LETTER

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The anthropocene biogeography of alien birds on islands: Drivers of their functional and phylogenetic diversities

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Abstract

A branch of island biogeography has emerged to explain alien species diversity in the light of the biogeographic and anthropogenic context, yet overlooking the functional and phylogenetic facets. Evaluating alien and native birds of 407 oceanic islands worldwide, we built structural equation models to assess the direct and indirect influence of biotic, geographic, and anthropogenic contexts on alien functional diversity (FD) and phylogenetic diversity (PD). We found that alien taxonomic richness was the main predictor of both diversities. Anthropogenic factors, including colonization pressure, associated with classic biogeographical variables also strongly influenced alien FD and PD. Specifically, habitat modification and human connectivity markedly drove alien FD, especially when controlled by taxonomic richness, whereas the human population size, gross domestic product, and native PD were crucial at explaining alien PD. Our findings suggest that humans not only shape taxonomic richness but also other facets of alien diversity in a complex way.

KEYWORDS
alien birds, biodiversity drivers, biological invasions, functional diversity, islands, phylogenetic diversity

INTRODUCTION

Natural eco-evolutionary processes have shaped insular ecosystems and biota for millions of years. Since MacArthur and Wilson's book *The Theory of Island Biogeography* (MacArthur & Wilson, 1967), there has been a growing interest in estimating and predicting species taxonomic richness on islands using geophysical factors (Whittaker et al., 2017). However, human arrivals on islands disturbed the natural processes by accelerating the introduction of alien species (Fernández-Palacios et al., 2021). A new branch of insular biogeography in the Anthropocene has thus emerged to study the diversity of alien species, such as birds, mammals, and plants (Capinha et al., 2017; Dawson et al., 2017; Dyer, Cassey, et al., 2017; Seebens & Kaplan, 2022; Van Kleunen et al., 2015). This branch has shown several consistent patterns with the theory of island biogeography (e.g., species-area relationship) (Baiser et al., 2018; Blackburn et al., 2021; Matthews et al., 2023). However, the classic species-isolation relationship (SIR; i.e., remote islands contain less species) has weakened due to more alien species established in remote islands (Helmus et al., 2014; Moser et al., 2018).

Previous studies of alien diversity on islands have focused on only one facet of diversity (i.e., taxonomic diversity). There are only few studies assessing functional and phylogenetic diversities of native and alien biota with a special focus on diversity-area relationships (Matthews et al., 2023; Sayol et al., 2021; Soares et al., 2022), and

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to our knowledge, there is no study to date that investigated how the multiple facets of alien diversity on islands, including functional diversity (FD) and phylogenetic (PD) diversity, are affected by biogeographic and anthropogenic drivers. This knowledge gap is surprising, as both FD and PD are crucial to understand invasion dynamics and properly explore island biogeography in the anthropocene.

FD represents the set of ecological strategies hosted by an assemblage (Mouillot et al., 2013), reflecting the ecological assembly rules of this assemblage (Mouchet et al., 2010). By studying alien FD, we can determine how alien species mediate their response to disturbances and contribute to ecosystem functioning given they may replace native species (Soares et al., 2022). Phylogenetic diversity (PD) captures the evolutionary history of species, their features and future options (Faith, 1992; Purvis et al., 2019). Because alien species are introduced by humans for specific purposes (Dyer, Cassey, et al., 2017), we can expect that alien PD is not only affected by biogeographical factors but also by human ones, and mediated by native biota. By identifying the factors determining alien FD and PD, we could anticipate the fate of insular diversity in a disturbed environment and provide guidelines to effective conservation strategies. Our aim here is to provide the first global evaluation of the drivers of FD and PD patterns for island alien birds, in one single analytical framework.

Birds are taxonomically well described and are the object of the most comprehensive resource on the global distribution of alien species (Dyer, Redding, & Blackburn, 2017; Jetz et al., 2012; Tobias et al., 2022). During European colonization, many birds were intentionally introduced, particularly specific families (e.g., Galliformes) originating from Western Europe (Cassey et al., 2015), and species with peculiar traits (e.g., diurnal and granivorous birds foraging on the ground and in artificial terrestrial habitats (Soares et al., 2021)). This period resulted in numerous introductions on remote islands marked by a taxonomic selection for probability of alien establishment (Lockwood, 1999), representing a biased sample of global avian evolutionary history and ecology. Moreover, Dyer, Cassey, et al. (2017) showed that the identity of introduced birds and the relative importance of colonization pressure, i.e., the number of species introduced to an area (Blackburn et al., 2020), varied through time. Birds are thus an excellent model for exploring global distribution of FD and PD of alien species.

Here, we investigate the spatial pattern of FD and PD for alien birds and their drivers on 407 oceanic islands worldwide. Notably, we aim to test how 15 island contextual variables related to the geographic (e.g., area, distance to mainland, elevation), biotic (i.e., taxonomic richness, FD and PD of native birds), and anthropogenic (e.g., human population size, connectivity, habitat modification, colonization pressure) contexts shape alien bird FD and PD. We expect that species richness of alien assemblages will partially drive alien FD and PD. Moreover, we seek to determine the effects of insular contexts on alien FD and PD which may be mediated by species richness. We further explore how critical the anthropogenic context is compared to the biogeographic context to explain alien diversities. To investigate these effects, we apply structural equation models (SEMs) by defining a priori directional links between the contextual variables and alien diversities (Table 1; Table S1 describes the links connecting contextual variables). Finally, we calculate the deviations of FD and PD from expected values given the taxonomic richness, allowing us to detect the drivers of the relative variation of FD and PD beyond taxonomic richness (i.e., standardized effect size (SES) of FD and PD; Bach et al., 2022).

MATERIALS AND METHODS

Alien bird diversities on oceanic islands

Study islands and species

Our dataset is based on the oceanic islands from Weigelt et al. (2013), defined as land masses larger than 1km^2 not connected to the mainland during the last glacial maximum. Alien assemblages were obtained by overlapping the distribution of current established alien bird populations from the global avian invasion atlas (GAVIA) (Dyer, Redding, & Blackburn, 2017) and the oceanic island contours from GADM (http://www.gadm.org/version1). We restricted our dataset to oceanic islands that harboured at least four alien birds ($n = 407$ islands, for a total of 188 alien bird species), which was the minimum number of species to calculate FD on one island.

Functional and phylogenetic diversities

We defined an alien assemblage as the pool of all alien birds with an established population on an island. Alien bird FD of an island was the ratio between the convex hull encompassing species from the alien assemblage and the convex hull encompassing the global bird pool in a three-dimensional trait space (Mouillot et al., 2013). To calculate alien FD, we collected seven species-level traits related to morphology (i.e., beak length, beak depth, hand-wing index, body mass) and ecological preferences (i.e., trophic level, foraging niche and habitat breadth) for 10,862 bird species from AVONET (Tobias et al., 2022) and IUCN (2022). Then, we reduced the dimensionality of the species-trait matrix by computing a principal coordinate analysis (PCoA) on the Gower's distance

TABLE 1 Hypotheses on the factors driving alien bird diversities.

Response	Driver	Variable	Hypothesized relationship	Source
Alien FD, PD	Alien taxonomic richness	Alien SR	(+) Alien FD and PD are partially dependent on alien SR	(Faith, 1992; Mouchet et al., 2010)
Alien SES-FD, SES-PD	Alien taxonomic richness	Alien SR	(+/−) Depending on the assembly rules, species close to each other can be favoured by habitat filtering or disfavored to limit competition	(Mouchet et al., 2010; Tilman, 2004)
Alien SR, FD	Area	Area	(+) Species-area relationship applied to aliens (alien SR); (+) FD-area relationship posits that FD will increase with area but will reach a plateau because of functional redundancy between species (alien FD)	(Blackburn et al., 2008, 2016; Case, 1996; MacArthur & Wilson, 1967)
Alien FD, PD	Elevation	Elevation	(+) Habitat heterogeneity promotes the establishment of species with distinct traits	(Case, 1996, Walsh et al., 2012)
Alien SR	Latitude	Latitude	(+) Alien taxonomic richness higher towards temperate zones	(Dyer et al., 2020)
Alien SR	Isolation	Distance to continent; Surrounding landmass	(+) Isolated islands more prone to alien species introduction and establishment	(Moser et al., 2018)
Alien SR, FD, PD	Native biota	Native taxonomic richness; Native FD; Native PD	(−) *Biotic resistance* hypothesis; (+) *Rich-get-richer* hypothesis	(Levine & D'Antonio, 1999; Stohlgren et al., 2006; Dyer, Cassey, et al., 2017)
Alien SR	Colonization pressure	Alien CP	(+) A high number of introduced species promotes a high number of established species	(Blackburn et al., 2020; Dyer, Cassey, et al., 2017)
Alien SR, FD, PD	Human exchanges and intensity of presence	GDP; Population size; Human connectivity	(+) Colonization pressure increases with human exchanges which are driven by population density, tourism, island accessibility and wealth	(Dawson et al., 2017; Dyer, Cassey, et al., 2017)
Alien SR, FD	Habitat modification	Static habitat modification; Change habitat modification	(+) Alien species thrive in disturbed habitats (alien SR); (+) Disturbed habitats offer new niches and favour new species traits (alien FD)	(Sánchez-Ortiz et al., 2020)

Abbreviations: FD, functional richness; PD, phylogenetic richness; SR, species richness.

between species. We finally obtained a synthesized 3D-trait space representing 54.1% of the total variation among bird species (see Supporting text, Tables S2, S3 in SI for more details on functional space computation). Alien FD was computed for each island using the *alpha.fd.multidim* function from the *mFD* package (Magneville et al., 2021). We calculated alien PD as the minimum total length of all phylogenetic branches required to span all alien birds in the assemblage on a phylogenetic tree. Phylogenetic trees were extracted from VertLife database (https://vertlife.org), and PD was calculated on 1000 trees using the *pd* function from the *picante* package (Kembel et al., 2010).

Deviation from taxonomic diversity

As we expect both FD and PD depend on alien taxonomic richness, we also computed standardized effect size indices (SES-FD and SES-PD) following Bach et al. (2022) to exclude the effect of alien taxonomic richness from these indices and explore the drivers of the relative variation of FD and PD. To do so, we performed null models using a matrix swap randomization by recalculating FD and PD (on 100 phylogenetic trees) on 100 randomly generated island-species matrices, while keeping a constant number of species per assemblage. These random assemblages were simulated on the global pool of alien birds documented in GAVIA ($n = 952$) with each species having the same chance to become alien in each of the islands. SES indices were calculated as $SES = \frac{observed\ value - mean(simulated\ values)}{standard\ deviation\ (simulated\ values)}$. Negative values of SES indicate a lower value FD or PD than expected by chance for an equal taxonomic richness, representing a more clustered assemblage in terms of traits or evolutionary history.

Potential drivers of functional and phylogenetic diversities of alien birds on islands

Geographic variables

We extracted the geographic variables for all islands from Weigelt et al. (2013). We retrieved three variables related to habitat heterogeneity (i.e., *Latitude*, *Area*, *Elevation*) and two variables linked to isolation (i.e., *Distance to the continent* and *Surrounding land mass*). Since native and alien bird diversities vary regarding geographic regions (Dyer, Cassey, et al., 2017; Holt et al., 2013), we also classified each island into the corresponding zoogeographic region delineated by Holt et al. (2013). For islands without information on the zoogeographic region ($n = 260$), we attributed them to the closest region (Figure S1).

Biotic variables

To account for the insular biotic context, we calculated the taxonomic richness of native birds for each island by computing the spatial overlap between the native ranges of all birds in the world (Birdlife International, 2020) and the islands. We also calculated native FD and PD following the same methodology as for alien species.

Anthropogenic variables

We compiled seven variables associated with the anthropogenic context of each island. *Population size* was calculated as the sum of human population counts in the area of each island using the CIESIN database (2018). The *gross domestic product* (*GDP*) was calculated as the sum of all GDP values in the cells falling into each island using the data from Wang and Sun (2022). *Human connectivity* was calculated by mirroring the surrounding landmass as a metric of human isolation of each island. We summed each island's number of ports (https://data.humdata.org/dataset/world-port-index) and airports (http://www.partow.net/miscellaneous/airportdatabase/) within the island and in a buffer of 100 km around the perimeter of the island. Finally, we retrieved two metrics related to habitat modification by human activities (Theobald et al., 2020). *Static habitat modification* refers to the median value of the current state of habitat modified by humans in 2017, while *Change habitat modification* depicts the dynamics of habitat modifications between 1990 and 2015. Both variables were aggregated at the island scale as the median of the values of habitat modification. Using the GAVIA dataset, we also retrieved information of *Colonization pressure* (i.e., the total number of alien species introduced to each island) for 96 islands, and of *Time since first introduction* for 83 islands (see the Supporting text for details on the method).

A priori hypotheses

We set 17 hypotheses to assess the links among the different variables (Table S1), including 10 hypotheses of direct links between absolute and relative values of alien diversities and the insular contexts (Table 1). For instance, larger and more remote islands are known to host a higher number of alien species, following known species-area and reverse SIRs (Blackburn et al., 2016; Moser et al., 2018). Besides the absolute values of FD/PD, we also seek to understand the variation and the drivers of FD/PD that are not explained by species richness (i.e., SES-FD/PD). For instance, islands containing heterogeneous habitats are the place for

hosting species with more diversified ecological strategies (Kadmon & Allouche, 2007) and hypothetically more FD than expected given their taxonomic richness (positive SES-FD). Moreover, native communities are likely to exert a biotic filter on alien species and we can hypothesize lower SES-FD/PD than expected, if competition or human selection exert a filter on alien species.

Statistical analyses

All statistical analyses were conducted in R (version 4.2.1; R Core Team, 2022).

To assess the direct, indirect, and total effects of biogeographic, anthropogenic, and biotic factors on alien bird diversities, we performed SEMs using the *piecewiseSEM* package (Lefcheck, 2016). We built four SEMs on the 407 islands to explain each of the endogenous variables related to alien diversity, i.e., alien FD, PD, SES-FD, and SES-PD, using our set of a priori hypotheses (Table 1; Table S1), excluding *Colonization pressure* and *Time since first introduction* due to the existence of missing data in the two variables. We conducted models with and without those two variables on sub-samples of islands ($n=96$ and $n=83$, respectively, when data were available) to compare the effects of those variables on the outputs (Supplementary text). All variables with a right-skewed distribution were log-transformed (*Area, Distance to the continent, Surrounding landmass, Elevation, Native richness, Native PD, Native FD, Alien richness, Alien PD*, and *Alien FD*), and *Latitude* was converted as an absolute value. Finally, we scaled all the variables ($\mu=0$, sigma=1) to get comparable effects.

For each endogenous variable (i.e., a variable supposedly explained by one or several exogenous variables), we derived a linear mixed-effects model, including the zoogeographic region as a random effect. The SEMs were then built upon these individual linear mixed-effects models (*psem* function from *piecewiseSEM* package). We evaluated SEM fit using Fisher's *C* statistic and considered it incomplete if the associated P-value was below 0.05. In the case of an incomplete model, we recursively added potential missing paths (i.e., paths that were not included in the initial model because lacking any causal relationship), based on pairwise tests of directed separation on unstated relationships between variables in the a priori model (*dSep* function from *piecewiseSEM* package). The four final models had a Fisher's *C* of 41.5 ($p=0.24$) for FD, 43.6 ($p=0.18$) for PD, 50.8 ($p=0.12$) for SES-FD, and 40.9 ($p=0.19$) for SES-PD. They contained 51 paths between explanatory and endogenous variables, and a correlated error was specified between anthropogenic variables and native biotic variables.

We analysed the results of the models by retrieving the R^2 associated with each endogenous variable. As we used linear mixed-effects models, R^2 values were decomposed into marginal (accounting for fixed effects) and conditional (accounting for both fixed and random effects) R^2. Finally, we derived the explanatory variables' direct, indirect, and total effects on the response variables by using a non-parametric bootstrapping method ($n=10,000$ samples) through the *bootEff* function from the *semEff* package (Murphy, 2022).

RESULTS

Functional and phylogenetic diversities of alien birds

Functional and phylogenetic diversities of alien birds varied markedly across islands worldwide (Figure 1). The Novozelandic and Hawaiian regions harboured islands with the higher FD and PD values, while alien birds in Saharo-Arabian, Indo-Malayan or Sino-Japanese regions had a lower diversity (Figure 1a). We also observed a strong spatial variation of FD and PD values within regions among islands (e.g., Papua-Melanesian and Novozelandic; Figure 1b,c). Overall, FD and PD of alien birds were highly correlated across all islands (Pearson's correlation=0.95, $p<0.001$, Figure S2a), but considering each region separately, we found varying shapes of relationships between both metrics (Figure S2b). Both diversity facets were also highly correlated with alien taxonomic richness (Pearson's correlation=0.94 for FD, 0.96 for PD). After controlling for alien taxonomic richness, we found that both SES-FD and SES-PD were significantly smaller than zero (Student tests, respectively, mean=−0.92, $t=−33.6$, $p<0.001$; mean=−0.89, $t=−13.6$, $p<0.001$). Thus, on average and especially in the Novozelandic region, alien assemblages were less phylogenetically and functionally diversified than expected from random assemblages of birds with the same taxonomic diversity (Figure 2; Figure S3). By contrast, assemblages from the Oriental, Panamanian and Saharo-Arabian regions had positive SES-PD values close to zero, representing a PD that was nearly expected given the taxonomic richness (Figure 2).

Drivers of alien diversities

Six variables had a significant total effect on alien FD (R^2 marginal=0.60), namely alien taxonomic richness, native taxonomic richness, static habitat modification, human connectivity, elevation, and distance to continent (confidence intervals (CIs) at 95% not crossing zero, Figures 3a, 4a). Eight variables had a significant total effect on alien PD (R^2 marginal=0.90), namely alien taxonomic richness, native PD, human connectivity, population size, GDP, surrounding landmass, distance to continent, and area (Figures 3b, 4b).
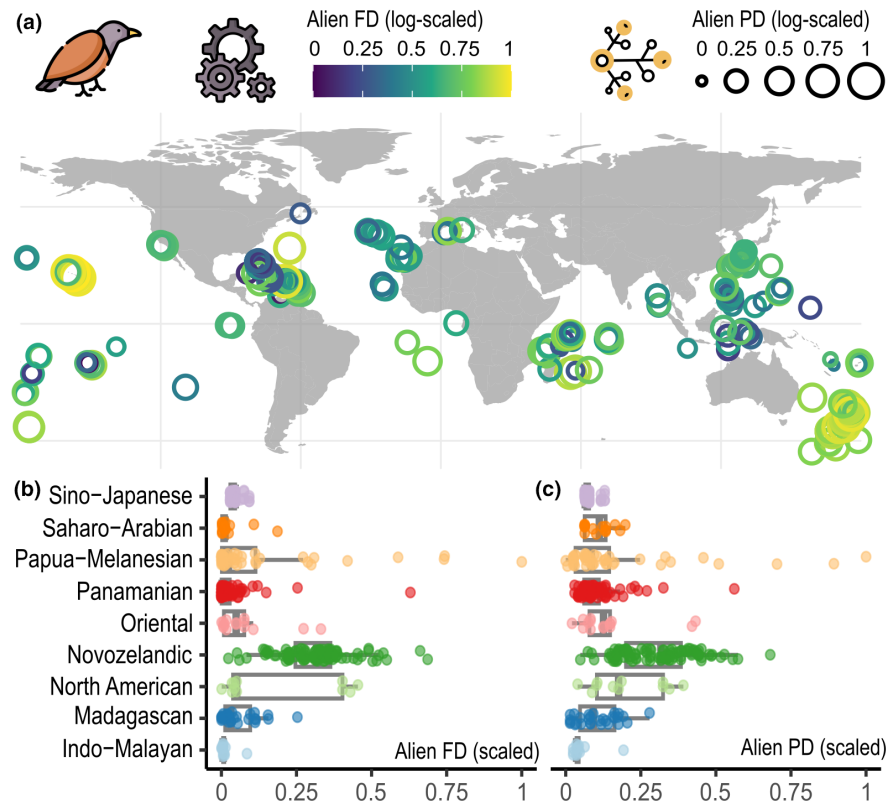
FIGURE 1 Global association between functional and phylogenetic diversities of alien birds on oceanic islands. (a) Spatial variation of FD (Alien FD, colour of the rings) and phylogenetic diversity (Alien PD, size of the rings) of alien birds on the 407 islands. Values of alien FD (b) and alien PD (c) for islands within each region. Only regions with more than 10 islands are shown.
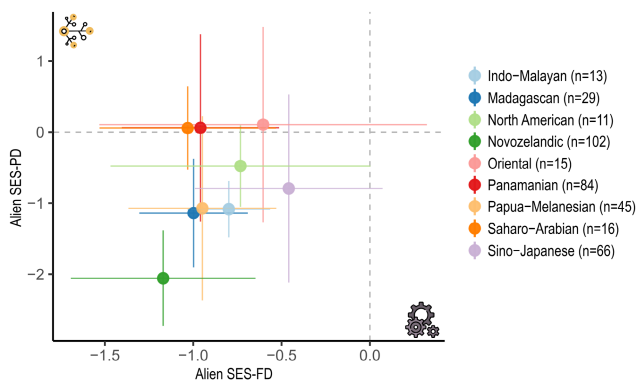

FIGURE 2 Deviations of functional and phylogenetic diversities from taxonomic diversity on islands. Mean standardized effect sizes (SES) of functional and phylogenetic diversities across all islands separated by region. The points represent the mean SES-FD and SES-PD per region, and horizontal and vertical bars represent the standard deviation of SES-FD and SES-PD within each region, respectively. Only regions with more than 10 islands are shown. Among the 407 islands, respectively 15 and 100 islands had SES-FD and SES-PD below −1.96, which is the threshold for assemblages being significantly more clustered than expected by chance. Three islands had SES-PD above 1.96, meaning their alien assemblages were significantly more dispersed than expected by chance.

Overall, alien taxonomic richness had the largest total effect on alien FD and PD (mean total effect = 0.58 and 0.79, respectively) followed by the geographic context

(mean combined total effect = 0.40 and 0.57), the anthropogenic context (mean combined total effect = 0.39 and 0.44) and, to a lesser extent, by the biotic context (mean combined total effect = 0.15 and 0.15; Table S4). Moreover, when anthropogenic variables were included in the SEM, the R^2 of alien FD and PD were identical but the R^2 of alien taxonomic richness increased by 12 to 15% compared with the SEM with biogeographical variables only (Figure S4).

Alien taxonomic richness had a substantial direct effect on both alien FD (95% CI: [0.46; 0.72]; Figures 3a, 4a) and PD (95% CI: [0.76; 0.90]; Figures 3b, 4b). By contrast, native taxonomic richness had a total negative effect on alien FD (95% CI: [−0.22; −0.04]; Figure 3a) and a weak negative effect on alien PD (95% CI: [−0.22; 0.04]; Figure 3b). Moreover, native PD had a moderate direct negative effect on alien PD (95% CI: [−0.20; −0.03]; Figure 3b), whereas native FD had no significant effect on alien FD (Figure 3a).

Regarding anthropogenic drivers, connectivity, population size, and GDP had a total positive effect on alien PD mediated by positive effects on alien taxonomic richness. By contrast, connectivity and static habitat modification positively affected alien FD (Figures 3, 4). Human connectivity was the anthropogenic driver with the most considerable total effect on both alien FD and PD (95% CI: [0.04; 0.23] and [0.04; 0.23], respectively; Figures 3, 4). When considering colonization pressure
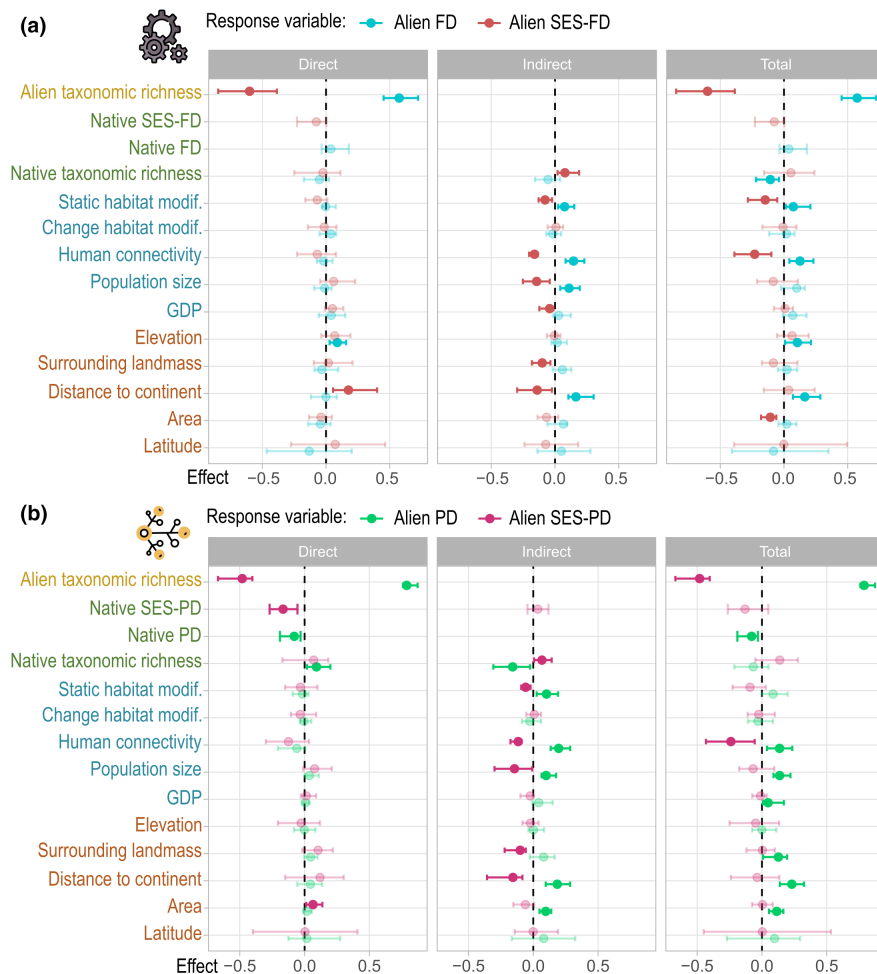
FIGURE 3 Direct, indirect, and total effects of all explanatory variables on (a) functional diversity (FD; and its associated SES) and (b) phylogenetic diversity (PD, and its associated SES) of alien birds. The zoogeographic region for birds of each island was integrated as a random effect in all relationships. Dots represent standardized mean effects, and error bars depict 95% CIs (shaded colours represent intervals crossing zero). Variable names are coloured following their context: biotic (green), human (blue), and biogeographical (orange).

(and time since first introduction) on the subset of 96 (83) informed islands for this variable, colonization pressure had the strongest total effect on alien FD and PD among anthropogenic drivers (Figure S5), while time since first introduction had no effect (Figure S6). The presence of colonization pressure in the predictors led to a decrease in the importance of the other anthropogenic effects compared to models without it, for both alien FD and PD. However, CIs largely overlapped in the two types of models for all predictors.

Biogeographic variables posed different effects on alien FD and PD. Distance to continent had a positive direct effect on alien taxonomic richness and a positive indirect effect on both alien FD and PD (95% CI: [0.11; 0.30] and [0.10; 0.28], respectively; Figures 3, 4). Island area had a total positive effect on alien PD (95% CI: [0.06; 0.17]), but not on alien FD, while island elevation had a positive direct effect on alien FD (95% CI: [0.08; 0.22]), but not on alien PD (Figure 3). The total effect of biogeographic variables was similar in models accounting for

the colonization pressure. Moreover, the zoogeographic regions included as a random effect increased the explanatory power of the SEMs (conditional R^2: 0.74 for FD; 0.93 for PD).

The final models obtained for SES strongly differed from the ones obtained for FD and PD values. While alien taxonomic richness remained a major driver of SES-FD and SES-PD (so when controlled by taxonomic richness), it had a strong negative direct effect on both SES-FD and SES-PD (Figure 3). This means that alien bird assemblages with higher richness are more likely to be phylogenetically and functionally clustered. Anthropogenic variables had a more substantial influence on the SES than biogeographic variables (Figure 3), with evidence of a total negative effect of human connectivity on SES-FD and SES-PD and of static modification on SES-FD. Among biogeographic variables, only island area showed moderate evidence of a total negative effect on SES-FD (Figure 3).
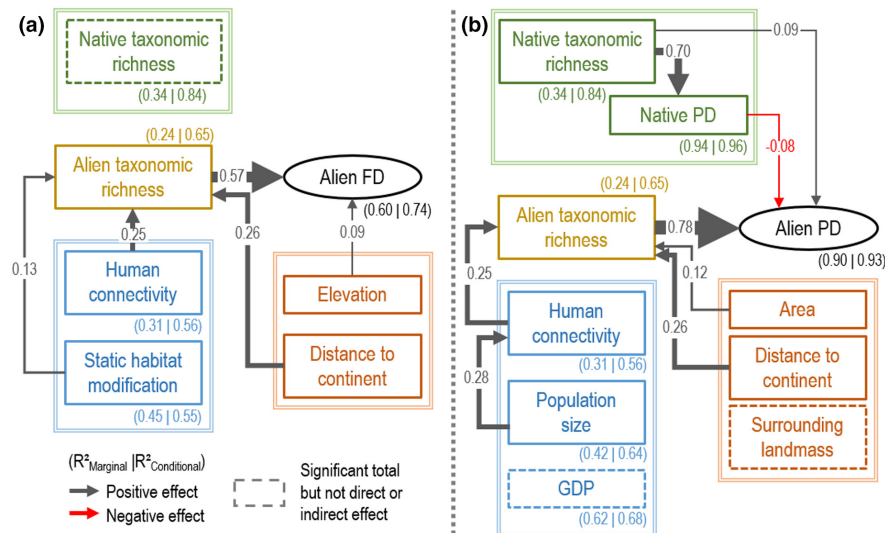
FIGURE 4 Schematic path diagram representing causal relationships between the geological, human, and biotic insular context and the alien functional diversity (FD, panel a) and phylogenetic diversity (PD; panel b). Line width is scaled to the absolute value of effects. Standardized R^2 coefficients are specified in brackets for each endogenous variable. Variable names are coloured following their context: biotic (green), human (blue) and biogeographical (orange). We only represented the effects for variables with a significant total effect on FD or PD. Dashed lines represent variables with a significant total effect (resulting from adding direct and multiple indirect effects through other variables), but no direct or indirect significant effect. All links between endogenous variables are depicted in Figure S7.

DISCUSSION

Global spatial variation of alien diversities

Our study provided important insights on the global spatial variation of alien diversities. Relative values of alien FD and PD varied across and within regions. The Novozelandic and Hawaiian regions harboured the highest levels of alien bird FD and PD, as well as some islands of Papua-Melanesia. Previous studies have pointed out the specificity of the Hawaiian archipelago related to its extremely high richness of alien plant species (Denslow et al., 2009; Wohlwend et al., 2021), as well as the long history of New Zealand for dealing with biological invasions (Simberloff, 2019). Those regions are well-known hotspots of invasions regarding taxonomic (Bellard et al., 2017; Dawson et al., 2017) and PD (Baiser et al., 2018), but this is the first time it is also demonstrated for the different facets of diversity at the global scale. Looking at SES, we found that islands from the Novozelandic region bear assemblages of aliens with less PD than expected from a random community assembly, as highlighted by Baiser et al. (2018), but also a poorer FD. This pattern can be explained by the invasion history of those islands for which most of their exotic species were imported from Britain and belong to few families (Baiser et al., 2018; Blackburn & Duncan, 2001). Moreover, some hotspots of alien bird FD and PD were not previously highlighted when focusing only on taxonomic diversity, including some islands of the Papua-Melanesian and Panamanian regions.

The relative contribution of biogeographic, anthropogenic and biotic factors

While alien taxonomic richness most strongly affected alien FD and PD, both anthropogenic and biogeographic contexts also had remarkable and comparable total effects on these diversities. Anthropogenic variables exceed by far the effects of biogeographic variables when considering SES-FD and SES-PD. This revealed that besides classical biogeographic variables, the anthropogenic context is highly important to understand the absolute (FD, PD) and relative (SES-FD, SES-PD) richness of birds. Therefore, neglecting anthropogenic variables significantly decreased our ability to explain the observed alien diversity on islands.

Including anthropogenic factors to fully address the diversity patterns of alien species

Our results suggest a substantial effect of anthropogenic factors on alien FD and PD, which have also been documented for alien species from several taxa on continents (Pyšek et al., 2010). First, we found a strong positive effect of human connectivity on absolute and relative alien bird richness, indirectly affecting alien FD, PD, SES-FD and SES-PD. Human connectivity reshapes environmental barriers between isolated places, the distance to a human facility that introduces species on islands being a primary determinant of alien distribution (Gleditsch et al., 2023). Human

connectivity is also a proxy of colonization pressure, a critical factor in alien taxonomic richness (Blackburn et al., 2020). Indeed, when included, we found that colonization pressure was the most important anthropogenic factor in the SEMs contributing to alien FD and PD, and it reduced the direct effect of connectivity on alien species richness and thus the indirect effect on alien PD (Figure S5).

Second, habitat modification positively influenced alien taxonomic richness and indirectly alien FD. Habitats with stronger human activities are considered more favourable for alien species establishment, partly because alien species do not have to compete with native species that are excluded from those disturbed habitats (Sol et al., 2022). Moreover, aliens adapt more to human-associated habitats due to their proximity and evolution with societies. The effect of habitat modification on FD rather than PD supports the idea that alien species exploit environmental niches in disturbed environments that differ from native ones (Soares et al., 2021).

We also observed contrasting effects of specific factors on SES-PD and SES-FD, which were negatively affected by static habitat modification and connectivity. This suggests that apart from increasing the number of alien species, a high human presence implies a clustering of alien species in terms of traits and evolutionary history. At some point, with the introduction of alien birds, a plateau is reached for alien FD and PD, and the supplemental addition of species does not lead to further functional or phylogenetic novelties. This also suggests that humans tend to bring the same type of species in terms of evolutionary history and ecological characteristics. Combined with native extinctions, alien species introductions favour the global homogenization of insular biota on the multiple facets of diversity (Baiser et al., 2018; Sayol et al., 2021; Soares et al., 2022; Sobral et al., 2016). The introduction of alien species might thus reinforce the observed FD-area non-linear relationship (i.e., the increase in area and native species richness does not imply a proportional increase in trait space), with even more species clustered in already well-represented parts of the trait space (Karadimou et al., 2016; Matthews et al., 2023).

Native communities as a weak biotic filter to alien diversities

Our study confirms that the biotic context (native taxonomic richness or their associated FD and PD) has a weaker influence on invasion success than anthropogenic or biogeographic contexts at this scale (Redding et al., 2019). For instance, the SEM analysis showed that native taxonomic richness had a direct positive effect on alien PD counterbalanced by an indirect negative effect through native PD. We also found a negative effect of native SES-PD on alien SES-PD (and a weak negative effect

on alien SES-FD), suggesting that when native species are evolutionarily or ecologically clustered (negative SES), alien species are more widespread across the tree of life and trait space (positive SES). Despite previous works showing evidence of filters exerted by native communities on alien ones (Jeschke & Heger, 2018), our study confirms the importance of abiotic and anthropogenic factors for shaping alien diversities.

Biogeographic factors continue to drive alien diversities

Distance to the closest continent was the strongest biogeographic driver explaining alien FD and PD, and also negatively affected alien SES-FD and SES-PD. Remote islands tend to contain more alien species than closer islands following a reverse SIR, and thus a more diverse alien assemblage regarding traits or evolutionary history. Our results are consistent with previous findings for other groups like plants or reptiles (Blackburn et al., 2016; Gleditsch et al., 2023; Moser et al., 2018). Interestingly, this pattern has never been confirmed for alien birds, with contrasting effects of remoteness on alien bird richness, either a negative indirect effect through native taxonomic richness (Blackburn et al., 2016), no effect (Moser et al., 2018), or a positive effect (Blackburn et al., 2008). We can confirm that reverse SIR is also validated for alien birds globally, thanks to the SEM analysis. For native birds, the original SIR was verified: taxonomic richness on islands declined with distance to continent (Figure S7). The negative indirect effect of distance to continent on alien SES-FD and SES-PD suggests that remote islands with higher alien species richness also tend to contain more redundant species in terms of traits or evolutionary history. Yet we also found a positive direct effect of distance to continent on alien SES-FD, meaning that, independently of species richness, islands farther from continents favour more diverse traits. This could be due either to humans that select birds with different characteristics for various purposes, or to a high competition with congeners on remote islands, favouring the establishment of more diverse traits.

We additionally found that both surrounding land mass and area positively affected alien PD indirectly through alien taxonomic richness but had no total effect on alien FD. The overall effect of island area was weak, suggesting that this is not a primary determinant in alien bird diversities, contrasting with previous studies (Blackburn et al., 2008, 2016). The log–log species-area relationship stands for alien species in many taxa, such as plants (Rojas-Sandoval et al., 2020) and insects (Mally et al., 2022). Still, the slope of the relationship is steeper than for native species with anthropogenic variables complementing the effect of biogeographic ones (Rojas-Sandoval et al., 2020), the available area for alien species to invade islands being non-saturated (Guo et al., 2020).

Another explanation is that both human population size and connectivity increase with island area as well as colonization pressure. Thus, the effect of island area on alien diversities is masked by the effect of anthropogenic variables (Blackburn et al., 2008; Moser et al., 2018), while area has a direct effect for native diversities (Figure S7). Our study sheds light on the importance of mediators to explain the impact of biogeographic variables on alien diversities. Indeed, direct effects of biogeographic drivers on birds FD, PD, SES-FD, and SES-PD were often non-significant, and their total effects were related to indirect effects mediated by anthropogenic and biotic drivers.

Limitations

Although our study provided new insights on biological invasions on islands, there are limitations to be acknowledged. First, while the GAVIA database is the most comprehensive source for alien bird distributions worldwide, it is not regularly being updated, and for 10 species known to have an established population on an oceanic island, the alien range map was not available. We were able to retrieve the colonization pressure only for 96 out of 407 islands, partly limiting our analyses using this variable. Yet, we could prove it was a critical factor for explaining alien taxonomic richness, but which did not have any direct effect on alien FD or PD (Supplementary text, Figure S5). Second, SEM is usually designed for causal relationships. However, it is unlikely to precisely get the direct links between predictors at such a spatial scale, forcing us to deal with many latent variables. As such, model construction led to the inclusion of a correlated error between the human-related variables and the native biotic context, based on two a priori hypotheses: (i) expert-derived maps for calculating native richness tend to overestimate species presence on islands, scaling with human presence (Nori et al., 2022); (ii) islands with more resources and thus with a higher native richness are more attractive to humans, resulting in an increased human presence (Luck, 2007).

CONCLUSION

We found that humans provoked drastic changes in ecosystem compositions across all facets of diversity. Our study allowed us to identify the drivers of multiple facets of alien diversity as a first step towards anticipating the risk posed by biological invasions. We believe that examining new insular communities, thus rethinking the island biogeography in the anthropocene, is of primary interest for forecasting the impacts of other global threats on islands, such as climate or land-use changes.

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SUPPORTING INFORMATION

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