

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

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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

INTRODUCTION

Oceanic islands are simplified, near-closed ecosystems hosting small populations with limited gene flow and simplified biotic interaction networks (MacArthur & Wilson, 1963, 1967; Grant, 1997; Kier *et al.*, 2009; Itescu *et al.*, 2020). 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 takes the form of gigantism or dwarfism, or the complete or partial loss of flight ability (McNab, 1994; Grant, 1997; Lomolino, 2005).

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 (Case, 1978; Lomolino, 2005; Boyer *et al.*, 2010; Leisler & Winkler, 2015), life history (Blondel, 1985; Covas, 2012), phenomenological (Prodon *et al.*, 2002) and behavioral (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 or to elucidate species’ roles in ecosystem processes and services (Sobral *et al.*, 2016; Cardador & Blackburn, 2019, 2020; Leclerc *et al.*, 2020). 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 (Diaz et al., 2016; Violle et al., 2007). For instance, geographical patterns in bird diets (Kissling *et al.*, 2011), species' propensity to mobility (McNab, 1994; Kirchman, 2009) 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, 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 (*Hieraaetus 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 favoring the diversity of frugivores and nectarivores; Kissling *et al.*, 2007; Jetz *et al.*, 2009; Barnagaud *et al.*, 2019).

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 (Whittaker, 1998; Blackburn *et al.*, 2008; Si *et al.*, 2017). Extensive hunting of island endemic species, the introduction of mammalian predators since the earliest human colonizations (Courchamp *et al.*, 2003; Blackburn *et al.*, 2004; Simberloff *et al.*, 2013), and novel competitors (Mandon-Dalger *et al.*, 2004; Blackburn *et al.*, 2011; Baker *et al.*, 2014; 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 have 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 non-random 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 (Olden *et al.*, 2004; Whittaker *et al.*, 2007; Mahoney *et al.*, 2015; Si *et al.*, 2017; Otto *et al.*, 2020).

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; Si *et al.*, 2016; Sobral *et al.*, 2016; Sayol *et al.*, 2021). 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 non-invaded 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 non-invaded 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 (Rosenzweig, 2001; Olden *et al.*, 2004; Otto *et al.*, 2020). 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.

METHODS

Data

Ecological traits

We retrieved the ecological traits of the world's 11,117 extant bird species from Şekercioğlu *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 for our research questions focused on the geographic 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 non-insular 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 biogeographic realms as defined by Olson et al. (2001; i.e. 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, post-fledging nomadism), and log-transformed body mass (descriptions of ecological traits in Table 1).

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 & Nature Serve (2012)'s extent-of-occurrence database (uploaded from <http://datazone.birdlife.org/home> in 2021), which contains vector extent-of-occurrence 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 to 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 having 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.

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 1km 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 total sample size for analysis since, in our modeling 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 correlation close to a Pearson’s correlation coefficient of -0.3); other variables were uncorrelated.

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 Swenson *et al.*, 2012; Si *et al.*, 2017). Gower’s distance allows dealing

with non-independent 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 randomises 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 biogeographic 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, Eq. 1, Webb *et al.*, 2008) :

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

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 were 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).

Trait structure - environment associations

We used spatial generalized additive models (GAM) to fit non-linear 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:

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

(Equation 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, α is an intercept, ϵ is an independent and normally distributed error and ν 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 (Rue *et al.*, 2009; Lindgren *et al.*, 2011), using the INLA package in R (Gomez-Rubio, 2020)

RESULTS

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 Fig. 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 dietary traits than expected in the null model. Consequently, the global distribution of SES_{diet} was shifted towards positive values (Fig. 1 a–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_{diet} , indicative of clustered dietary traits (located in the Neotropic and Palearctic realms, Fig. 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'

dietary strategies 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 (Fig. 1b, $SES_{mob} = 1.50 \pm 1.77 [-3.24, 8.83]$). Native species' mobility traits were significantly overdispersed in 2118/4628 islands (30%), 81% of positive SES_{mob} being located in the southern hemisphere (*e.g.*, $SES_{mob} > 8.00$ for Pulau Timor, Pulau Semau and the other islands of the Malay Archipelago, Fig. 1b). By contrast, 840 islands had clustered mobility traits (negative SES_{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, $SES_{mob} = -3.24$ and Iceland, $SES_{mob} = -3.04$, Fig. 1c), except Madagascar ($SES_{mob} = -1.51$, non-significantly different from the null model, Fig. 1b and Fig. 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_{mob} (25 significantly overdispersed assemblages and 23 significantly clustered assemblages over 774 islands).

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

were dominated by non-significant negative values when accounting for all species or for alien species (see figures in Appendix S3).

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 non-linear trends, but without a consistent pattern among variables and traits (Fig. 2-3-4, estimated parameters are provided in Appendix S4). Overdispersion of diets increased towards northern latitudes (Fig. 2a), while clustering increased southwards for mobility and body mass (Fig. 3a, Fig. 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 (Fig. 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 (Fig. 2u, Fig. 3u).

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 (Fig. 5). The average positions of invaded islands along environmental gradients were statistically different from those of non-invaded islands (Welch's t tests, p-values $< 10^{-11}$ with 1629 invaded islands and 3031 non invaded islands for all variables except human impact : 1621 invaded and 2952 non-invaded islands, and NPP : 1169 invaded and 1684 non-invaded islands). However, these statistical differences are partly

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

Influence of alien species on the trait structures of invaded islands

On average, the 1629 invaded islands hosted 2.59 ± 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 : $t = -13.71$, $df = 769$, $p < 0.0001$, Fig. 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: $\Delta = 1.69$, Fig. 1c-f) to overdispersion in the other atolls of French Polynesia ($\Delta = -1.24$, Fig. 1c-f). However, in spite of these shifts in the distributions of SES, the relationships between SES values and environmental variables were virtually not altered by alien species (Figs. 3-4-5, 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 (Figs. 2, 3 and 4), variations of the SES_{diet} of alien species alone differed noticeably for latitude (more overdispersed at northern latitudes, compare Fig. 2b-c, yellow curves), isolation (more clustered at large distances, Fig. 2e-f, yellow curves) and species richness (strong overdispersion in the richest species assemblages, Fig. 2n-o, yellow curves). Similar discrepancies occurred for SES_{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 Fig. 3a-c, yellow curves). SES_{mobility} was further unrelated to species richness in alien species, contrary to the pattern for all species (compare Fig. 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 (Fig. 4b-c, yellow curves).

DISCUSSION

Results overview

Since Mac Arthur & Wilson (1963, 1967), island biogeography has emphasized geographic 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 non-invaded 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.

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 (Gotelli & McCabe, 2002; Pautasso & Gaston, 2005; Cavender-Bares *et al.*, 2009), 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 (MacArthur & Wilson, 1963, 1967; Heaney, 2001; Whittaker *et al.*, 2008), local competition over limited resources and habitats (Diamond, 1975; Cardillo *et al.*, 2008), 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 (Pianka, 1972; Blondel, 1990; Crowell & Rothstein, 2008). 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; Duncan & Blackburn, 2004; Hansford & Turvey, 2018; Walker *et al.*, 2019; Chinsamy *et al.*, 2020).

Geographic 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 favor 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 behavior). Surprisingly, Madagascar was systematically clustered for the three set of traits in spite of 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; Turvey & Fritz, 2011; Hansford *et al.*, 2021) 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 (McNab, 1994; Ferrer *et al.*, 2011). 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; Lomolino, 2005; Itescu *et al.*, 2020). 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 (Mandon-Dalger *et al.*, 2004; Blackburn *et al.*, 2009; Cardador & Blackburn, 2020).

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 toward 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 (Milberg & Tyrberg, 1993; Biber, 2002; Ficetola

& Padoa-Schioppa, 2009; Boyer & Jetz, 2014). 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 because 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.*, Polynesia, Thibault & Cibois, 2017). Furthermore, some of these filters may have acted far earlier than the post-1500AD 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).

Impact of alien species on island trait structures

Mots islands invaded by alien species are located in the intertropical band, at lower latitudes than non-invaded 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). In spite of 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; Nogué *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; Mc Kinney & Lockwood, 1999; Olden *et al.*, 2002). 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 (α diversity), while between-islands dissimilarity decreases due to the relative homogeneity in the traits of the introduced species pool (β 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 non-random selection of alien species by settlers (Pipek *et al.*, 2020) was associated with a post-introduction filtering of alien species' traits based on their ability to cope with local environmental conditions (Blackburn *et al.*, 2009; Mahoney *et al.*, 2015; Cardador & Blackburn, 2019; Barnagaud *et al.*, 2022). 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 (Cassey *et al.*, 2004; Shirley & Kark, 2009; Blackburn *et al.*, 2013; Mahoney *et al.*, 2015). 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 Réunion, Mandon-Dalger *et al.*, 2004; or New Zealand, Pipek *et al.*, 2020).

CONCLUSION

In spite of 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 β -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.

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DATA ACCESSIBILITY STATEMENT

The data files and scripts necessary to replicate the analyses of this article can be found at

<https://doi.org/10.5061/dryad.hqbzkh1n3> .

TABLES

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

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, post-fledgling nomadism.	Categorical with 3 modalities: 0, sedentary; 1, strict migrant; 2, partial migrant	Tendency to sedentariness, at least for non-passerines.
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 2. Environmental variables considered in our analyses. All variables are quantified for 4660 oceanic islands unless otherwise stated.

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 ²)	Area	584.60 \pm 10508.35 [1, 590547.40]
Net primary production* (g carbon/year)	NPP	1.32e+11 \pm 2.16e+11 [1.42e+09, 1.12e+12] (1807 missing values)
Human impact (HMc)**	Human	0.14 \pm 0.14 [0, 0.88] (87 missing values)
Species richness	SP	30.25 \pm 29.63 [1, 256]

*Net primary production is a median per island

**HMc = cumulative degree of human modification of land

FIGURES

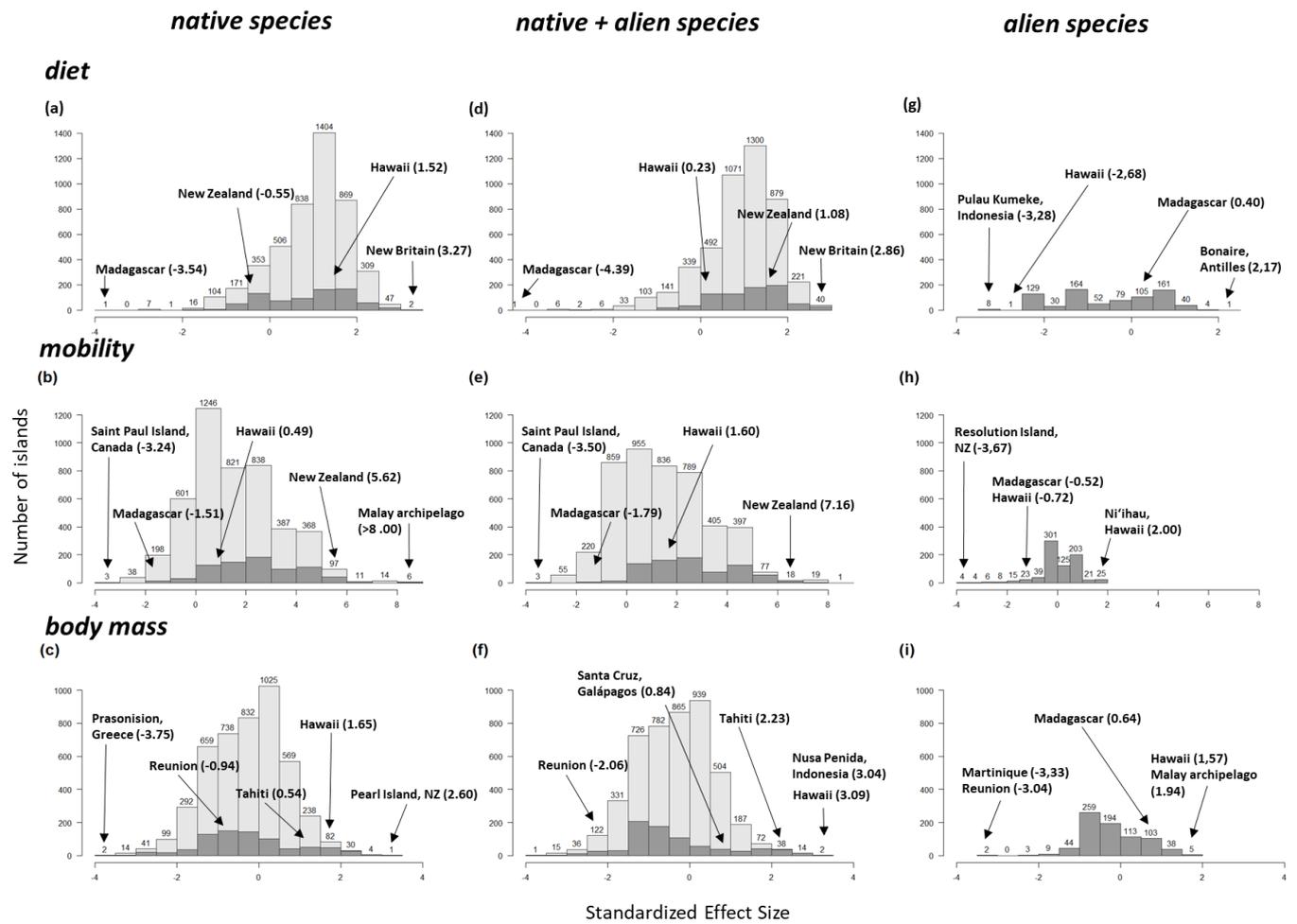


Figure 1. Distributions of the trait structures of island bird assemblages with respect to dietary traits (a, d, g), for mobility-related traits (b, e, h) and body mass (c, f, i). Trait structure is quantified as the standardized effect size (SES) of mean pairwise trait distances compared to a null model, and is computed for islands with at least two species with trait data. Light gray: SES values for all oceanic islands with at least two species (diet n=4628, migration n=4628, body mass n=4626); dark gray: 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 (center column).

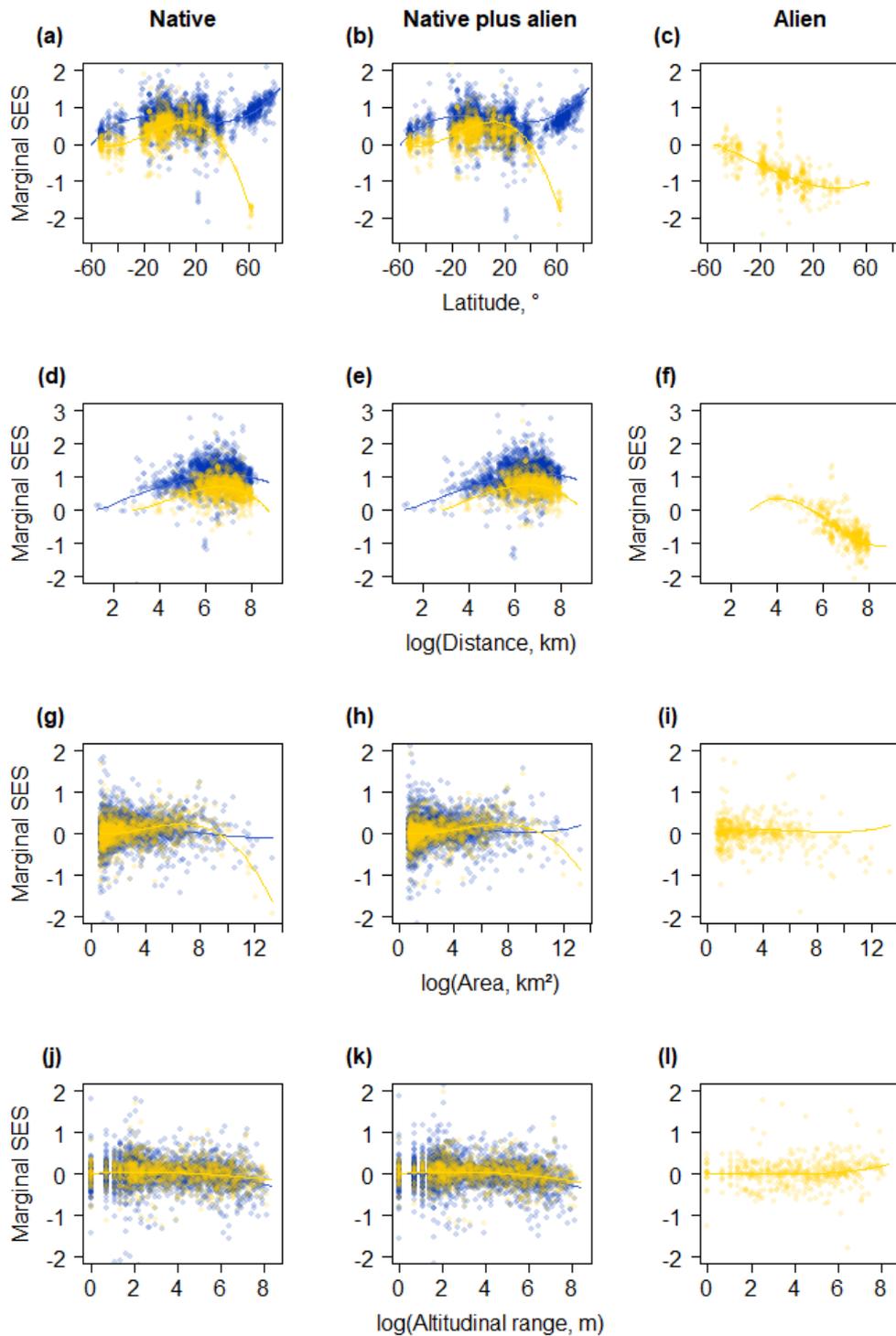


Figure 2. Variations in the trait structure of bird assemblages along environmental gradients for traits related to diet (marginal standardized effect size in spatial additive models; 0 = null trait structure, positive values = overdispersion, negative values = clustering), with median curve (blue: all 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.

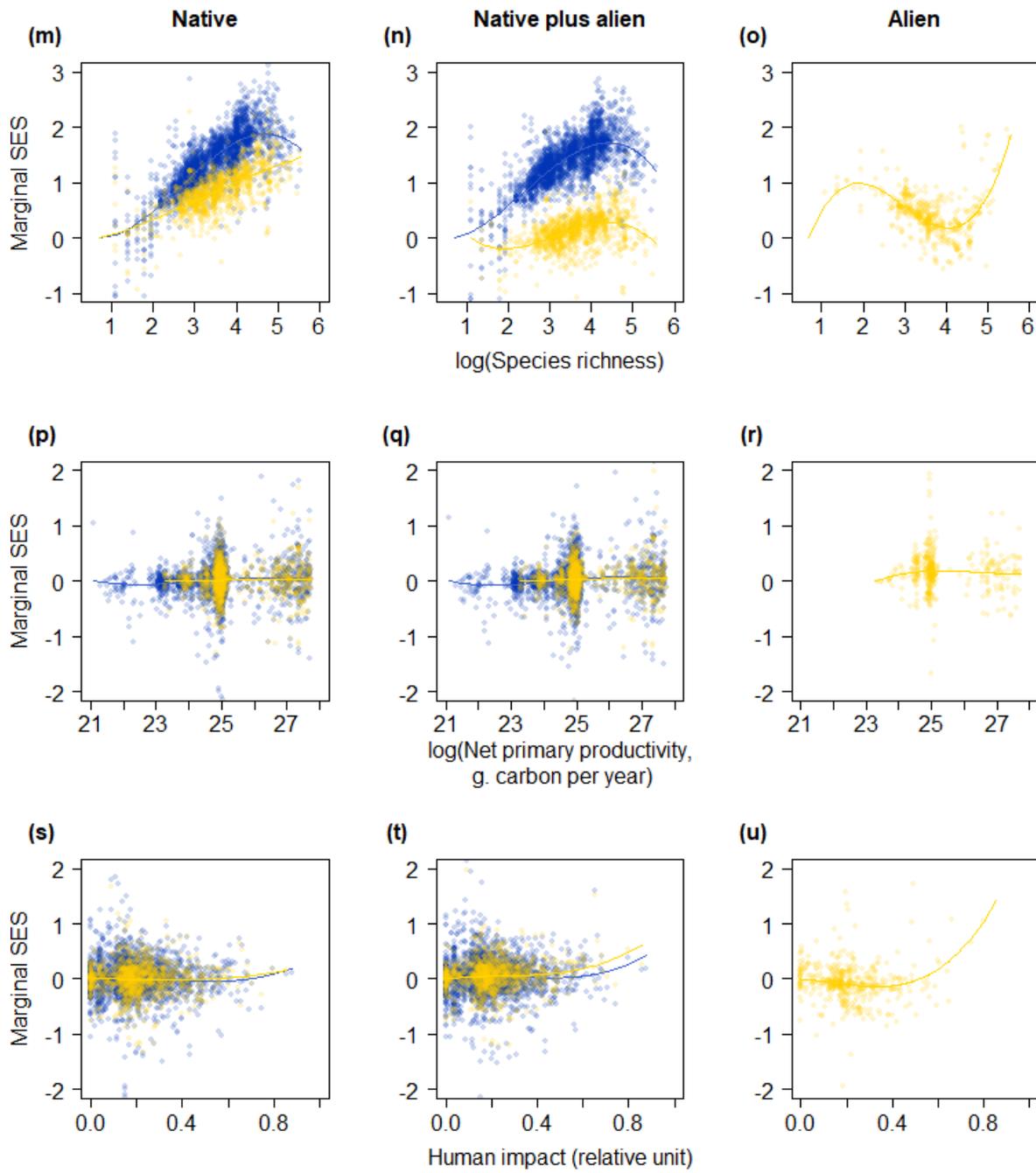


Figure 2 (continued)

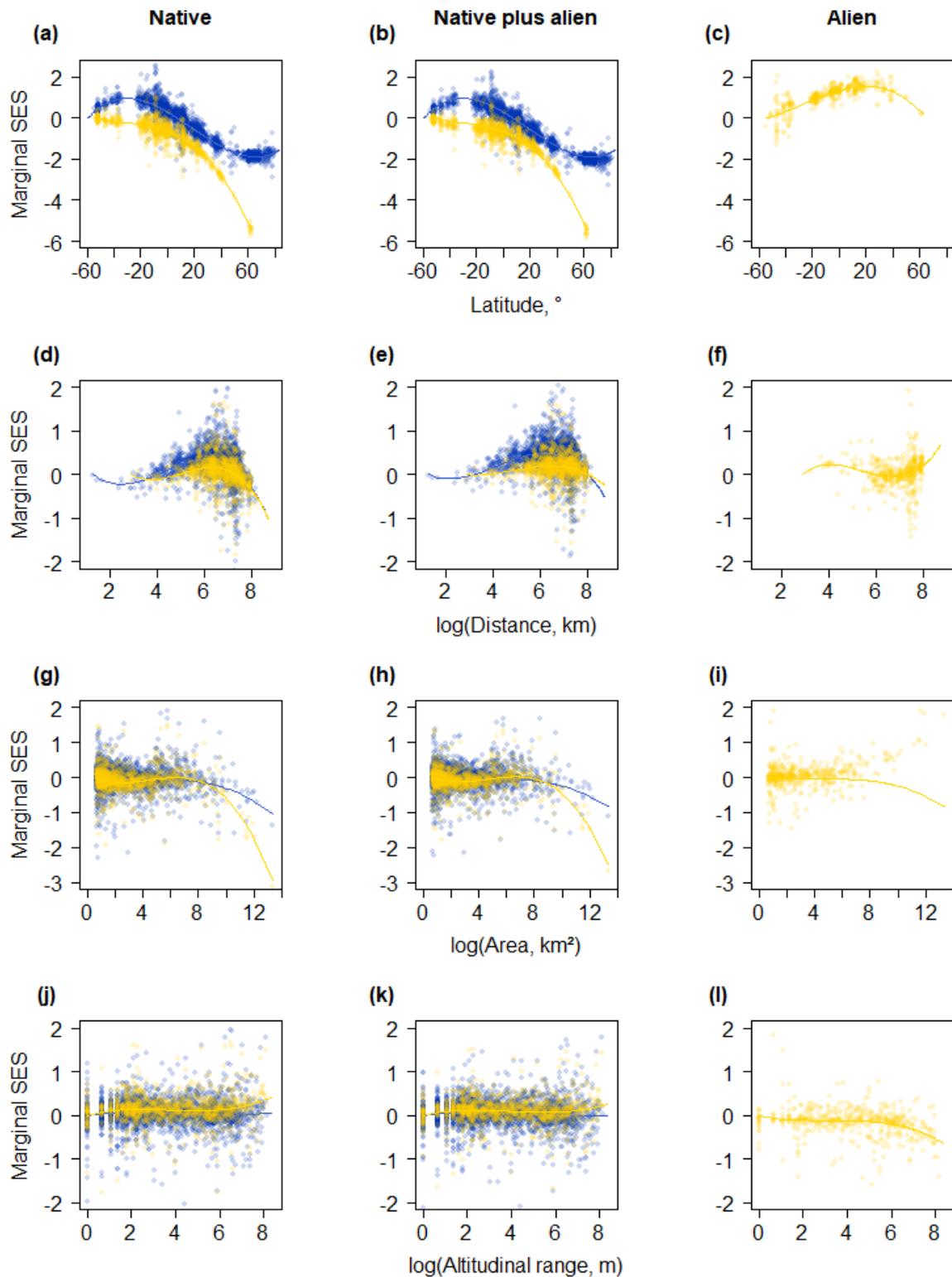


Figure 3. Variations in the trait structure of bird assemblages along environmental gradients for traits related to mobility (marginal standardized effect size in spatial additive models; 0 = null trait structure, positive values = overdispersion, negative values = clustering), with median curve (blue: 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.

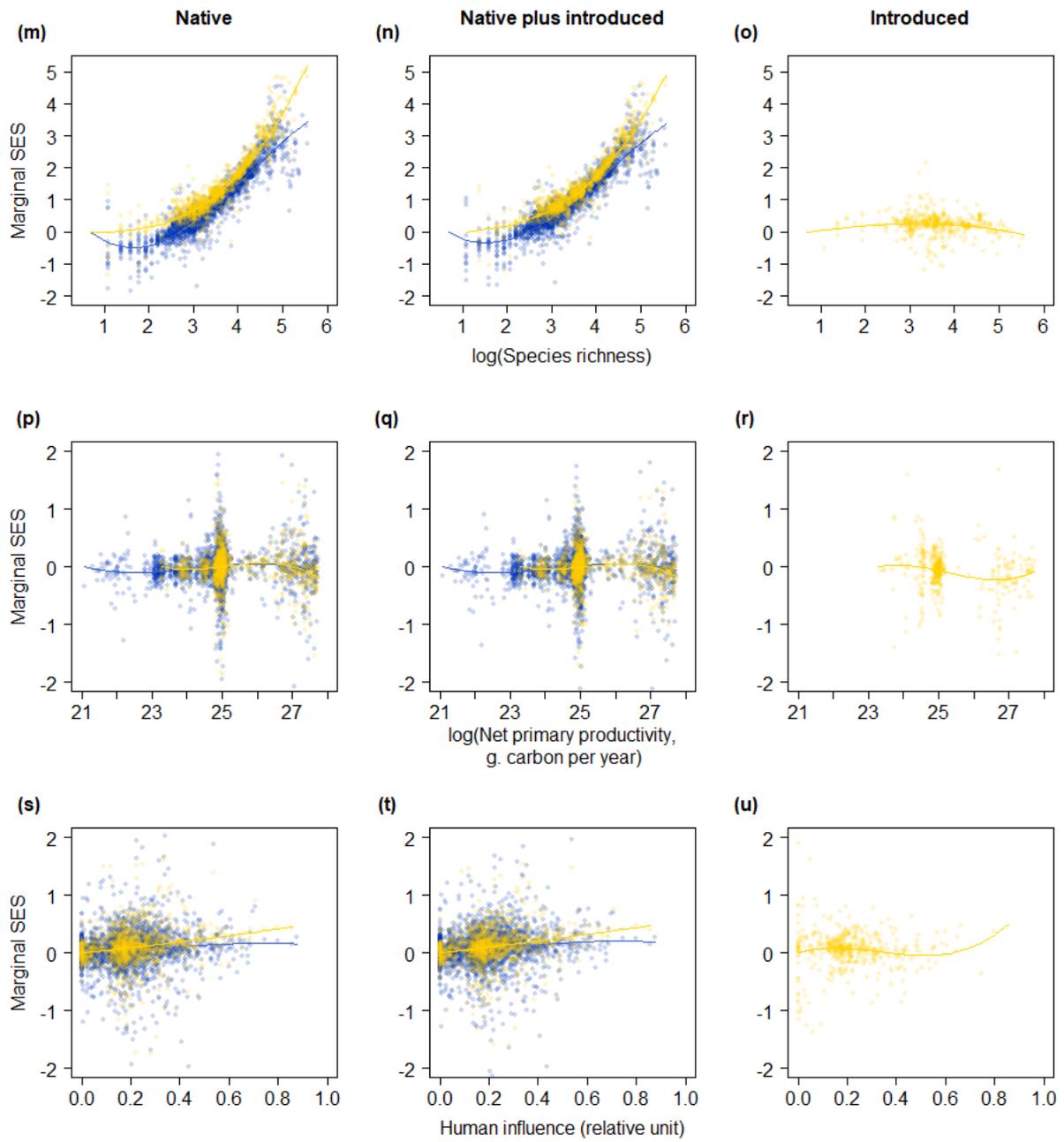


Figure 3 (continued).

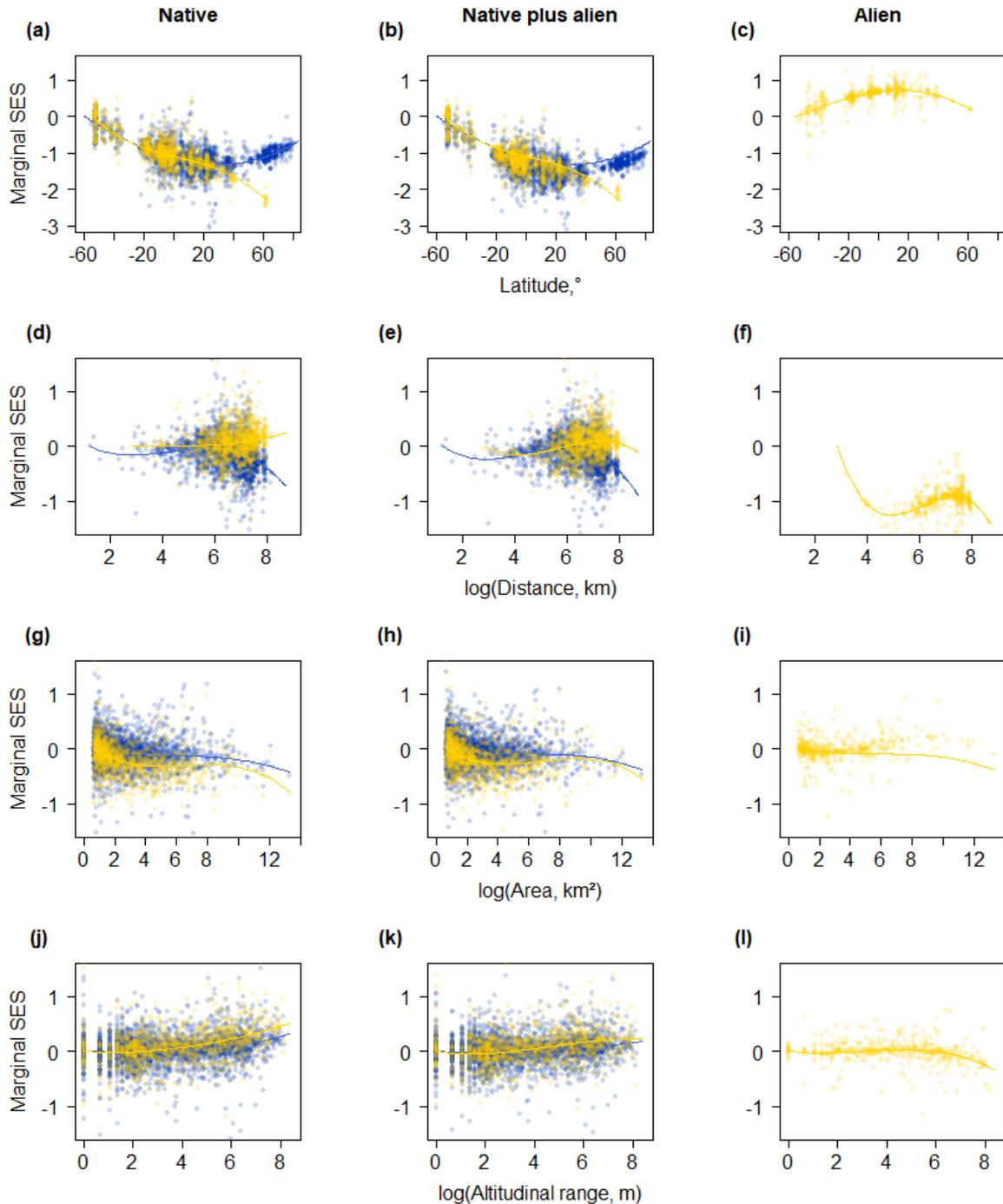


Figure 4. Variations in the trait structure of bird assemblages along environmental gradients for body mass (marginal standardized effect size in spatial additive models; 0 = null trait structure, positive values = overdispersion, negative values = clustering), with median curve (blue: all oceanic islands 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.

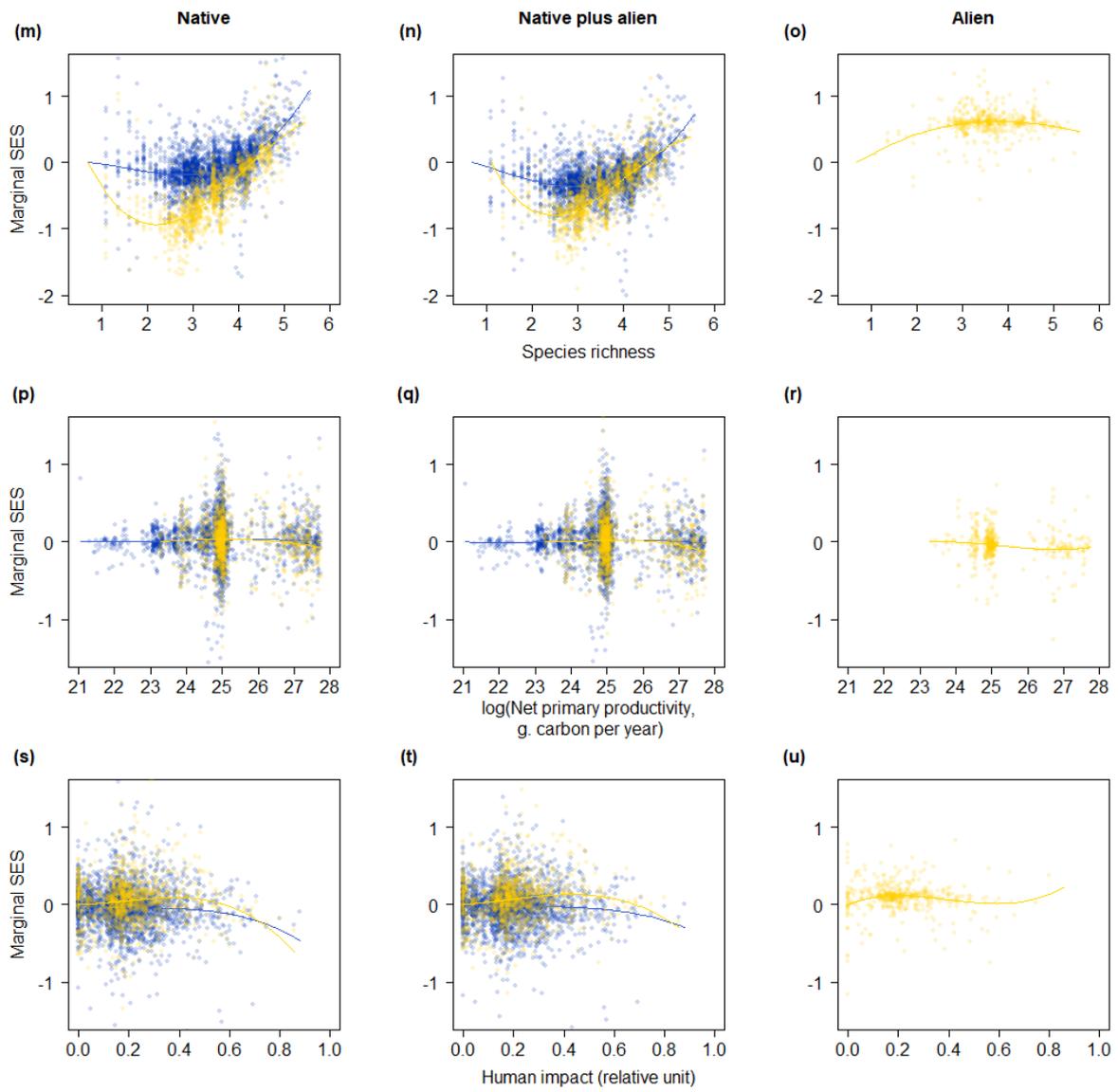


Figure 4 (continued).

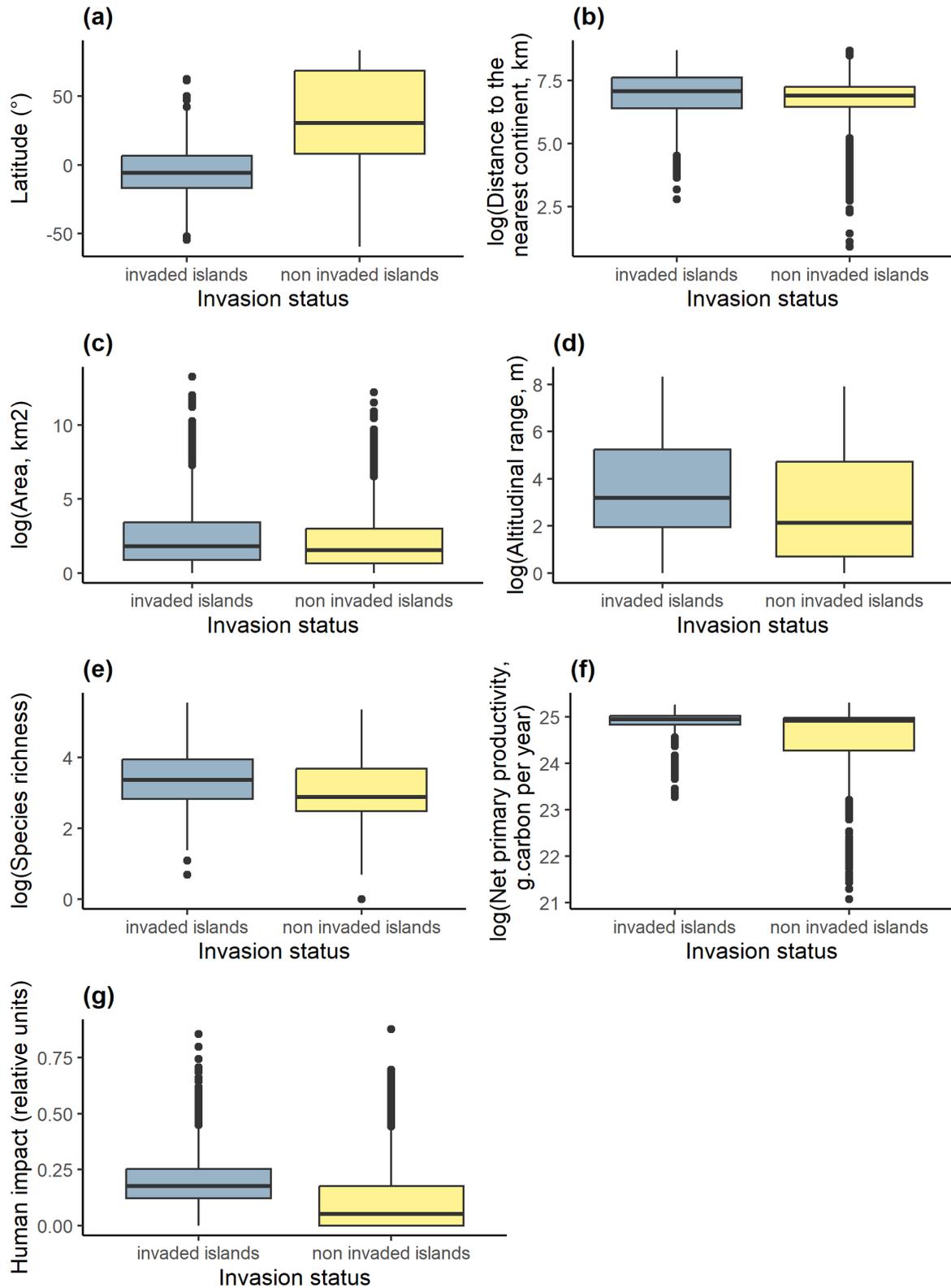


Figure 5. Latitudinal (a) and environmental position of the 1629 invaded islands and the 3031 non-invaded oceanic islands encompassed in the study (for Net Primary Productivity : 1169 invaded islands and 1684 non-invaded islands ; for Human impact : 1621 invaded islands and 2952 non-invaded islands).

SUPPLEMENTARY INFORMATION

Appendix S1: Summaries of environmental variables in the 8 biogeographical realms.

Appendix S2: Maps of trait structures for the 4628 islands and three traits considered.

Appendix S3: Distributions of standardized effect sizes and associated p-values.

Appendix S4: table of estimated parameters of INLA models