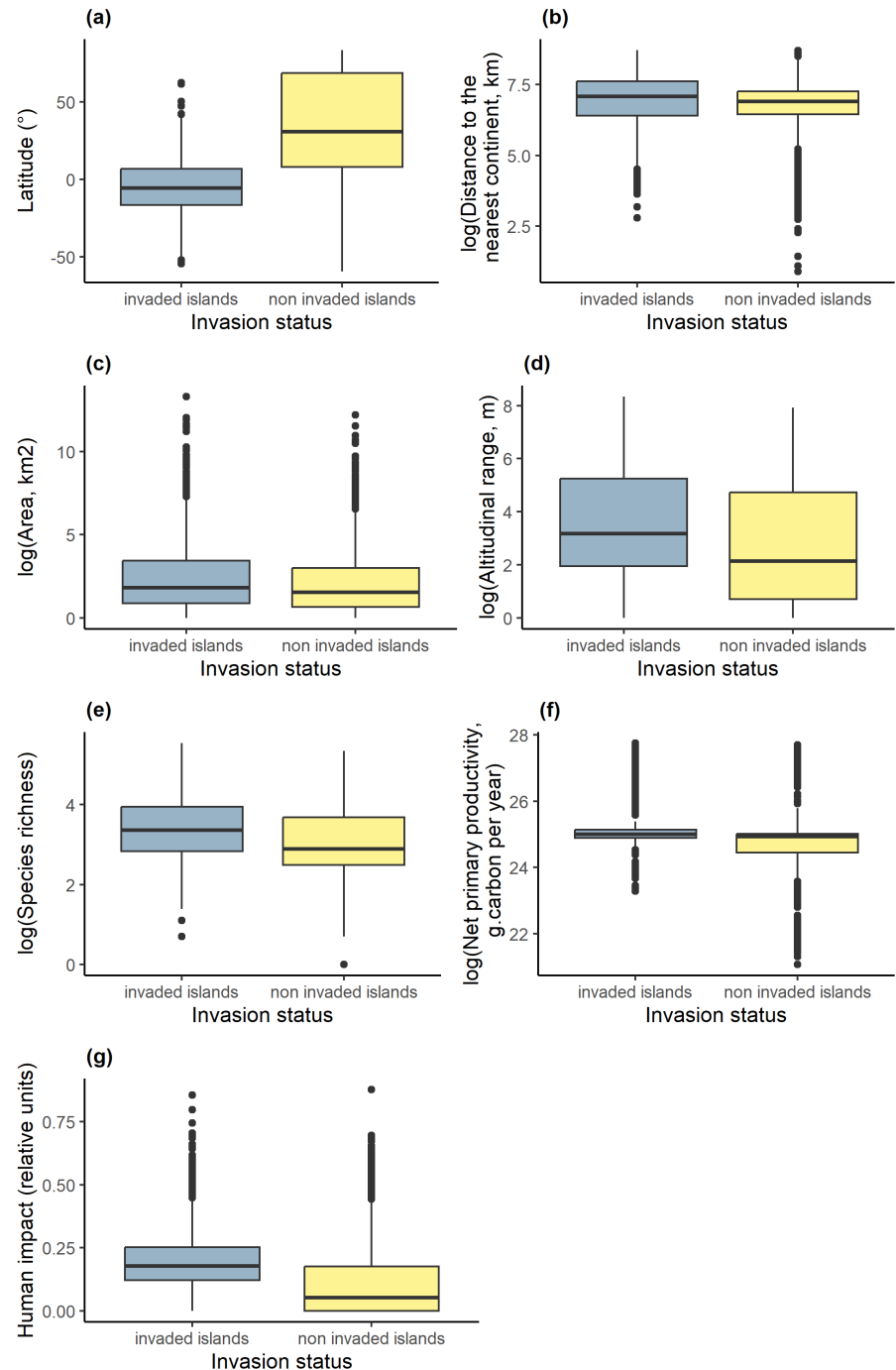


**FIGURE 3** Variations in the trait structure of bird assemblages along environmental gradients for traits related to mobility (marginal standardized effect size in spatial additive models; 0 = null trait structure, positive values = overdispersion, negative values = clustering), with median curve (blue: all oceanic islands with at least two bird species ( $n = 4628$ ); yellow: only oceanic islands with at least two alien species ( $n = 774$ )). Credibility intervals are uninformative (too small due to high sample size) and are thus not displayed.



**FIGURE 4** Variations in the trait structure of bird assemblages along environmental gradients for body mass (marginal standardized effect size in spatial additive models; 0 = null trait structure, positive values = overdispersion, negative values = clustering), with median curve (blue: all oceanic islands with at least two bird species ( $n = 4626$ ); yellow: only oceanic islands with at least two alien species ( $n = 770$ ). Credibility intervals are uninformative (too small due to high sample size) and are thus not displayed.

**FIGURE 5** Latitudinal (a) and environmental position of the 1629 invaded islands and the 3031 noninvaded oceanic islands encompassed in the study (for net primary productivity: 1169 invaded islands and 1684 noninvaded islands; for human impact: 1621 invaded islands and 2952 noninvaded islands).



## 4 | DISCUSSION

### 4.1 | Results overview

Since MacArthur and Wilson (1963, 1967), island biogeography has emphasized geographical location, isolation and area as major drivers of island ecosystems combined with secondary influences of local biotic and abiotic processes (Whittaker & Fernández-Palacios, 2007). Accordingly, in our results, latitude, distance to the nearest continent and species richness were the three key factors explaining the variations in the ecological trait structure

of bird assemblages on oceanic islands. Local environmental conditions (including island area) and anthropogenic imprint had more equivocal influences. We showed that the ecological trait structures of islands invaded by naturalized alien species did not substantially differ from those of noninvaded islands, although alien species tended to augment slightly pre-existing patterns in invaded islands. Furthermore, variations of trait structures differed among native and alien species assemblages on invaded islands along several of the environmental gradients considered, suggesting that both assemblages are shaped by distinct processes.

## 4.2 | Possible processes underlying trait structures

Combining all species, diet and mobility strategies were overdispersed relative to the null model but were clustered for body mass. Trait overdispersion in species assemblages is often attributed to competitive exclusion or fine-grained heterogeneity in the distribution of resources (Cavender-Bares et al., 2009; Gotelli & McCabe, 2002; Pautasso & Gaston, 2005), although various other ecological and evolutionary processes may result in similar patterns (Si et al., 2017). A plausible explanation for trait overdispersion in oceanic island assemblages lies in a combination of low colonization rates (Heaney, 2001; MacArthur & Wilson, 1963, 1967; Whittaker et al., 2008), local competition over limited resources and habitats (Cardillo et al., 2008; Diamond, 1975), and the co-occurrence of contrasting strategies in species-poor assemblages (e.g. the co-occurrence of granivorous and insectivorous passerines in small oceanic islands such as the Azores). Conversely, species assemblages composed of species with similar body size (i.e. clustering, as observed in our results) are expected under strong environment-related selective pressures, such as those leading to the strategy shift from *r* to *K*-selected species predicted by hypotheses related to island syndromes (Blondel, 1990; Crowell & Rothstein, 2008; Pianka, 1972). Nevertheless, clustering in body size is also attributable, to an unknown extent, to human-mediated extinctions that have narrowed the body size distributions through the removal of many large flightless species (such as the moas in New Zealand and elephant birds in Madagascar, Blackburn et al., 2004; Chinsamy et al., 2020; Duncan & Blackburn, 2004; Hansford & Turvey, 2018; Walker et al., 2019).

## 4.3 | Geographical patterns

SES were spatially variable, either because no systematic environmental pressure filters ecological traits, or because regional and local contexts overwhelm such filters. The mobility and diet of bird assemblages, but not their body mass, were to varying extents overdispersed in the tropics. However, when controlling for the other variables that we considered, our model showed that diet became more overdispersed towards northern latitudes. This finding contrasts with continental patterns (Pellissier et al., 2018) and reflects the coexistence of diverse trophic strategies in species-poor Arctic insular assemblages where trophic redundancy is low (Holt, 2009; Massol et al., 2017). For instance, all the diet categories considered in our study, except nectarivory, are represented in the 75 bird species breeding regularly in Iceland. This pattern corresponds to a situation of niche expansion, in which high resource heterogeneity and low carrying capacity favour a higher diversity of niches than expected from species richness (Pautasso & Gaston, 2005). Tropical islands were comparatively closer to the null expectation or were more clustered, corresponding to a situation of niche packing that occurs when resource quantities are less limiting, a pattern similar to that found on continents (Pellissier et al., 2018). Conversely, the greater seasonality of resources at higher latitudes could explain the northward decrease

in SES, indicative of clustered mobility strategies (greater prevalence of migratory behaviour). Surprisingly, Madagascar was systematically clustered for the three sets of traits despite its location in the tropics, speculatively due to its large size and its history of extensive avian species losses since the arrival of humans ~1500–2000 years ago (Culotta, 1995; Hansford et al., 2021; Turvey & Fritz, 2011) and increasingly pervasive anthropogenic pressures (Ganzhorn et al., 2001; Goodman & Benstead, 2005).

Assemblages on the most remote and smallest islands were clustered with respect to mobility strategies and to a lesser extent to the two other traits. A clustering effect of isolation is expected since some land bird species secondarily become sedentary and less mobile once they become permanent island residents (Ferrer et al., 2011; McNab, 1994). Consistent with this result, only the highest distances to the nearest continent were associated with clustered body masses, a result consistent with various empirical studies (Case, 1978; Itescu et al., 2020; Lomolino, 2005). The fact that this effect was restricted to the most isolated islands can be linked to strong effects of regional species pools and local colonization and extinction contexts (Blackburn et al., 2009; Cardador & Blackburn, 2020; Mandon-Dalger et al., 2004).

## 4.4 | Effects of environmental variables

Net primary productivity, topographic heterogeneity and human impact had a low or highly variable influence on all traits, except a slight tendency towards overdispersion in diet and body mass at high levels of human impact on habitats and, for body mass, as a result of high topographic heterogeneity. The lack of a strong statistical effect of human-mediated alterations of land is consistent with a combination of past extinction filters having homogenized the functional compositions of the world's islands (Biber, 2002; Boyer & Jetz, 2014; Ficetola & Padoa-Schioppa, 2009; Milberg & Tyrberg, 1993). Extinction filters may also explain reduced diet overdispersion on islands invaded by alien species and the surprisingly low variation in assemblage structure along gradients of net primary productivity and island size. However, the role of extinction filters could not be tested formally in the present study since lists of extinct species are incomplete or unverified on many of the world's oceanic islands, limiting such studies to the best-documented regions (e.g., Thibault & Cibois, 2017). Furthermore, some of these filters may have acted far earlier than the post-1500 AD records available through the BirdLife data (BirdLife International & Nature Serve, 2012), requiring paleontological data on a restricted set of islands, which may themselves induce a sampling bias based on trait structures (Hortal et al., 2015).

## 4.5 | Impact of alien species on island trait structures

Mots islands invaded by alien species are located in the intertropical band, at lower latitudes than noninvaded ones. This is not surprising

since temperate and boreal northern hemisphere islands were not subjected to major bird naturalization events, except for a few game species. Invaded islands also tended to exhibit slightly wider altitudinal ranges, higher species richness and human impacts, in accordance with known relationships (Biber, 2002; Blackburn et al., 2004; Sanchez-Ortiz et al., 2019). Despite these environmental differences, ecological trait structures in the 770 invaded islands followed the same distributions as the 4628 islands considered, which apparently contrasts with the increase in taxonomic and functional similarity among islands reported in birds and lizards and interpreted as a biotic homogenization process (Capinha et al., 2020; Ficetola & Padoa-Schioppa, 2009; Soares et al., 2022). However, a substantial part of biotic homogenization in island avifaunas is likely more attributable to introduced mammalian predators than to alien bird themselves, as well as to anthropogenic correlates of bird introductions such as habitat conversion and hunting (Blackburn et al., 2004; Ficetola & Padoa-Schioppa, 2009; Nogu e et al., 2021; Sayol et al., 2021).

Accounting for alien species even increased slightly the level of overdispersion in diet and mobility on invaded islands, indicative of niche expansion (i.e. less similarity among species within an assemblage than expected from its species richness, Pellissier et al., 2018) rather than homogenization (i.e. a reduction of trait diversity, Devictor et al., 2008; McKinney & Lockwood, 1999; Olden et al., 2004). This pattern is inconsistent with the homogenizing effect of alien species observed in the world's largest islands (Soares et al., 2022), but it conforms with studies showing that alien and native species overlap little in their ecological traits and are predominantly separated by habitat rather than competitive exclusion (Barnagaud et al., 2014, 2022; Blackburn et al., 2008; Sayol et al., 2021). This discrepancy is most likely explained by differences in the geographical scope and extent among studies, since the ecological structure of local species assemblages remains relatively constant after species introductions within islands ( $\alpha$  diversity), while between-islands dissimilarity decreases due to the relative homogeneity in the traits of the introduced species pool ( $\beta$ -diversity, as studied in Soares et al., 2022).

Alien species did not modify the patterns of variation in ecological trait structures along environmental gradients when pooled with native species. A plausible hypothesis to explain this result could be that the nonrandom selection of alien species by settlers (Pipek et al., 2020) was associated with a postintroduction filtering of alien species' traits based on their ability to cope with local environmental conditions (Barnagaud et al., 2022; Blackburn et al., 2009; Cardador & Blackburn, 2019; Mahoney et al., 2015). These processes can explain why patterns are consistent between native and alien species with respect to variables that determine niche availability, such as net primary productivity and island size. However, they do not account for the marked discrepancy between the variations of the ecological structures of native and alien species assemblages with respect to latitude, species richness and distance to the nearest continent, which we consistently observed for all traits.

The absence of any clear variation in alien species' mobility among islands, except a peak of overdispersion at tropical latitudes, could

stem from the propensity of settlers to naturalize sedentary and generalist species, and to these species' higher abilities to produce viable populations (Blackburn et al., 2009). With respect to diet and, to a lesser extent, body size, alien species were increasingly clustered towards northern latitudes and isolated islands, but overdispersed towards high species richness and high human impacts. These patterns are also more consistent with species' unequal survival to shipment and ability to settle populations under local conditions rather than with respect to macroecological processes, in accordance with studies showing that the conditions of introduction explain a large proportion of species' establishment success (Blackburn et al., 2013; Cassey et al., 2004; Mahoney et al., 2015; Shirley & Kark, 2009). A formal test of these interpretations requires extensive investigations in historical ecology regarding the documented importance of propagules (ship-assisted introductions), paired with the quantification of species' habitat preferences along intra-island gradients, which can only be done on the best-known islands (such as La R union, Mandon-Dalger et al., 2004; or New Zealand, Pipek et al., 2020).

## 5 | CONCLUSION

Despite increasing anthropogenic pressures on island habitats, island bird assemblages still exhibit strong associations between environmental variables and ecological traits. Hence, as observed on continents (Dornelas et al., 2014), patterns of local trait composition and diversity have not entirely been erased by human pressures although major changes have affected the taxonomic composition of species assemblages, resulting in a global decrease of  $\beta$ -diversity. Overall, the distributions of native and alien species among islands seem to be driven by distinct processes, suggesting that bird species introductions on islands have not led to a global homogenization of local assemblages comparable to those driven by habitat conversion, pathogens or predation from introduced mammals. However, the scale relation between within- and inter-island variations in these patterns, as well as their regional variability, needs to be further investigated. This requires improving the availability and comparability of species distribution data within islands, protocols for temporal monitoring of species assemblages at the island scales and most critically continued effort for the conservation of insular avifaunas.

## AUTHOR CONTRIBUTIONS

Charlotte Rault compiled and analysed the data, performed methodological developments, interpreted results and led the writing. Fabien Leprieur contributed to the conceptual and methodological development, participated in data interpretations and contributed to the writing. Luc Barbaro contributed to the conceptual development and to the writing. Holger Kreft contributed to the conceptual development and to the writing. Nicolas Mouquet contributed to the conceptual development and to the writing. Julien Papa x contributed to methodological development, developed the spatial model and contributed to the writing.  a an H.  ekercio lu compiled the trait data and contributed to methodological development and to the writing.

Cyrille Violle contributed to the conceptual and methodological development, participated in data interpretations and contributed to the writing. Jean-Yves Barnagaud supervised the project, elaborated the original idea, contributed to conceptual and methodological developments and contributed to the writing.

## ACKNOWLEDGEMENTS

We thank Cyril Bernard and Laura Mannocci for their assistance with geographical data; Christian Hof, Pavel Pipek and Ana-Maria Bastidas-Urrutia for discussions on the data, methods and results; and Hannah Wheatley for BirdLife International for helpful comments on bird distribution data. We also thank the associate editor and two anonymous referees for their input on previous versions of this manuscript. This article was funded by the Labex CEMEB's project BIOTA. HK acknowledges funding by the German Science Foundation to the DynaCom project (Research Unit number FOR 2716).

## FUNDING INFORMATION

This article is funded by LabEx CeMEB (project BIOTA). HK acknowledges funding by the German Science Foundation to the DynaCom project (Research Unit number FOR 2716).

## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

The data files and scripts necessary to replicate the analyses of this article can be found at <https://doi.org/10.57745/1BRHFC>.

## ORCID

Fabien Leprieur  <https://orcid.org/0000-0001-6869-342X>

Luc Barbaro  <https://orcid.org/0000-0001-7454-5765>

Holger Kreft  <https://orcid.org/0000-0003-4471-8236>

Nicolas Mouquet  <https://orcid.org/0000-0003-1840-6984>

Julien Papaix  <https://orcid.org/0000-0003-2273-5334>

Çağan H. Şekercioğlu  <https://orcid.org/0000-0003-3193-0377>

Cyrille Violle  <https://orcid.org/0000-0002-2471-9226>

Jean-Yves Barnagaud  <https://orcid.org/0000-0002-8438-7809>

## REFERENCES

- Ackerly, D. D., Schilck, D. W., & Webb, C. O. (2006). Niche evolution and adaptive radiation: testing the order of trait divergence. *Ecology*, *87*, 550–561.
- Anderson, S. H., Kelly, D., Ladley, J. J., Molloy, S., & Terry, J. (2011). Cascading effects of bird functional extinction reduce pollination and plant density. *Science*, *331*, 1068–1071.
- Baker, J., Harvey, K. J., & French, K. (2014). Threats from introduced birds to native birds. *Emu-Austral Ornithology*, *114*, 1–12.
- Barnagaud, J.-Y., Barbaro, L., Papaix, J., Deconchat, M., & Brockerhoff, E. G. (2014). Habitat filtering by landscape and local forest composition in native and exotic New Zealand birds. *Ecology*, *95*, 78–87.
- Barnagaud, J.-Y., Brockerhoff, E. G., Mossion, R., Dufour, P., Pavoine, S., Deconchat, M., & Barbaro, L. (2022). Trait-habitat associations explain novel bird assemblages mixing native and alien species across New Zealand landscapes. *Diversity and Distributions*, *28*, 38–52.
- Barnagaud, J.-Y., Mazet, N., Munoz, F., Grenié, M., Denelle, P., Sobral, M., Kissling, W. D., Şekercioğlu, Ç. H., & Violle, C. (2019). Functional biogeography of dietary strategies in birds. *Global Ecology and Biogeography*, *28*, 1004–1017.
- Biber, E. (2002). Patterns of endemic extinctions among Island bird species. *Ecography*, *25*, 661–676.
- BirdLife International & NatureServe. (2012). *Bird species distribution maps of the world*. BirdLife International & NatureServe.
- Blackburn, T. M., Cassey, P., Duncan, R. P., Evans, K. L., & Gaston, K. J. (2004). Avian extinction and mammalian introductions on oceanic islands. *Science*, *305*, 1955–1958.
- Blackburn, T. M., Cassey, P., & Lockwood, J. L. (2008). The Island biogeography of exotic bird species. *Global Ecology and Biogeography*, *17*, 246–251.
- Blackburn, T. M., Cassey, P., & Lockwood, J. L. (2009). The role of species traits in the establishment success of exotic birds. *Global Change Biology*, *15*, 2852–2860.
- Blackburn, T. M., Prowse, T. A. A., Lockwood, J. L., & Cassey, P. (2013). Propagule pressure as a driver of establishment success in deliberately introduced exotic species: Fact or artefact? *Biological Invasions*, *15*, 1459–1469.
- Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošík, V., Wilson, J. R. U., & Richardson, D. M. (2011). A proposed unified framework for biological invasions. *Trends in Ecology & Evolution*, *26*, 333–339.
- Blondel, J. (1985). Breeding strategies of the blue tit and coal tit (Parus) in mainland and Island Mediterranean habitats: A comparison. *Journal of Animal Ecology*, *54*, 531–556.
- Blondel, J. (1990). Long term studies on bird communities and populations in mainland and Island Mediterranean forests. In A. Keast (Ed.), *Biogeography and ecology of forest bird communities* (pp. 167–182). SPB Academic Publishings.
- Boyer, A. G., Cartron, J.-L. E., & Brown, J. H. (2010). Interspecific pairwise relationships among body size, clutch size and latitude: Deconstructing a macroecological triangle in birds. *Journal of Biogeography*, *37*, 47–56.
- Boyer, A. G., & Jetz, W. (2014). Extinctions and the loss of ecological function in Island bird communities. *Global Ecology and Biogeography*, *23*, 679–688.
- Capinha, C., Marcolin, F., & Reino, L. (2020). Human-induced globalization of insular herpetofaunas. *Global Ecology and Biogeography*, *29*, 1328–1349.
- Cardador, L., & Blackburn, T. M. (2019). Human-habitat associations in the native distributions of alien bird species. *Journal of Applied Ecology*, *56*, 1189–1199.
- Cardador, L., & Blackburn, T. M. (2020). A global assessment of human influence on niche shifts and risk predictions of bird invasions. *Global Ecology and Biogeography*, *29*, 1956–1966.
- Cardillo, M., Gittleman, J. L., & Purvis, A. (2008). Global patterns in the phylogenetic structure of Island mammal assemblages. *Proceedings of the Royal Society B: Biological Sciences*, *275*, 1549–1556.
- Case, T. J. (1978). A general explanation for insular body size trends in terrestrial vertebrates. *Ecology*, *59*, 1–18.
- Cassey, P., Blackburn, T. M., Sol, D., Duncan, R. P., & Lockwood, J. L. (2004). Global patterns of introduction effort and establishment success in birds. *Proceedings of the Royal Society B: Biological Sciences*, *271*, S405–S408.
- Cavender-Bares, J., Ackerly, D. D., Baum, D. A., & Bazzaz, F. A. (2004). Phylogenetic overdispersion in Floridian oak communities. *The American Naturalist*, *163*, 823–843.
- Cavender-Bares, J., Keen, A., & Miles, B. (2006). Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. *Ecology*, *87*, S109–S122.

- Cavender-Bares, J., Kozak, K. H., Fine, P. V. A., & Kembel, S. W. (2009). The merging of community ecology and phylogenetic biology. *Ecology Letters*, 12, 693–715.
- Chinsamy, A., Angst, D., Canoville, A., & Göhlich, U. B. (2020). Bone histology yields insights into the biology of the extinct elephant birds (Aepyornithidae) from Madagascar. *Biological Journal of the Linnean Society*, 130, 268–295.
- Courchamp, F., Chapuis, J. L., & Pascal, M. (2003). Mammal invaders on islands: Impact, control and control impact. *Biological Reviews*, 78, 347–383.
- Covas, R. (2012). Evolution of reproductive life histories in Island birds worldwide. *Proceedings of the Royal Society B-Biological Sciences*, 279, 1531–1537.
- Crowell, K., & Rothstein, S. (2008). Clutch size and breeding strategies among Bermudan and North American passerines. *Ibis*, 123, 42–50.
- Culotta, E. (1995). Many suspects to blame in Madagascar extinctions. *Science*, 268, 1568–1569.
- Del Hoyo, J., Elliott, A., & Sargatal, J. (2013). *Handbook of the birds of the world*. Lynx Edicions.
- Devictor, V., Julliard, R., Clavel, J., Jiguet, F., Lee, A., & Couvet, D. (2008). Functional biotic homogenization of bird communities in disturbed landscapes. *Global Ecology and Biogeography*, 17, 252–261.
- Diamond, J. M. (1975). Assembly of species communities. In M. L. Cody & J. M. Diamond (Eds.), *Ecology and evolution of communities* (pp. 342–444). Cambridge.
- Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönsch, G., Westoby, M., Poorter, H., Reich, P. B., Moles, A. T., Dickie, J., Gillison, A. N., Zanne, A. E., ... Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, 529, 167–171.
- Dornelas, M., Gotelli, N. J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., & Magurran, A. E. (2014). Assemblage time series reveal biodiversity change but not systematic loss. *Science*, 344, 296–299.
- Duncan, R. P., & Blackburn, T. M. (2004). Extinction and endemism in the New Zealand avifauna. *Global Ecology and Biogeography*, 13, 509–517.
- Ferrer, M., Bildstein, K., Penteriani, V., Casado, E., & De Lucas, M. (2011). Why birds with deferred sexual maturity are sedentary on islands: A systematic review. *PLoS One*, 6, e22056.
- Ficetola, G. F., & Padoa-Schioppa, E. (2009). Human activities alter biogeographical patterns of reptiles on Mediterranean islands. *Global Ecology and Biogeography*, 18, 214–222.
- Ganzhorn, J. U., Lowry, P. P., Schatz, G. E., & Sommer, S. (2001). The biodiversity of Madagascar: One of the world's hottest hotspots on its way out. *Oryx*, 35, 346–348.
- Gomez-Rubio, V. (2020). *Bayesian inference with INLA*. Chapman & Hall/CRC Press.
- Goodman, S. M., & Benstead, J. P. (2005). Updated estimates of biotic diversity and endemism for Madagascar. *Oryx*, 39, 73–77.
- Gotelli, N. J., & McCabe, D. J. (2002). Species co-occurrence: A meta-analysis of J. M. Diamond's assembly rules model. *Ecology*, 83, 2091–2096.
- Gower, J. C. (1966). Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika*, 53, 325–338.
- Grant, P. R. (Ed.). (1997). *Evolution on islands*. Oxford University Press.
- Hansford, J., & Turvey, S. (2018). Unexpected diversity within the extinct elephant birds (Aves: Aepyornithidae) and a new identity for the world's largest bird. *Royal Society Open Science*, 5, Article 181295.
- Hansford, J., Wright, P. C., Rasoamiramanana, A., Pérez, V. R., Godfrey, L. R., Errickson, D., Thompson, T., & Turvey, S. T. (2021). Early Holocene human presence in Madagascar evidenced by exploitation of avian megafauna. *Science Advances*, 4, eaat6925.
- Heaney, L. R. (1978). Island area and body size of insular mammals: Evidence from the tri-colored squirrel (*Callosciurus prevosti*) of Southeast Asia. *Evolution*, 32, 29.
- Heaney, L. R. (2001). Small mammal diversity along elevational gradients in The Philippines: An assessment of patterns and hypotheses. *Global Ecology and Biogeography*, 10, 15–39.
- Herk, K. M. B., Skidmore, A. K., & Fahr, J. (2017). Macroecological conclusions based on IUCN expert maps: A call for caution. *Global Ecology and Biogeography*, 26, 930–941.
- Holt, R. D. (2009). Toward a trophic Island biogeography reflections on the interface of Island biogeography and food web ecology. In *The theory of island biogeography revisited* (pp. 143–185). Princeton University Press.
- Hortal, J., de Bello, F., Diniz-Filho, J. A. F., Lewinsohn, T. M., Lobo, J. M., & Ladle, R. J. (2015). Seven shortfalls that beset large-scale knowledge of biodiversity. In D. J. Futuyma (Ed.), *Annual review of ecology, evolution, and systematics* (Vol. 46, pp. 523–549). Annual Reviews.
- Imhoff, M. L., & Bounoua, L. (2006). Exploring global patterns of net primary production carbon supply and demand using satellite observations and statistical data. *Journal of Geophysical Research: Atmospheres*, 111(D22), 1–8.
- Itescu, Y., Foufopoulos, J., Pafilis, P., & Meiri, S. (2020). The diverse nature of Island isolation and its effect on land bridge insular faunas. *Global Ecology and Biogeography*, 29, 262–280.
- Jetz, W., Ashton, K. G., & La Sorte, F. A. (2009). Phenotypic population divergence in terrestrial vertebrates at macro scales. *Ecology Letters*, 12, 1137–1146.
- Kennedy, C. M., Oakleaf, J. R., Theobald, D. M., Baruch-Mordo, S., & Kiesecker, J. (2019). Managing the middle: A shift in conservation priorities based on the global human modification gradient. *Global Change Biology*, 25, 811–826.
- Kier, G., Kreft, H., Lee, T. M., Jetz, W., Ibsch, P. L., Nowicki, C., Mutke, J., & Barthlott, W. (2009). A global assessment of endemism and species richness across Island and mainland regions. *Proceedings of the National Academy of Sciences*, 106, 9322–9327.
- Kirchman, J. J. (2009). Genetic tests of rapid parallel speciation of flightless birds from an extant volant ancestor. *Biological Journal of the Linnean Society*, 96, 601–616.
- Kissling, W. D., Rahbek, C., & Böhning-Gaese, K. (2007). Food plant diversity as broad-scale determinant of avian frugivore richness. *Proceedings of the Royal Society B: Biological Sciences*, 274, 799–808.
- Kissling, W. D., Sekercioglu, C. H., & Jetz, W. (2011). Bird dietary guild richness across latitudes, environments and biogeographic regions. *Global Ecology and Biogeography*, 21, 328–340.
- Leclerc, C., Villéger, S., Marino, C., & Bellard, C. (2020). Global changes threaten functional and taxonomic diversity of insular species worldwide. *Diversity and Distributions*, 26, 402–414.
- Leisler, B., & Winkler, H. (2015). Evolution of Island warblers: Beyond bills and masses. *Journal of Avian Biology*, 46, 236–244.
- Lindgren, F., Rue, H., & Lindström, J. (2011). An explicit link between gaussian fields and gaussian Markov random fields: The stochastic partial differential equation approach. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 73, 423–498.
- Lomolino, M. V. (1985). Body size of mammals on islands: The Island rule reexamined. *The American Naturalist*, 125, 310–316.
- Lomolino, M. V. (2005). Body size evolution in insular vertebrates: Generality of the Island rule. *Journal of Biogeography*, 32, 1683–1699.
- MacArthur, R. H., & Wilson, E. O. (1963). An equilibrium theory of insular zoogeography. *Evolution*, 17, 373–387.
- MacArthur, R. H., & Wilson, E. O. (1967). *The theory of Island biogeography*. Princeton University Press.
- Mahoney, P. J., Beard, K. H., Durso, A. M., Tallian, A. G., Long, A. L., Kindermann, R. J., Nolan, N. E., Kinka, D., & Mohn, H. E. (2015). Introduction effort, climate matching and species traits as

- predictors of global establishment success in non-native reptiles. *Diversity and Distributions*, 21, 64–74.
- Mandon-Dalger, I., Clergeau, P., Tassin, J., Rivière, J.-N., & Gatti, S. (2004). Relationships between alien plants and an alien bird species on Reunion Island. *Journal of Tropical Ecology*, 20, 635–642.
- Massol, F., Dubart, M., Calcagno, V., Cazelles, K., Jacquet, C., Kéfi, S., & Gravel, D. (2017). Island biogeography of food webs. In D. A. Bohan, A. J. Dumbrell, & F. Massol (Eds.), *Advances in ecological research networks of invasion: A synthesis of concepts* (pp. 183–262). Academic Press.
- McKinney, M. L., & Lockwood, J. L. (1999). Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, 14, 450–453.
- McNab, B. K. (1994). Energy conservation and the evolution of flightlessness in birds. *The American Naturalist*, 144, 628–642.
- Milberg, P., & Tyrberg, T. (1993). Naive birds and Noble savages—A review of man-caused prehistoric extinctions of Island birds. *Ecography*, 16, 229–250.
- Nogué, S., Santos, A. M. C., Birks, H. J. B., Björck, S., Castilla-Beltrán, A., Connor, S., De Boer, E. J., De Nascimento, L., Felde, V. A., Fernández-Palacios, J. M., Froyd, C. A., Haberle, S. G., Hooghiemstra, H., Ljung, K., Norder, S. J., Peñuelas, J., Prebble, M., Stevenson, J., Whittaker, R. J., ... Steinbauer, M. J. (2021). The human dimension of biodiversity changes on islands. *Science*, 372, 488–491.
- Novosolov, M., Raia, P., & Meiri, S. (2013). The island syndrome in lizards: Life history evolution in island lizards. *Global Ecology and Biogeography*, 22, 184–191.
- Olden, J. D., Poff, N. L., Douglas, M. R., Douglas, M. E., & Fausch, K. D. (2004). Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology & Evolution*, 19, 18–24.
- Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'Amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P., & Kassem, K. R. (2001). Terrestrial ecoregions of the worlds: A new map of life on earth. *Bioscience*, 51, 933–938.
- Otto, R., Fernández-Lugo, S., Blandino, C., Manganelli, G., Chiarucci, A., & Fernández-Palacios, J. M. (2020). Biotic homogenization of oceanic islands depends on taxon, spatial scale and the quantification approach. *Ecography*, 43, 747–758.
- Pautasso, M., & Gaston, K. J. (2005). Resources and global avian assemblage structure in forests. *Ecology Letters*, 8, 282–289.
- Pavlek, M., & Mammola, S. (2021). Niche-based processes explaining the distributions of closely related subterranean spiders. *Journal of Biogeography*, 48, 118–133.
- Pavoine, S., Vallet, J., Dufour, A.-B., Gachet, S., & Daniel, H. (2009). On the challenge of treating various types of variables: Application for improving the measurement of functional diversity. *Oikos*, 118, 391–402.
- Pellissier, V., Barnagaud, J.-Y., Kissling, W. D., Şekercioğlu, Ç., & Svenning, J.-C. (2018). Niche packing and expansion account for species richness–productivity relationships in global bird assemblages. *Global Ecology and Biogeography*, 27, 604–615.
- Pianka, E. R. (1972). R and K selection or b and d selection? *The American Naturalist*, 106, 581–588.
- Pianka, E. R. (1974). Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences*, 71, 2141–2145.
- Pimm, S., Raven, P., Peterson, A., Sekercioğlu, C. H., & Ehrlich, P. R. (2006). Human impacts on the rates of recent, present, and future bird extinctions. *Proceedings of the National Academy of Science*, 103, 10941–10946.
- Pipek, P., Blackburn, T. M., Delean, S., Cassey, P., Şekercioğlu, Ç. H., & Pyšek, P. (2020). Lasting the distance: The survival of alien birds shipped to New Zealand in the 19th century. *Ecology and Evolution*, 10, 3944–3953.
- Prodon, R., Thibault, J.-C., & Dejaifve, P.-A. (2002). Expansion vs. compression of bird altitudinal ranges on a Mediterranean Island. *Ecology*, 83, 1294–1306.
- Rosenzweig, M. (2001). The four questions: What does the introduction of exotic species do to diversity? *Evolutionary Ecology Research*, 3, 361–367.
- Rue, H., Martino, S., & Chopin, N. (2009). Approximate Bayesian inference for latent gaussian models by using integrated nested Laplace approximations. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 71, 319–392.
- Sam, K., Koane, B., Jeppy, S., Sykorova, J., & Novotny, V. (2017). Diet of land birds along an elevational gradient in Papua New Guinea. *Scientific Reports*, 7, 44018.
- Sanchez-Ortiz, K., Gonzalez, R. E., Palma, A. D., Newbold, T., Hill, S. L. L., Tylianakis, J. M., Börger, L., Lysenko, I., & Purvis, A. (2019). Land-use and related pressures have reduced biotic integrity more on islands than on mainlands. *bioRxiv*, 576546.
- Sax, D. F., Gaines, S. D., Brown, J. H., & Doak, A. E. D. F. (2002). Species invasions exceed extinctions on islands worldwide: A comparative study of plants and birds. *The American Naturalist*, 160, 766–783.
- Sayol, F., Cooke, R. S. C., Pigot, A. L., Blackburn, T. M., Tobias, J. A., Steinbauer, M. J., Antonelli, A., & Faurby, S. (2021). Loss of functional diversity through anthropogenic extinctions of Island birds is not offset by biotic invasions. *Science Advances*, 7, eabj5790.
- Şekercioğlu, Ç. H., Daily, G. C., & Ehrlich, P. R. (2004). Ecosystem consequences of bird declines. *Proceedings of the National Academy of Sciences*, 101, 18042–18047.
- Şekercioğlu, Ç. H., Wenny, D. G., & Whelan, C. J. (2016). *Why birds matter: Avian ecological function and ecosystem services*. University of Chicago Press.
- Shirley, S. M., & Kark, S. (2009). The role of species traits and taxonomic patterns in alien bird impacts. *Global Ecology and Biogeography*, 18, 450–459.
- Si, X., Baselga, A., Leprieur, F., Song, X., & Ding, P. (2016). Selective extinction drives taxonomic and functional alpha and beta diversities in Island bird assemblages. *Journal of Animal Ecology*, 85, 409–418.
- Si, X., Cadotte, M. W., Zeng, D., Baselga, A., Zhao, Y., Li, J., Wu, Y., Wang, S., & Ding, P. (2017). Functional and phylogenetic structure of Island bird communities. *Journal of Animal Ecology*, 86, 532–542.
- Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D. A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E., & Vilà, M. (2013). Impacts of biological invasions: What's what and the way forward. *Trends in Ecology & Evolution*, 28, 58–66.
- Soares, F. C., de Lima, R. F., Palmeirim, J. M., Cardoso, P., & Rodrigues, A. S. L. (2022). Combined effects of bird extinctions and introductions in oceanic islands: Decreased functional diversity despite increased species richness. *Global Ecology and Biogeography*, 31, 1172–1183.
- Soares, F. C., Leal, A. I., Palmeirim, J. M., & De Lima, R. F. (2021). Niche differences may reduce susceptibility to competition between native and non-native birds in oceanic islands. *Diversity and Distributions*, 27, 1507–1518.
- Silvertown, J., Dodd, M., Gowing, D., Lawson, C., & McConway, K. (2006). Phylogeny and the hierarchical organization of plant diversity. *Ecology*, 87, S39–S49.
- Sobral, F. L., Lees, A. C., & Cianciaruso, M. V. (2016). Introductions do not compensate for functional and phylogenetic losses following extinctions in insular bird assemblages. *Ecology Letters*, 19, 1091–1100.
- Stamps, J. A., & Buechner, M. (1985). The territorial defense hypothesis and the ecology of insular vertebrates. *The Quarterly Review of Biology*, 60, 155–181.

- Swenson, N. G., Stegen, J. C., Davies, S. J., Erickson, D. L., Forero-Montaña, J., Hurlbert, A. H., Kress, W. J., Thompson, J., Uriarte, M., Wright, S. J., & Zimmerman, J. K. (2012). Temporal turnover in the composition of tropical tree communities: Functional determinism and phylogenetic stochasticity. *Ecology*, *93*, 490–499.
- Taylor, A., Keppel, G., Weigelt, P., Zotz, G., & Kreft, H. (2021). Functional traits are key to understanding orchid diversity on islands. *Ecography*, *44*, 703–714.
- Thibault, J.-C., & Cibois, A. (2017). *Birds of Eastern Polynesia: A biogeographic Atlas* (1st ed.). LYNX EDICIONS.
- Thioulouse, J., Dray, S., Dufour, A.-B., Siberchicot, A., Jombart, T., & Pavoine, S. (2018). *Multivariate analysis of ecological data with ade4*. Springer-Verlag.
- Turvey, S. T., & Fritz, S. A. (2011). The ghosts of mammals past: Biological and geographical patterns of global mammalian extinction across the Holocene. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *366*, 2564–2576.
- van Heteren, A. H., Wroe, S., Tsang, L. R., Mitchell, D. R., Ross, P., Ledogar, J. A., Attard, M. R. G., Sustaita, D., Clausen, P., Scofield, R. P., & Sansalone, G. (2021). New Zealand's extinct giant raptor (*Hieraetus moorei*) killed like an eagle, ate like a condor. *Proceedings of the Royal Society B: Biological Sciences*, *288*, 20211913.
- Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, *116*, 882–892.
- Walker, S., Monks, A., & Innes, J. (2019). Thermal squeeze will exacerbate declines in New Zealand's endemic forest birds. *Biological Conservation*, *237*, 166–174.
- Webb, C. O., Ackerly, D. D., & Kembel, S. W. (2008). Phylocom: Software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics*, *24*, 2098–2100.
- Weigelt, P., Jetz, W., & Kreft, H. (2013). Bioclimatic and physical characterization of the world's islands. *Proceedings of the National Academy of Sciences*, *110*, 15307–15312. <https://doi.org/10.1073/pnas.1306309110>
- Whittaker, R. J. (1998). *Island biogeography: Ecology, evolution, and conservation*. Oxford University Press.
- Whittaker, R. J., & Fernández-Palacios, J. M. (2007). *Island biogeography: Ecology, evolution, and conservation* (2nd ed.). Oxford University Press.
- Whittaker, R. J., Rigal, F., Borges, P. A. V., Cardoso, P., Terzopoulou, S., Casanoves, F., Pla, L., Guilhaumon, F., Ladle, R. J., & Triantis, K. A. (2014). Functional biogeography of oceanic islands and the scaling of functional diversity in the Azores. *Proceedings of the National Academy of Sciences*, *111*, 13709–13714.
- Whittaker, R. J., Triantis, K. A., & Ladle, R. J. (2008). A general dynamic theory of oceanic Island biogeography. *Journal of Biogeography*, *35*, 977–994.

## BIOSKETCH

**Charlotte Rault** is a master student with broad interests in the application of data analysis to the conservation of ecosystems and their faunas at various spatial scales. Her master project focussed on the ecological structure of island bird assemblages over a macroecological extent, with a specific emphasis on the role of introduced species. The BIOTA project aims to explore the imprint of climate, land use and introduced species on the bird faunas of oceanic islands through a functional biogeography approach.

## SUPPORTING INFORMATION

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

**How to cite this article:** Rault, C., Leprieur, F., Barbaro, L., Kreft, H., Mouquet, N., Papaix, J., Şekercioğlu, Ç. H., Violle, C., & Barnagaud, J.-Y. (2023). Trait-environment associations diverge between native and alien breeding bird assemblages on the world's oceanic islands. *Global Ecology and Biogeography*, *00*, 1–17. <https://doi.org/10.1111/geb.13729>