Bird extinctions and introductions are causing taxonomic and functional homogenization in oceanic islands

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Bird extinctions and introductions are causing taxonomic and functional homogenization in oceanic islands

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Abstract

1. Humans are quickly reshaping species assemblages through the loss and gain of species at multiple scales. Extinctions and introductions are non-random events known to be contributing to taxonomic homogenization. However, it is not yet clear if they also promote functional homogenization. Here, we assess whether extinctions and introductions are leading to taxonomic and functional homogenization of 64 oceanic island bird assemblages, belonging to 11 archipelagos.

2. Based on island lists of extinct and extant, native and introduced species and on species traits, we use probabilistic hypervolumes in trait space to calculate functional beta-diversity before and after extinctions and introductions. Bird extinctions and introductions promoted taxonomic and functional homogenization on most oceanic islands. These results follow our expectations, considering previous studies on taxonomic homogenization, the predictable link between taxonomic and functional diversity, and the trait similarity of many introduced species, often adapted to anthropogenic habitats, linked to the non-randomness of bird introductions on islands.

3. Taxonomic homogenization was more common across than within archipelagos, also corroborating previous studies describing stronger homogenization on islands that are further apart and thus had distinctive native assemblages. Surprisingly, the widespread loss of species with similar traits, namely large flightless birds, often led to functional differentiation across archipelagos. However, this differentiation effect tended to be offset by the homogenizing effect of introductions.

4. Functional homogenization increases the vulnerability to global changes, by reducing the variability of responses to disturbance and thus the resilience of ecosystem services, posing a threat to human societies on islands. Our results highlight subtle variations in taxonomic and functional beta-diversity of bird assemblages in oceanic islands, providing important insights to allow a better assessment of how anthropogenic changes might alter ecosystem functioning, which is vital to develop effective long-term conservation strategies.

1 | INTRODUCTION

Humans have been reshaping species assemblages at a fast pace and across multiple spatial scales (McKinney & Lockwood, 1999; Olden et al., 2018). Changes in species richness result from the balance between the loss and gain of species. At the global scale, species losses occur through extinction, which can be a swift process, whereas gains occur through speciation, which is typically a drawn-out process. Humans have substantially accelerated extinction rates (Sax & Gaines, 2003), leading to a decline in global species diversity. In contrast, at smaller spatial scales, species diversity can increase when introductions outweigh extirpations (i.e. local extinctions; Olden et al., 2018). Some species are particularly prone to anthropogenic extinction (e.g. those with large body sizes), while others are often introduced (e.g. those with affinity to anthropogenic environments; Chichorro et al., 2019; Olden et al., 2004; Sobral et al., 2016). Together, these two non-random effects are decreasing the distinctiveness of assemblages and contribute to biotic homogenization at all scales (Baiser et al., 2012; Li et al., 2020; Sax & Gaines, 2003).

Much research on the temporal dynamics of assemblages has focused on oceanic islands, which have been disproportionately impacted by human activities (Russell & Kueffer, 2019; Whittaker et al., 2017). A substantial part of this work was done with island birds, with numerous recorded extinctions and introductions (Hume, 2017; Sax & Gaines, 2003), that tend to cause taxonomic homogenization (Baiser et al., 2012; Cassey et al., 2007; McKinney & Lockwood, 1999; Otto et al., 2020; Rosenblad & Sax, 2017). However, it is not yet clear whether this translates into functional homogenization (Olden, 2006; Olden et al., 2018), since introductions and extinctions can have very distinct effects on the functional traits of species assemblages. For example, the extinction of single-island endemic species and the introduction of one species across multiple islands are both likely to cause taxonomic and functional homogenization, while the extinction of a species found across multiple islands and the establishment of distinct introduced species in multiple islands are both likely to lead to taxonomic and functional differentiation (Baiser & Lockwood, 2011; Clavel et al., 2011). Nevertheless, taxonomic homogenization does not necessarily imply functional homogenization: when two functionally similar species go extinct on distinct islands, they cause taxonomic homogenization because each island lost a species that was not shared, but cause functional differentiation because they lost functionally similar species (Baiser & Lockwood, 2011; Olden et al., 2018). This was the case for the five extinct rail species from Madeira and Azores (Alcover et al., 2015). Likewise, taxonomic differentiation also does not imply functional differentiation, for instance, if different but functionally similar species are introduced across islands (Baiser & Lockwood, 2011). Taxonomic and functional homogenization can

thus show contrasting signals, especially if the species going extinct or being introduced are not functionally very distinctive from others in the assemblage (Baiser & Lockwood, 2011; Villéger et al., 2014).

On oceanic islands, the number of introduced bird species exceeds that of known extinctions (Seebens et al., 2017). However, these introductions do not compensate for the functional diversity lost through extinction (Sayol et al., 2021; Soares et al., 2022; Sobral et al., 2016), indicating that island bird assemblages are losing functionally unique species while gaining others that tend to be functionally redundant. Hence, we expect to find a global tendency for the functional homogenization of oceanic islands, possibly being more common than taxonomic homogenization. Taxonomic homogenization tends to be more frequent at regional and global scales given the lower similarity of the original assemblages, whereas islands that are closer to each other tend to have similar original avifaunas that differentiate taxonomically (Baiser et al., 2012; Olden et al., 2018). As such, we expect islands of different archipelagos to have lower original similarities and thus become more homogenized. The separate effect of extinctions and introductions on taxonomic homogenization appear to be stronger when the original assemblages are more distinct (Olden, 2006): the introduction of the same species to two distant islands have a propensity for stronger homogenizing effect than on neighbouring islands, which tend to share native species and thus to have original avifaunas that are more similar (Rosenblad & Sax, 2017); likewise, the loss of shared native species has a stronger differentiating effect when the original avifaunas are less similar (Otto et al., 2020). Therefore, given that many introduced birds are functionally redundant (Sayol et al., 2021; Soares et al., 2022) and that introductions are common events, within and across archipelagos, we expect them to continue contributing for the functional homogenization of island bird assemblages.

Here, we ask whether anthropogenic extinctions and introductions are leading to taxonomic and functional homogenization of bird assemblages in oceanic islands worldwide. Focusing on 64 oceanic islands belonging to 11 archipelagos, we (1) quantify taxonomic and functional homogenization among island assemblages; (2) investigate the relationship between the two; (3) compare taxonomic and functional homogenization within and across archipelagos; and (4) investigate the separate effects of extinctions and introductions in taxonomic and functional homogenization.

2 | MATERIALS AND METHODS

2.1 | Island selection

We focused on oceanic islands larger than 100km². From an initial list of 87 islands (Weigelt et al., 2015), we excluded 13 for which we were unable to obtain a species checklist, or that do not have

terrestrial or freshwater breeding bird species (see Table S1 in Supporting Information). We excluded 10 additional islands that were not in the same archipelago as other islands in the dataset. In total, we analysed 64 islands, belonging to 11 archipelagos, and spread across the Pacific, Atlantic and Indian Oceans (Table S1, Figure S1).

2.2 | Bird species database

We extracted data for the abovementioned 64 islands from an existing database (a detailed methodology can be found in Soares et al., 2022), which is based on multiple open sources (i.e. del Hoyo et al., 2014; Dyer, Redding, et al., 2017; IUCN, 2020; Lepage, 2018) and specific literature (i.e. regional field guides; Hume, 2017; Paleobiology Database, 2018). Namely, we obtained a list of known breeding bird species for each island, including established introduced species, extant native species and native extinct species (we use the term 'extinct species' for both globally extinct and locally extirpated species). For each island, we considered all bird species that went extinct after human arrival, and all successfully established introduced bird species, where were intentionally or accidentally transported to the islands by humans. Extant native species correspond to native species that currently exist on the island. We followed the taxonomy used by Birdlife International (Handbook of the Birds of the World &

BirdLife International, 2018). We use the term 'population' to refer to a species occurrence on an island; a species will thus have more than one population if it is present on more than one island in our dataset.

We excluded marine birds as well as non-breeding migrants, occasional breeders, vagrant and accidental species, to focus on regularly breeding terrestrial and freshwater species. These are the ones clearly highly dependent on island resources, also having particularly high rates of extinction and introduction on oceanic islands (del Hoyo et al., 2014).

2.3 | Bird species traits

For each species, we gathered information on body mass, foraging time, diet, foraging strata, volancy and habitat (Table 1 and Table S2). These traits are commonly used in studies evaluating bird functional diversity, as they are considered to effectively summarize the effects of species on ecological processes and are important determinants of responses to environmental change (Boyer, 2008; Luck et al., 2012; Sobral et al., 2016). Nectivores had to be included as a separate trait to be explicitly accounted for species with missing traits (40 out of 617 extant species, and 96 out of 214 extinct species), we inferred traits from the closest species in the genus or, for extinct species only, obtained information from descriptions of the species (Soares et al., 2022).

TABLE 1 Description of the 10 traits used to build the trait space

Trait	Type	Description
Diurnal	Dichotomous	Diurnal (1), nocturnal (0)
Nectivore[a]	Dichotomous	Nectivore (1), non-nectivore (0)
Water forager[b]	Dichotomous	Yes (1), no (0)
Forest specialist	Dichotomous	Forest specialist (1), non-forest specialist (0)
Wetland specialist	Dichotomous	Wetland specialist (1), non-wetland specialist (0)
Diet	Nominal	Granivore, herbivore, frugivore, invertivore, carnivore, omnivore
Average body mass	Continuous	Natural log-transformed body mass
Habitat specialization	Ordinal	Number of suitable habitats listed by IUCN
Volancy	Ordinal	Flightless (1), weak flyer (2), volant (3)
Terrestrial foraging strata[c]	Ordinal	Ground (1), understory (2), mid–high (3), non-specialized (3.5), canopy (4), aerial (5)

[a] Contrarily to the other six diet categories, nectivore was not obtained directly from Wilman et al. (2014) and had to be included as an independent trait to be explicitly account for (if not these would be diluted in 'frugivore' class), despite its increased contribution to the functional changes; nectivore species play a critical ecological role in the ecosystem and are essential to accurately capture important changes in functional diversity associated with the loss of these species (Soares et al., 2022); excluding these species would be an important oversight, considering that they were almost entirely wiped out in some archipelagos (e.g. Hawaiian Islands; Boyer, 2008).

[b]Water and terrestrial foraging strata are not mutually exclusive, because a species can be, for example, both water and ground forager, as in most Anatidae species.

[c]Species that forage in most strata between ground and aerial were considered non-specialized and attributed the value of 3.5.

2.4 | Data analysis

Data processing and statistical analyses were undertaken in R (v.4.0.4; R Core Team, 2021). Our study did not require ethical approval.

2.4.1 | Quantifying taxonomic homogenization

Given a pair of islands, we considered that they homogenized taxonomically if their bird species composition became more similar over time (decreasing beta-diversity), and conversely that they differentiated if it became less similar (increasing beta-diversity).

We measured the taxonomic dissimilarity between island pairs using the Jaccard pairwise dissimilarity, calculated by the *beta* function in the BAT package (Cardoso et al., 2015). This index ranges from 0, when two islands have the same species composition, to 1 when they have no species in common. Given that Jaccard index is sensitive to small sample sizes, we assessed the correlation between the changes in taxonomic beta-diversity and the original species richness, using Spearman's rank correlation, and plotted these two variables to help visualize their relationship (Appendix S2).

For each pair of islands, we measured dissimilarity at two stages: originally, before anthropogenic extinctions and introductions (i.e. including all native species, extant and extinct); and presently, after extinctions and introductions (i.e. including extant native and introduced species). As such, the effects of extinctions and introductions were combined to analyse changes to the assemblages. Then, we calculated the change in dissimilarity as the difference between the dissimilarities of the present and original avifaunas. Positive values indicated that islands differentiated taxonomically (increased beta-diversity), whereas negative values indicated that they homogenized (decreased beta-diversity).

2.4.2 | Quantifying functional homogenization

Similar to taxonomic changes, we considered that a pair of islands homogenized functionally (lost functional beta-diversity) if the functional trait space of their bird species assemblages became more similar after the combined effect of anthropogenic extinctions and introductions, and differentiated functionally (increased functional beta-diversity) if the reverse occurred. Subsequently, we used the Jaccard pairwise dissimilarity to calculate the functional beta-diversity of island pairs over time, using probabilistic hypervolumes to represent the trait space of each island bird assemblage (Mammola & Cardoso, 2020). This index ranges from 0, when two hypervolumes are the same, to 1, when they do not overlap.

A trait space was generated separately for each island assemblage, using a matrix comprising all species and traits of all 64 analysed islands. First, we computed the pairwise functional distances between each pair of species using the Gower dissimilarity index, giving the same weight to each trait (range of pairwise functional distances: 0–0.887), and calculated the contribution of each trait to the resulting distance matrix, using *dist.ktab* and *kdist.cor* in the ADE4 package (Table S3; Dray & Dufour, 2007). Then, to extract orthogonal axes for the hypervolume delineations, we analysed the distance matrix through a principal coordinate analysis (PCoA) with Cailliez correction for negative eigenvalues, using the *pcoa* function in the APE package (Paradis et al., 2004). We retained the first eight PCoA axes, which cumulatively explained 81.3% of the total variation (Figure S2).

The trait space of each assemblage was constructed using a kernel density hypervolume, approximated to a cloud of stochastic points based on the species in the assemblage, positioned based on their traits. These kernel density hypervolumes were built using the Gaussian method with a 95% bandwidth so that hypervolumes represent an estimated 95% of the cloud density and even weight across traits (Blonder et al., 2018), using the *kernel.build* function in BAT package (Mammola & Cardoso, 2020). In this probabilistic hypervolume approach, the functional richness (i.e. functional alpha-diversity) of each assemblage is estimated as the volume of the hypervolume delineated by the cloud of stochastic points, and the functional beta-diversity between two assemblages is measured as the dissimilarity between the two hypervolumes (Figure S3; Mammola et al., 2021). This approach does not assume a homogeneous trait space, and thus it responds to variations in point density within the multidimensional space.

We measured the functional dissimilarity (functional beta-diversity) of each island pair in the original and present avifaunas, using the *kernel.beta* function in the BAT package, and then evaluated changes as the difference between the dissimilarities of the present and original avifaunas. Positive values indicated that islands differentiated functionally (increased functional beta-diversity), whereas negative values indicated that they homogenized (decreased functional beta-diversity).

2.4.3 | Effects of species turnover on the taxonomic and functional homogenization of island assemblages

We investigated whether anthropogenic species turnover (the combined effect of extinctions and introductions) is leading to homogenization or differentiation, by contrasting each island with each of the remaining 63 (global scale). We averaged the results to obtain, for each island, a value of change in taxonomic beta-diversity, and another one of change in functional beta-diversity, to measure taxonomic and functional homogenization, respectively. Then, we analysed the relationship between taxonomic and functional beta-diversity by building a generalized linear mixed-effects model with Gaussian distribution and identity link function, using the GLMMTMB package (Brooks et al., 2017). Two models were built: one using the individual change in dissimilarity of all island pairs ($n = 64^2 = 4096$), and another using the average change of each island ($n = 64$). The change in functional beta-diversity of each island was the response variable and the change in taxonomic beta-diversity was the

only fixed effect, while archipelago was used as a random effect ($n = 11$). Model assumptions were validated using simulated residuals and the DHARMa package (Hartig, 2021).

To check if the proportion of homogenized islands was greater than that of differentiated islands, we performed a chi-squared test, which is a two-sample test for equality of proportions with a continuity correction for small sample sizes (continuity of Yates).

2.4.4 | Contrasting taxonomic and functional homogenization within and across archipelagos

We compared taxonomic and functional homogenization within and across archipelagos (Figure S4). For the analyses within archipelagos, we averaged the results of change in taxonomic and functional beta-diversity for each island contrasted to all other islands in the same archipelago, and then plotted a comparison between taxonomic and functional homogenization. We repeated the analysis across archipelagos, by contrasting each island with all islands in the other archipelagos, within the same ocean, following previous studies (Cassey et al., 2007). Comparisons among groups (within vs. across) were analysed with a two-sample chi-squared test for equality of proportions with a continuity correction for small sample sizes (continuity of Yates). Like for the global scale, we also analysed the relationship between taxonomic and functional beta-diversity both within and across archipelagos by performing a generalized linear mixed-effects model with Gaussian distribution and identity link function, using the glmmTMB package (Brooks et al., 2017). The average change in functional beta-diversity of each island was the response variable and the average change in taxonomic beta-diversity was the only fixed effect ($n = 64$), while archipelago was used as a random effect ($n = 11$). Model assumptions were validated using simulated residuals and the DHARMa package (Hartig, 2021).

To explore the relationship between the changes in taxonomic beta-diversity and original taxonomic beta-diversity, as well as the relationship between the changes in functional beta-diversity and original functional beta-diversity, we performed four generalized linear mixed-effects models with Gaussian distribution and identity link function, using the glmmTMB package. These were done both for within and across archipelagos. The average change in beta-diversity of each island was the response variable and the original beta-diversity was the only fixed effect ($n = 64$), while archipelago was used as a random effect ($n = 11$). Model assumptions were validated using simulated residuals and the DHARMa package (Hartig, 2021).

2.4.5 | Disentangling the effects of extinctions and introductions on taxonomic and functional homogenization

To disentangle the effects of extinctions and introductions in the patterns of taxonomic and functional homogenization,

we quantified taxonomic and functional homogenization (Sections 2.4.1 and 2.4.2, respectively), measuring dissimilarity at three different stages: originally, before extinctions and introductions (i.e. extant and extinct native avifauna); after extinctions alone (i.e. extant native avifauna) and presently, after extinctions and introductions (i.e. extant native and introduced avifauna). Then, we contrasted the extant native avifauna with the original avifauna to quantify the effect of extinctions and with the present avifauna to quantify the effect of introductions. As before, we used the Jaccard dissimilarity index to measure taxonomic and functional homogenization, within and across archipelagos (repeating analysis in Section 2.4.4).

3 | RESULTS

Our database included 2512 populations of 677 species (Table S1) distributed across 64 islands. Of these, 245 populations were extinct (178 species), 727 were introduced (162 species) and the remaining 1540 populations (397 species) were extant natives. Some species were included in more than one group (e.g. introduced to an island and native in another, or extinct from one island and extant in another).

3.1 | Effects of species turnover on the taxonomic and functional homogenization of island assemblages

There is strong evidence for taxonomic and functional homogenization of island bird assemblages: the bird taxonomic composition of the large majority of islands has become on average more similar to others (global scale: 57/64 islands = 89.1%, $\chi^2 = 75.031$, p-value < 0.001), as did the functional composition (global scale: 55/64 islands = 85.9%, $\chi^2 = 63.281$, p-value < 0.001; Figure 1a); and on average, islands experienced declines in taxonomic (–0.024, min = –0.076, max = 0.011), and functional beta-diversity (–0.041, min = –0.192, max = 0.037; Figure S5).

The potential limitation related to Jaccard index's sensitivity to small sample sizes was ignored in subsequent analysis because there was no or a small positive correlation between the changes in taxonomic beta-diversity and the original species richness, depending on the scale (Appendix S2).

There is a significant positive relationship between the change in taxonomic and functional beta-diversity across all island pairs (coef = 0.509, p-value < 0.001) and using the average change of each island (coef = 1.449, p-value < 0.001; Table S4, Figure 1a and Figure S6a). For the sake of simplicity, we focused on the latter in subsequent analyses. Although the strength of the relationship is strong (close to one), there is substantial variance that suggests that changes in taxonomic beta-diversity do not necessarily lead to proportional changes in functional beta-diversity. For the 55 islands that homogenized taxonomically and functionally, 44 (80%) experienced
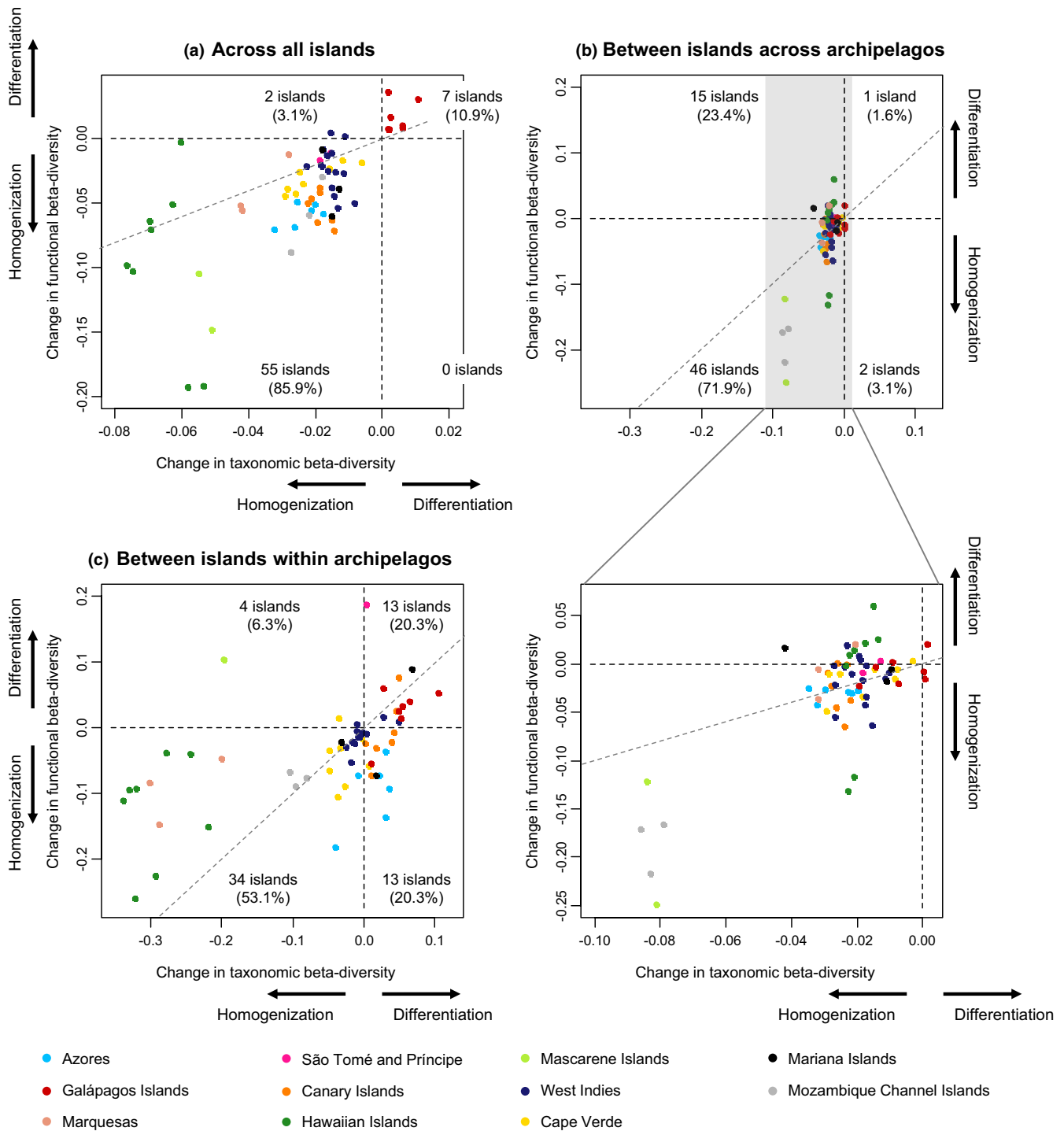
FIGURE 1 Relationship between the average change in taxonomic beta-diversity and the average change in functional beta-diversity between each island and (a) all others, (b) others across different archipelagos of the same ocean and (c) the others within the same archipelago. A positive value indicates that islands have, on average, differentiated from other islands, whereas a negative value indicates that islands have homogenized. The diagonal dashed grey line corresponds to the y = x line (change in taxonomic beta-diversity = change in functional beta-diversity). Each dot represents one of 64 islands analysed, coloured by archipelago (n = 11). Panels (b and c) are on the same scale for comparison, while the lower right panel is on a different scale to show individual islands.

stronger functional than taxonomic homogenization, and 11 did the reverse. For 7 islands (10.9%), namely all islands from the Galápagos, there was both taxonomic and functional differentiation, the latter being stronger (Figure 1a). For the remaining two islands (3.1%), there was taxonomic homogenization but functional differentiation (Figure 1a and Figure S5).

3.2 | Contrasting taxonomic and functional homogenization

Homogenization dominated both within and across archipelagos (Figure 1b,c): across archipelagos, 61 islands (95.3%) homogenized taxonomically, 48 (75%) functionally and 46 (71.9%) in both aspects; while within archipelagos, 38 islands (59.4%) homogenized taxonomically, 47 (73.4%) functionally and 34 (53.1%) in both aspects. Taxonomic homogenization was clearly stronger across and within archipelagos (61 vs. 38 islands, $\chi^2 = 21.579$, *p*-value < 0.001), while functional homogenization was similar across than within archipelagos (48 vs. 47 islands, $\chi^2 = 0$, *p*-value = 1).

Like for the global scale, there is a significant positive relationship between the change in taxonomic and functional beta-diversity both within (coef = 0.487, *p*-value = 0.002; Table S4, Figure 1c and Figure S6b) and across archipelagos (coef = 2.275, *p*-value < 0.001; Table S4, Figure 1b and Figure S6c). However, the strength of this relationship is much larger than 1 across archipelagos, indicating that changes in taxonomic beta-diversity result in greater changes in functional beta-diversity.

Despite the general homogenization trend, some islands homogenized taxonomically but differentiated functionally (e.g. the two Mascarene islands), especially across archipelagos (15

across vs. 4 within, $\chi^2 = 6.181$, *p*-value = 0.013). Others differentiated taxonomically while homogenizing functionally (e.g. four islands within the Azores), especially within archipelagos (13 within vs. 2 across, $\chi^2 = 7.552$, *p*-value = 0.006). Islands in the same archipelago tended to show similar changes in taxonomic and functional beta-diversity, both within and across archipelagos (Figure 1b,c).

3.3 | Homogenization within and across archipelagos

A little more than half of islands homogenized taxonomically both within and across archipelagos (38/64–59.4%, $\chi^2 = 3.781$, *p*-value = 0.052; e.g. all islands in the Indian Ocean, the Hawaiian Islands, and the Marquesas), while almost all the remaining islands became differentiated within archipelagos but homogenized across (23/64–35.9%; Figure 2a, Figures S7 and S8). The Hawaiian Islands were by far the islands that homogenized the most within the archipelago, while the Indian Ocean had the most homogenized islands (Mascarenes and Mozambique Channel Islands). Many islands became differentiated within archipelagos but homogenized across archipelagos (23/64), while a few differentiated both within
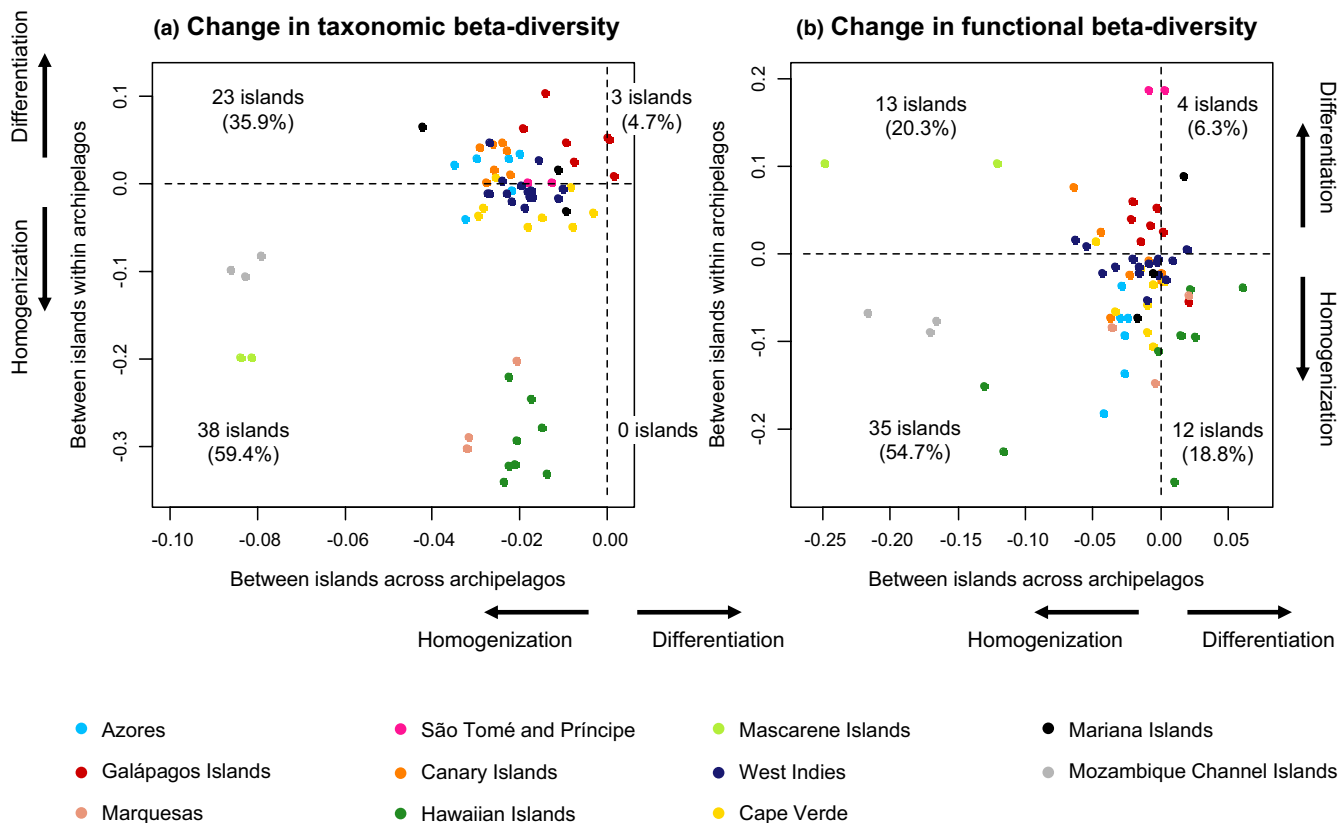

FIGURE 2 Average change in beta-diversity between islands within archipelagos and across archipelagos of the same ocean: (a) changes in taxonomic beta-diversity and (b) functional beta-diversity, both caused by anthropogenic species turnover. A positive value indicates that islands have, on average, differentiated from other islands, whereas a negative value indicates that islands have homogenized. Each dot represents one of 64 islands, coloured by archipelago (*n* = 11).

and across archipelagos (3/64). No island homogenized within their archipelago and differentiated across archipelagos. Overall, more islands homogenized taxonomically across archipelagos than within archipelagos (61 vs. 38, $\chi^2 = 21.579$, p-value < 0.001). In contrast, all the Galápagos differentiated taxonomically within the archipelago.

Similar to the changes in taxonomic beta-diversity, a little more than half of the islands homogenized functionally within and across archipelagos (35/64–54.7%, $\chi^2 = 0.781$, p-value = 0.377; e.g. most Atlantic Islands—Macaronesia and West Indies) and very few differentiated at both scales (4/64–6.3%; Figure 2b, Figures S9 and S10). A similar number of islands homogenized functionally within and across archipelagos (47 within vs. 48 across, $\chi^2 = 0$, p-value = 1).

There is a significant negative relationship between the change in taxonomic beta-diversity and the original taxonomic beta-diversity within archipelagos (coef = −0.135, p-value = 0.031), but not across (coef = 0.031, p-value = 0.784; Table S5, Figures S6 and S11). Moreover, there was a significant negative relationship between the change in functional beta-diversity and the original functional beta-diversity both within (coef = −0.490, p-value < 0.001) and across archipelagos (coef = −0.471, p-value < 0.001).

3.4 | Disentangling the effects of extinctions and introductions on taxonomic and functional homogenization

Both extinctions and introductions tended to cause taxonomic and functional homogenization within and across archipelagos (Figure 3), the single exception being that extinctions caused mostly functional differentiation across archipelagos (43/64–67.2%; Figure 3c).

Extinctions lead more often to taxonomic homogenization across archipelagos than within archipelagos (56 > 42, $\chi^2 = 7.358$, p-value = 0.007; Figure 3a), but the pattern inverts for functional homogenization (8 < 36, $\chi^2 = 25.247$, p-value < 0.001; Figure 3c). Similarly, introductions also led more often to taxonomic homogenization across archipelagos than within (61 > 38, $\chi^2 = 21.579$, p-value < 0.001; Figure 3b), and the pattern was the same for functional homogenization (56 > 40, $\chi^2 = 9.375$, p-value = 0.002; Figure 3d).

Taxonomic homogenization occurred most often when extinctions and introductions led simultaneously to homogenization (within: 23–35.9%, across: 53–82.8%; Figures S7 and S8, respectively). Functional homogenization also occurred most often when both extinctions and introductions led to homogenization within archipelagos (34.4%; Figure S9), but not across archipelagos where it was mostly caused by differentiation from extinctions and homogenization from introductions (59.4%; Figure S10). Islands in the same archipelago usually showed similar patterns.

4 | DISCUSSION

4.1 | Taxonomic homogenization does not always imply functional homogenization

Most island bird assemblages became taxonomically and functionally homogenized (global scale: 85.9%; Figure 1a). These results match those of previous studies (e.g. Baiser & Lockwood, 2011; Olden et al., 2018) that suggested that this homogenization pattern is probably attributed to the replacement of specialists by generalist species (Clavel et al., 2011). On oceanic islands, most extinct birds are known to be functionally unique species whose functional roles are not replaced by introduced birds (Sayol et al., 2021; Soares et al., 2022; Sobral et al., 2016). In contrast, birds that have been introduced tend to be open habitat granivores with ground or unspecialized foraging strategies, being thus better adapted to anthropogenic environments (Soares et al., 2021). However, despite the strong trend for homogenization, there were exceptions: Antigua and Saint Kitts (both in the West Indies) differentiated functionally, while all the Galápagos Islands differentiated taxonomically and functionally (Figure 1a). In Antigua and Saint Kitts, taxonomic homogenization and functional differentiation were led by the extinction of different but functionally similar species on each of these islands (Figures S12–S14). Both taxonomic and functional differentiations of the Galápagos were concomitantly promoted by the same species becoming extinct on multiple islands and by the introduction of distinct species on each island (Figures S12–S14; Si et al., 2017; Longman et al., 2018).

Moreover, taxonomic and functional homogenization were positively correlated (Figure 1a), as expected from previous studies (Baiser & Lockwood, 2011; Villéger et al., 2014).

Human impacts on island bird assemblages will always be underestimated because there is still incomplete knowledge regarding the original island avifaunas, which consequently creates uncertainty around the observed magnitude of species compositional changes. The number of extinct species is most likely underestimated (Boehm & Cronk, 2021), as new extinct species keep being described (e.g. Rheindt et al., 2020), and the identification of species as native or introduced is also frequently challenging (Essl et al., 2018). In addition, the functional roles of historically extinct species are often missing, which is a major constraint to measure the impacts on functional diversity. It is important to keep in mind that these results are simply a snapshot in time, which will likely change rapidly as extinctions and introductions continue to increase (Pereira et al., 2010; Seebens et al., 2017).

4.2 | Taxonomic and functional homogenization dominated within and across archipelagos

Most taxonomically homogenized islands also homogenized functionally, both within (34/38; Figure 1c) and across archipelagos
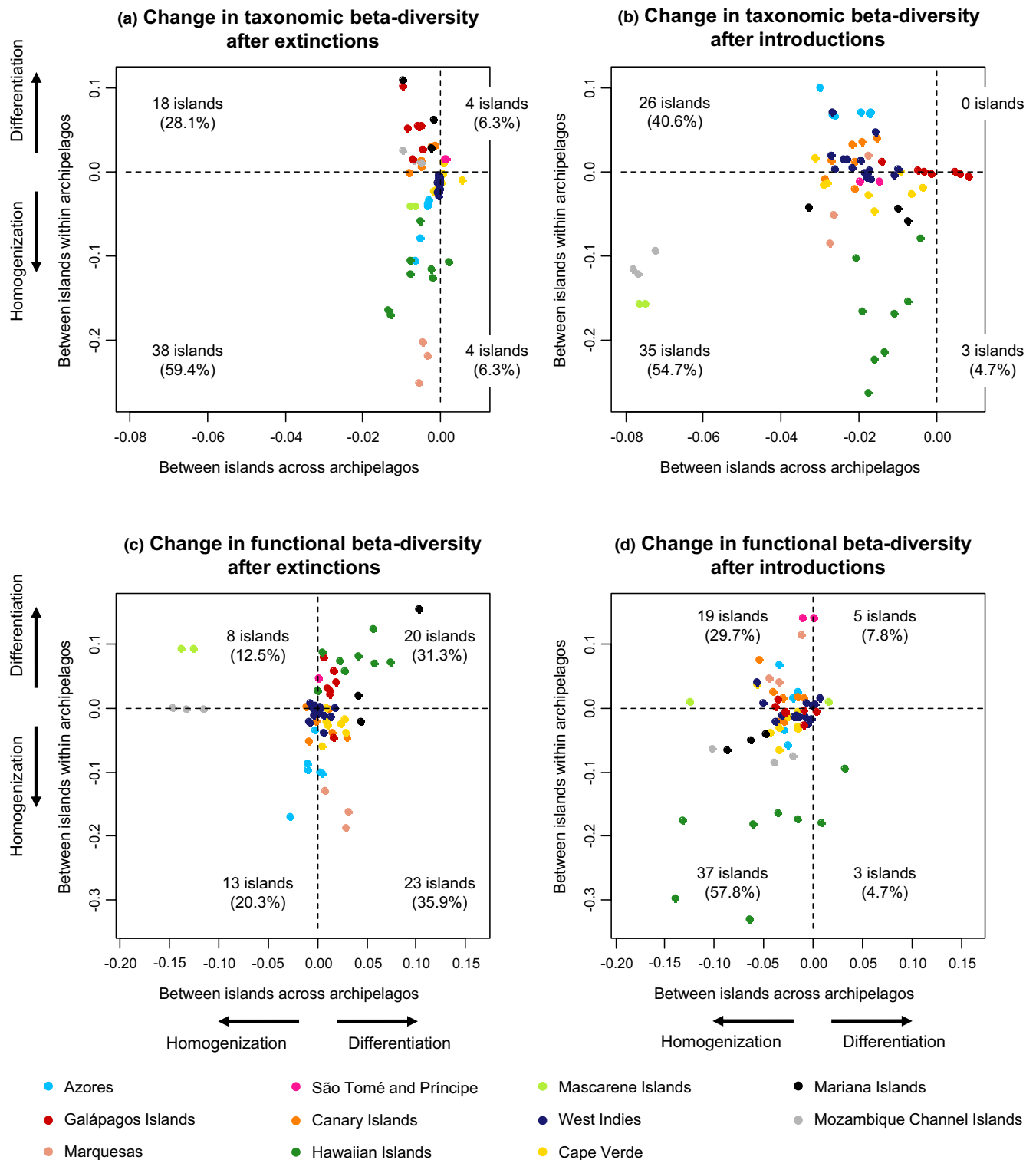
FIGURE 3 Average change in beta-diversity between islands within archipelagos and across archipelagos of the same ocean: (a) changes in taxonomic beta-diversity caused by extinctions, (b) changes in taxonomic beta-diversity caused by introductions, (c) changes in functional beta-diversity caused by extinctions and (d) changes in functional beta-diversity caused by introductions. A positive value indicates that islands have, on average, differentiated from other islands, whereas a negative value indicates islands have homogenized. Each dot represents one of 64 islands analysed, coloured by archipelago (n = 11).

(46/61; Figure 1b). The positive relationship between taxonomic and functional homogenization was preserved across scales, but changes in taxonomic beta-diversity across archipelagos reflected

much greater changes in functional beta-diversity compared to within archipelagos (Table S4). However, there were exceptions: 15 islands across archipelagos and 4 within archipelagos became

taxonomically homogenized but functionally differentiated. In almost all cases (18/19), introductions were the main driver of taxonomic homogenization (Figures S7 and S8), probably due to the introduction of the same species (Longman et al., 2018). Several bird species have been intentionally introduced and established populations across islands worldwide, especially across those with the same history of colonization (e.g. European colonization), such as islands belonging to the same archipelago (Blackburn et al., 2009). In the Hawaiian archipelago, the introduction of several species (e.g. common myna *Acridotheres tristis*, Eurasian skylark *Alauda arvensis*, rock partridge *Alectoris graeca*, black francolin *Francolinus francolinus*) across five islands caused strong taxonomic homogenization. Nowadays, some bird species are close to colonizing almost all of these archipelagos: for example, the common widespread rock dove *Columba livia* has been introduced to 62.5% of the islands in our database. On the other hand, extinction was the main factor responsible for functional differentiation (17/19; e.g. Tenerife, Antigua and Lana'i—Figures S8 and S10), despite having generally caused taxonomic homogenization (16/19). This suggests that extinct species tended to be functionally similar (Figure S14), having traits that resemble those of other species in different island assemblages (Li et al., 2020; Rosenblad & Sax, 2017). Human colonization of oceanic islands is known to have caused the extinction of bird species with similar traits, typical of species that evolved in isolation and with few to no predators, such as flightlessness, ground-foraging and specialized diets, and that are associated with high vulnerability to anthropogenic threats, like hunting, introduced predators and habitat loss (Carpenter et al., 2020; Kirchman & Steadman, 2006; Rando et al., 2020; Sayol et al., 2020). For example, the two Mascarene Islands lost different species of shelducks, night-herons and rails that were susceptible to human activities given their larger body size, low flight capacity (or flightlessness) and ground-foraging strategy (Hume et al., 2013). This pattern of high functional similarity among extinct birds has also been described for this island dataset (Soares et al., 2022), corroborating that the extinction of functionally similar species promoted the trend for overall functional differentiation of island bird assemblages.

Few islands became taxonomically differentiated but functionally homogenized, either within (13; Figure 1c) or across archipelagos (2; Figure 1b). Introductions were the main driver of taxonomic differentiation in most of these cases (within: 9/13—Figure S7; across: 2/2—Figure S8), suggesting that some introduced species are seldom shared among islands (Figure S14). On the other hand, most functional homogenization was due to extinctions (13/15; e.g. São Jorge, Gran Canaria and Tenerife—Figures S7 and S9), suggesting that these affected mostly functionally unique species. Interestingly, introductions led to functional homogenization in some of these cases (9/15), despite promoting taxonomic differentiation, which suggests that the species being introduced in different islands were not the same but were functionally redundant (e.g. Flores, Terceira and São Vicente—Figures S7 and S9). The introduction of species to a single assemblage promotes taxonomic differentiation, but it can promote functional homogenization if its traits are similar to those of species

in other islands (Baiser & Lockwood, 2011). Indeed, many bird species with similar ecological niches have been successfully introduced to oceanic islands, such as numerous ground-foraging granivores that prefer open areas, and this is promoting the global functional homogenization of oceanic islands (Blackburn et al., 2009; Soares et al., 2021).

4.3 | Homogenization is more common across than within archipelagos

A little more than half of the islands homogenized taxonomically both within and across archipelagos (38/64), including all islands of the Indian Ocean (Mascarenes and Mozambique Channel Islands), the Hawaiian Islands and the Marquesas (Figure 2a). Taxonomic homogenization across scales has been shown before (Olden et al., 2018; Otto et al., 2020), particularly for the islands of the Indian Ocean that have a high number of extinctions and introductions (Cassey et al., 2007). The Hawaiian Islands had some of the strongest taxonomic homogenization within archipelagos, which is expected since they had many extinctions, often referring to single-island endemics, and at least half of the introduced species are found on all main islands (Lockwood, 2006). The Indian Ocean islands exhibited the strongest taxonomic homogenization, corroborating previous studies that showed that these archipelagos received similar sets of introduced bird species that mostly derived from the same biogeographical region (Blackburn & Duncan, 2001; Cassey et al., 2007).

Taxonomic homogenization occurred more frequently across than within archipelagos (61 vs. 38; Figure 2a). This result agrees with our prediction that islands of different archipelagos have lower original similarities (this was also verified—original taxonomic beta-diversity ranging from 0.90 to 1—Figure S11b), and should therefore have higher homogenization. This pattern is mostly explained by extinctions: islands that are further away, namely those in different archipelagos, are less likely to share native species, meaning that, in these cases, extinctions usually refer to species that are restricted to single islands and whose extinction promotes taxonomic homogenization (extinctions promote more homogenization across archipelagos—see blue dots in Figures S7 and S8); by contrast, islands in the same archipelago will tend to share not only several native species but also extinctions (Russell & Kueffer, 2019; Whittaker et al., 2017), which will promote taxonomic differentiation. This high frequency of extinctions of species restricted to single islands across archipelagos caused their overall taxonomic homogenization, regardless of their original similarity level, which explains the non-significant relationship found across archipelagos (Table S5).

Recent studies have described an inverse relationship between taxonomic homogenization and initial similarity between islands, having linked it to the stronger homogenizing effect of introductions on islands with low original similarity: the original assemblages of distant islands tend to be more distinct, meaning that the introduction of the same species on both islands will have a stronger effect than on nearby islands that had more similar original assemblages

(Longman et al., 2018; Rosenblad & Sax, 2017). We showed that the original assemblages of islands on different archipelagos were indeed more distinct (Figure S11a,b), and that introductions tended to cause taxonomic homogenization on most islands (61/64; Figure S8).

Functional homogenization occurred within and across archipelagos for a little more than half of the islands (35/64; Figure 2b). Functional homogenization of island bird assemblages has been described before (Sayol et al., 2021; Soares et al., 2022; Sobral et al., 2016), but the effect of the distance between islands was not explored. We found that the patterns for functional homogenization are not as distinctive as for taxonomic homogenization (Figure 2), with functional homogenization occurring almost equally within (47) and across archipelagos (48). Functional differentiation was higher than taxonomic differentiation across archipelagos (16 vs. 3, $\chi^2 = 8.9$, p-value = 0.003), but within archipelagos, although statistically non-significant, it had the opposite direction with functional differentiation being lower than taxonomic differentiation (17 vs. 26, $\chi^2 = 2.241$, p-value = 0.134). The extinction of a species shared between islands has a stronger effect on taxonomic differentiation when the original similarity is low (Otto et al., 2020). In the same way, the extinction of functionally similar species should also promote stronger functional differentiation on islands that had an initial low functional similarity, such as those from different archipelagos. In fact, while the extinction of the same species on islands from different archipelagos is unlikely (discussed above), the extinction of functionally redundant species appears to have been common on oceanic islands (extinctions promote functional differentiation across archipelagos—see blue dots in Figure S10; Soares et al., 2021). The widespread loss of functionally similar species might explain why functional differentiation was higher than taxonomic differentiation across archipelagos, while the contrary was not as obvious and even had the opposite direction within archipelagos.

4.4 | Introductions offset extinction-driven differentiation

Extinctions led mostly to overall taxonomic homogenization (Figure 3a). Extinction-driven taxonomic homogenization was higher across than within archipelagos (56 vs. 42), which might be explained by endemic species that tend to be prone to extinction, being often shared between islands within archipelagos (Li et al., 2020; Otto et al., 2020; Rosenblad & Sax, 2017). Extinctions also led mostly to functional homogenization within (36/64) but not across archipelagos (21/64; Figure 3c). This can be attributed to the loss of species with highly distinctive traits that tend to evolve in remote archipelagos (Hume, 2017; McKinney & Lockwood, 1999): naïve, large-bodied, flightless or with poor flying abilities, ground foragers, frugivores and herbivores (Boyer & Jetz, 2014; Carpenter et al., 2020; Soares et al., 2022). The widespread loss of these species led to the functional differentiation of the islands that held them, which often belonged to different archipelagos that had low original functional similarity (Rosenblad & Sax, 2017).

Introductions also tended to promote taxonomic and functional homogenization (Figure 3b,d), as suggested before (Baiser et al., 2012; Cassey et al., 2007; Otto et al., 2020). These events are non-random, often favouring closely related species with similar traits (Blackburn et al., 2009; McKinney & Lockwood, 1999). Recent studies have shown that the introduction of functionally similar species is promoting functional homogenization of native bird assemblages on oceanic archipelagos (Sayol et al., 2021; Soares et al., 2022; Sobral et al., 2016). Introductions are currently happening at a faster pace, involving an increasing number of species and countries (Dyer, Cassey, et al., 2017). This means that even though introductions might have initially differentiated some assemblages, they might, later on, homogenize them (Olden, 2006). Birds are naturally vagile species, so they might disperse to neighbouring islands and homogenize entire archipelagos, as it happened to the common waxbill in Cape Verde (Otto et al., 2020).

The introduction of species is undoubtedly a major driver of both taxonomic and functional homogenization of island bird assemblages, frequently offsetting the functional differentiation effect of some extinctions and leading to overall functional homogenization (Figures S9 and S10). As the number of introduced bird species is expected to increase (Seebens et al., 2017), island bird assemblages will most likely continue to homogenize taxonomically and functionally. Moreover, considering the offsetting effect of introductions, functional homogenization may be even faster compared to taxonomic homogenization.

4.5 | Consequences of functional homogenization

Overall, bird extinctions and introductions promoted taxonomic and functional homogenization on oceanic islands, especially between those of different archipelagos. Since these patterns reflect functional changes in island bird assemblages, these will likely have strong cascading effects on other components of ecosystems and on ecosystem functioning. This was the case of the high species turnover of the Hawaiian bird assemblage, where functional traits important for seed dispersal (i.e. gape width and body mass) declined significantly, threatening the future of native plant communities, particularly larger-seeded plants (Case & Tarwater, 2020). Future research should aim to identifying which functional traits are contributing the most to these changes, linking homogenization patterns to species traits, and to ecosystems functions and services. Functional homogenization also increases the vulnerability to global changes, by reducing the variability of responses to disturbance (Clavel et al., 2011; Olden, 2006; Socolar et al., 2016) and thus the resilience of ecosystem services, posing a threat to human societies on islands (Russell & Kueffer, 2019; Whittaker et al., 2017).

Although there was a positive relation between the changes in taxonomic and functional beta-diversity at the global scale and both within and across archipelagos, it was not equally proportional across scales: the most extreme relation was found across archipelagos

where changes in taxonomic beta-diversity resulted in great changes in functional beta-diversity (1:2.275; Table S4). Moreover, despite the positive relationship and the overall homogenization pattern, not all taxonomically homogenized islands experienced functional homogenization (and vice versa). The opposite patterns between taxonomic and functional diversity reflect the non-randomness of species extinctions and introductions across oceanic islands. The variability between spatial scales and the opposite patterns highlights the need to consider the functional facet of biodiversity independently (Cadotte & Tucker, 2018; Devictor et al., 2010). Beta-diversity measures should be included in the development of future global conservation strategies to gain a better understanding of how extinctions and introductions might be affecting global biodiversity and ecosystem functioning (Brum et al., 2017; Cadotte & Tucker, 2018). Taxonomic beta-diversity is already increasingly being used to guide conservation (Olden et al., 2018; Socolar et al., 2016), but we call for the inclusion of functional beta-diversity, to allow a better assessment of how taxonomic changes might alter ecosystem functioning, which is vital to develop effective long-term conservation strategies.

AUTHOR CONTRIBUTIONS

Filipa C. Soares, Ricardo F. de Lima, Ana S. L. Rodrigues, Jorge M. Palmeirim and Pedro Cardoso conceived the ideas and designed the methodology. Filipa C. Soares collected the data. Filipa C. Soares analysed the data (with help from Pedro Cardoso, especially for the implementation and testing of the computer code and supporting algorithms). Filipa C. Soares led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

All data supporting the results in the paper are archived in figshare, https://figshare.com/s/6e3f02a21d78b06f5f5e.

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SUPPORTING INFORMATION

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