Patterns and drivers of taxonomic and functional changes in oceanic island bird assemblages

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Abstract

Oceanic islands are among the most transformed ecosystems in the world, with many having experienced major biotic changes through the combined effects of species extinctions and introductions. We map global patterns of taxonomic and functional change in 64 oceanic island bird assemblages and investigate whether these patterns can be explained by either island characteristics (geography, climate) or anthropogenic factors (human occupation, connectivity). The Hawaiian and Mascarene islands stand out as hotspots of taxonomic and functional change, but all islands changed taxonomically and functionally, mostly gaining species but losing functional richness. Island isolation and aridity can explain some of the observed variation in levels of change, but anthropogenic factors have a stronger effect. Remote humid islands have a stronger susceptibility to assemblage turnover and should be prioritized for conservation through the protection of native species and their ecosystems, and by preventing further introductions.

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Changes in island bird assemblages

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Abstract

Oceanic islands are among the most transformed ecosystems in the world, with many having experienced major biotic changes through the combined effects of species extinctions and introductions. We map global patterns of taxonomic and functional change in 64 oceanic island bird assemblages and investigate whether these patterns can be explained by either island characteristics (geography, climate) or anthropogenic factors (human occupation, connectivity). The Hawaiian and Mascarene islands stand out as hotspots of taxonomic and functional change, but all islands changed taxonomically and functionally, mostly gaining species but losing functional richness. Island isolation and aridity can explain some of the observed variation in levels of change, but anthropogenic factors have a stronger effect. Remote humid islands have a stronger susceptibility to assemblage turnover and should be prioritized for conservation through the protection of native species and their ecosystems, and by preventing further introductions.
Keywords
Beta-diversity; biogeography; dissimilarity; extinction; functional diversity; hypervolumes; island conservation; non-native species; species introductions

Introduction
Human activities are causing a global biodiversity crisis through increased extinction rates and major changes in biological communities worldwide (Johnson et al., 2017). Local and global extinctions and introductions are changing the distribution and abundance of species (McKinney & Lockwood, 1999), modifying ecosystem functioning and potentially impairing human well-being in the long term (Cardinale et al., 2012). Assessing how and why biodiversity is changing is essential to understand its implications and inform conservation strategies (Jarzyna & Jetz, 2017).

Most assessments of biodiversity change focus on taxonomic diversity, often investigating alpha-diversity using simple metrics, such as species richness (e.g., Dornelas et al., 2014). Conservation is also mostly guided by taxonomic diversity, focusing on species-rich sites, and under-representing other facets of biodiversity (Cadotte & Tucker, 2018; Devictor et al., 2010). Such facets include functional diversity, which reflects the combination of functional traits expressed by a group of species in a community, providing a link between species composition and ecosystem function and services (Jarzyna & Jetz, 2017).

Oceanic islands are not only areas of exceptional endemic biodiversity but also hotspots of species extinctions and introductions (Matthews et al., 2022; Whittaker et al., 2017). Previous studies found that whereas island avifaunas are mainly increasing in taxonomic diversity, they are losing functional diversity. Indeed, even though numbers of introduced species tend to be higher than those of extinctions, introductions do not offset the functional loss caused by bird extinctions, since many extinct island species were relatively functionally unique (Sayol et al., 2021; Soares et al., 2022a; Sobral et al., 2016). Island assemblages are also becoming taxonomically and functionally more similar, particularly through the homogenising effect of species introductions (Soares et al., 2022b). Nonetheless, there remains substantial variability in the extent to which oceanic island assemblages have been altered by human activities. The Hawaiian Island of Kahoolawe, for example, has endured a nearly complete transformation of its bird assemblages, with 29 new species introduced. In contrast, Isabela in the Galápagos only gained one non-native species. It is not clear which factors explain these variations, whether they correspond to intrinsic island characteristics such as isolation or geography, or instead to the history of their human transformation. These have different implications for management and conservation, given that island characteristics are fixed, whereas human presence can be changed.

Here, we map global patterns of biotic change across oceanic islands since human colonisation, as characterized by either taxonomic or functional changes to their bird assemblages. We focus on birds because besides their vital role within island ecosystems, recently compiled databases of species traits have render it possible to quantify functional diversity (e.g., Case & Tarwater, 2020; Heinen et al., 2018; Tobias et al., 2022), and the zooarchaeological record is relatively complete for this taxon. We highlight global hotspots of human-induced transformation by mapping multiple facets of biotic change: change in the taxonomic and functional richness of bird assemblages (as defined by high rates of species extinctions and introductions, and by change in functional richness); and hotspots of change in the composition of assemblages (as measured through taxonomic and functional dissimilarity).

We then investigate the drivers for the observed patterns by testing whether change can be explained by either intrinsic island characteristics (related to geography and climate) or by anthropogenic factors (human occupation and human connectivity). We expect to find higher rates of extinctions and introductions in isolated islands, given that their native assemblages tend to be more naïve and thus more vulnerable to extinction (Russell & Kueffer, 2019), and indeed recent studies showed that introductions increase with isolation (Moser et al., 2018). Bird introductions are known to increase with island area and human population size (Blackburn et al., 2008), therefore we expect larger islands, which usually have larger human populations, to have higher introduction rates. We also expect that islands more connected by harbours and airports

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will receive more introduced species. Most islands have suffered extensive deforestation since colonisation (Russell & Kueffer, 2019) but drier islands might be more resilient to extinctions because replacement of arid ecosystems by human-modified environments is often a less severe transformation than the deforestation of wetter islands. However, arid ecosystems might be more susceptible to competition from introduced human commensal bird species (e.g., associated with urban and agricultural landscapes; Soares et al., 2021). We do not have a priori prediction for the net effects of species extinctions and introductions on the functional richness and composition of island avifaunas, we thus hope this analysis will bring new insights into the net human impacts on bird functional diversity across oceanic islands.

Methods

Our analyses are based on a dataset (compiled by Soares et al. 2022a,b) that includes 64 oceanic islands larger than 100 km² with sufficient data and belonging to 11 archipelagos across the Pacific, Atlantic and Indian Oceans (Table S1, Fig. S1).

Bird species data

For each of the 64 islands, the dataset lists the occurrence of terrestrial and freshwater regularly breeding bird species, including all known species introductions and extinctions since human colonisation (following the taxonomy from the Handbook of the Birds of the World & BirdLife International, 2018). Out of a total of 677 species: 178 are extinct, 163 introduced, and 397 extant native species on at least one island. The term “extinct” is relative to an individual island and refers to both globally extinct and locally extirpated species.

For each species in the dataset, we sourced data on a range of functional traits (see Soares et al. 2022a,b - Tables 1 & S2) that are known to reflect bird species’ ecological roles and determine their responses to environmental changes (Luck et al., 2012; Tobias et al., 2022).

Island characteristics

For each of the 64 islands, we compiled information on characteristics that can plausibly influence changes in species and functional composition (Tables 2, S1). For information obtained from raster data (see Table 2), values correspond to the average of all pixels touching each island.

Data analysis

We undertook all data processing and statistical analyses in R (v.4.0.4; R Core Team, 2021).

Changes in taxonomic diversity

For each island, we define the ‘original’ species assemblage (i.e., the assemblage present when humans first colonised the island) as the set of native species that are either extant today plus any species that have become extinct. The ‘present’ assemblage includes native extant plus introduced species, but excluding extinct species. To quantify human-driven changes in taxonomic diversity, we calculated three indices per island:

- Extinction rate: number of extinct species divided by the original species richness.
- Introduction rate: number of introduced species divided by the original species richness.
- Taxonomic dissimilarity: measured as the Jaccard pairwise dissimilarity between the composition of the original and the present assemblages. Calculated using the beta function in the BAT package (Cardoso et al., 2015), to reflect species heterogeneity in time (Magurran et al., 2019). It ranges from 0 (species composition did not change) to 1 (no species in common between original and present assemblages), and is affected by species replacement and changes in species richness.

Changes in functional diversity

We assessed functional diversity based on hyperdimensional functional trait spaces (Soares et al. 2022a) created from probabilistic hypervolumes (Mammola & Cardoso, 2020). We first built a global trait space
encompassing all species and traits, by computing pairwise functional distances between each pair of species, using the Gower dissimilarity index and giving the same weight to each trait (range of pairwise functional distances: 0 – 0.887), in dist.ktab function in ade4 (Table S3; Dray & Dufour, 2007). Then, we did a principal coordinate analysis (PCoA) with Cailliez correction for negative eigenvalues and used the pcoa function in ape (Paradis et al., 2004) to extract the first PCoA axes that cumulatively explained more than 80% of the total variation. Eight axes (81.3% variation; Fig. S2) were then used to represent the global trait space.

From this global trait space, we derived two trait spaces for each island, representing their original and their present assemblages. Each was built based on the kernel density hypervolumes using even weight across traits, the Gaussian method representing an estimated 95% of the cloud density of stochastic points based on the position of each species in the assemblage (Blonder et al., 2018), and the default arguments of the kernel.build function in BAT (Mammola & Cardoso, 2020). We define functional richness as the volume of the cloud of stochastic points, calculated using the kernel.alpha function in BAT (Cardoso et al., 2015; Mammola & Cardoso, 2020).

To quantify changes in functional diversity for each island, we used:

Rate of change in functional richness: difference between present and original functional richness, divided by the original functional richness (positive when there was volume expansion).

Functional dissimilarity: dissimilarity between present and original functional composition, using Jaccard pairwise dissimilarity, calculated with the kernel.beta function in BAT (Cardoso et al., 2015; Mammola, 2019; ranges from zero if no change in functional composition, to one if no overlap between trait spaces).

Links between taxonomic and functional dissimilarity

We investigated the relationship between taxonomic and functional dissimilarity through a generalized linear mixed-effects model (GLMM) with a beta distribution and a logit link function, using the glmmTMB package (Magnusson et al., 2017). Functional dissimilarity was the response variable, taxonomic dissimilarity was considered a fixed effect (n = 64) and archipelago a random effect (n = 11). Model assumptions were validated using simulated residuals and the DHARMa package (Hartig, 2021).

Drivers of taxonomic and functional change

We used GLMMs to identify which island characteristics best explain changes in taxonomic and functional diversity. We improved the symmetry and linearity of explanatory variables through logarithmic or square root transformations (Table 2). To reduce dimensionality (from 15 predictors), we divided the variables into 5 types (three related to island biogeography and two associated with anthropogenic factors):

- Isolation: summarising isolation to surrounding landmass, and distance to the mainland;
- Surface: summarising island area and elevation range;
- Climate: summarising annual precipitation, precipitation seasonality, aridity index, mean annual temperature, temperature seasonality, and percentage of forest cover (included here as vegetation reflects climate);
- Human connectivity: summarising airport capacity, and harbour capacity;
- Human occupation: summarising human population density, percentage of roadless areas, and percentage of cultivated and managed vegetation.

We then undertook a principal component analysis (PCA) for each type (prcomp function in stats ), retaining the first set of PCA axes needed to cumulatively explain at least 75% of the total variation in each PCA (Fig. S3 and Table S4).

We built GLMMs to explain (i) extinction rate, (ii) introduction rate, (iii) rate of change in functional richness, (iv) taxonomic dissimilarity, and (v) functional dissimilarity, using the above-mentioned PCA axes as fixed effects and archipelago as a random effect. Models i, iv and v were fitted using a beta distribution with logit link function and the glmmTMB function in glmmTMB , while models ii and iii were fitted using Gaussian distribution and the lmer function in lme4 (Bates et al., 2014).
We identified the most important variables in each GLMM through a multi-model comparison using Akaike’s information criterion corrected for small sample sizes (AICc), using the `dredge`function in MuMIn (Barton, 2019). Then, for each fixed effect, we (1) averaged conditional coefficients across all models (‘full set’), and (2) estimated the relative variable importance (RVI) by summing the Akaike weights (wAICc) of models in which each variable was included with the `sw` function in MuMIn. We validated model assumptions using simulated residuals and the DHARMa package (Hartig, 2021). To avoid multicollinearity, we excluded all explanatory variables that had a (generalised) variance inflation factors (VIFs) above 2 (highlighted in grey in Table S5), according to the `check_collinearity` function in performance (Lüdecke et al., 2021).

Results

Spatial patterns of species extinction and introduction

Extinctions occurred on 44 out of the 64 islands, with losses averaging 15% of the original avifauna (Fig. 1 and S1, Table S1). Islands within archipelagos had generally similar extinction rates, with the greatest losses occurring in the Hawaiian Islands (average = 54%; up to 73% in Lanai), the Mascarenes (58%; up to 62% in La Réunion) and the Mariana Islands (31%; up to 72% in Guam), while islands without extinctions are concentrated in the West Indies (n = 4), Galápagos (n= 4), Azores (n = 3), and Cape Verde (n = 3).

Introductions occurred on all islands, which gained, on average, 58% of the original species richness (Fig. 1). Islands within archipelagos tended to have similar gains, the lowest being in the Galápagos (average = 5%; down to 3% in Isabela), and the highest in the Hawaiian Islands (average = 284%; up to 725% in Kahoolawe).

Nearly all islands gained more species through introductions than they lost from extinctions, exceptions being Floreana, San Cristóbal (both in Galápagos), and Guam (Mariana Islands). The Hawaiian and Mascarenes archipelagos stand out as hotspots of both extinctions and introductions.

Spatial patterns of change in functional richness

Only 11 out of 64 islands had a net gain of functional richness (Fig. 2 and S1, Table S1), and on average each island lost 34% of its original functional richness. The Hawaiian Islands, the Mascarenes, and the Marquesas stand out as hotspots of functional richness loss, losing up to 96% of their original functional richness in the Hawaiian Island of Lanai.

Patterns were again generally consistent within archipelagos. All islands lost functional richness in the Marquesas, Azores, Canaries, Mascarenes, and Marianas. The same was also true for over 85% of islands in each archipelago of Hawaii, West Indies, and Cape Verde, while in the Galápagos five out of seven islands gained functional richness, including the two with the highest gains (38% in Floreana and 44% in San Cristóbal).

Spatial patterns of taxonomic and functional compositional changes

We found a positive relationship between taxonomic and functional dissimilarity (beta-GLMM: coefficient = 4.114, p < 0.001; Fig. S4). Functional dissimilarity was higher than taxonomic dissimilarity on all islands (averaging 0.59 and 0.33, respectively; Fig. 3). The Hawaiian Islands, the Mascarenes and Guam (Mariana Islands) stand out as hotspots of both taxonomic and functional dissimilarity ([?]. 0.78 and [?]. 0.91, respectively).

Drivers of taxonomic and functional change

Island isolation and human occupation were significantly positively associated with the extinction rate, the latter also being positively related to the introduction rate (Fig. 4a, 4b and S6, Table S5). Aridity had a positive significant effect on change in functional richness, whereas isolation and human connectivity had a negative effect (Fig. 4c and S10). Taxonomic and functional dissimilarity were significantly positively associated with human occupation (Fig. 4d and e), although residual analysis suggests caution is needed in the interpretation of these results (Fig. S11 and S12).
Discussion

Pervasive anthropogenic changes across islands

All islands had species introductions and 69% suffered extinctions. On average, each island gained 58% of species in introductions compared to their original avifauna but lost just 15% due to extinctions (Fig. 1). Our results agree with previous findings (e.g., Sayol et al., 2021; Soares et al., 2022a; Sobral et al., 2016), showing that although introductions exceed extinctions on almost all islands, they do not compensate for the loss of functional richness (Fig. 2), because extinct species represented a disproportionally high fraction of the original functional richness. Many extinct birds were functionally unique, assuming functions that are not covered by extant native or introduced birds (Case & Tarwater, 2020; Soares et al., 2022a; Sayol et al., 2021).

Anthropogenic taxonomic and functional dissimilarity varied across islands (Fig. 3), being positively correlated. This indicates that changes in species composition led to changes in function, as expected since most species have a unique combination of traits (Fig. S5; Baiser & Lockwood, 2011; Fonseca & Ganade, 2001). However, functional dissimilarity was higher than taxonomic dissimilarity for all islands (Fig. 3), suggesting that bird extinctions on oceanic islands are non-random events that disproportionately affect functionally distinct species (e.g., Baiser et al., 2018; Matthews et al., 2022; Soares et al., 2022a; Sayol et al., 2021). These differences warn against using taxonomic diversity as a proxy for functional diversity (Cadotte & Tucker, 2018; Carmona et al., 2021; Devictor et al., 2010).

Only 11 islands gained functional richness, five of which were in the Galapagos (Fig. 2). This resulted from the loss of a few not-very-distinct species and the introduction of functionally distinct species. In Floreana and San Cristobal (Galapagos), introductions were so functionally distinct that functional richness increased despite decreasing species richness. Loosing functionally similar species while gaining distinct species can thus lead to disproportionally high gains in functional richness, despite modest or even negative changes in species richness (Fonseca & Ganade, 2001; Jarzyna & Jetz, 2017).

Hotspots (and coldspots) of taxonomic and functional change

T axonomic and functional changes are often consistent across islands within archipelagos (Fig. 1-3), some of which exhibit extraordinarily high levels of change, such as Hawaii and the Mascarenes. These are not only hotspots of bird extinctions and introductions (Cheke, 2013; Lockwood, 2006), but also of loss in functional richness. Almost all Hawaiian and Mascarene Islands more than doubled their original species richness, while losing over 80% of their functional richness (Boyer & Jetz, 2014). The replacement of the original frugivores and granivores by introduced species that are functionally different is affecting seed predation and dispersal patterns, with cascading effects on vegetation dynamics and forest regeneration across these islands (Carpenter et al., 2020; Case & Tarwater, 2020). Besides decreasing pollination (Anderson et al., 2011) and impairing seed dispersal (Heinen et al., 2018), insular bird extinctions are also known to alter herbivory (Forsyth et al., 2010).

Many islands have several introduced species, many of which are functionally similar to each other, sometimes even belonging to the same family (Blackburn & Duncan, 2001). Island bird introductions are non-random regarding origin, function and recipient location, so the probability of introduced birds being similar to each other increases as more species are introduced (Baiser et al., 2018; Blackburn & Duncan, 2001), resulting in a progressively smaller contribution for functional richness.

Some archipelagos, such as the Galapagos and Sao Tome and Principe, are ‘coldspots’, having experienced relatively small taxonomic and functional changes (Fig. 1 and 2). In particular, Isabela, Santiago, Fernandina and Marchena (Galapagos) had no extinctions and experienced introduction rates of only 3-5% (Fig. 1). Even though this translated into small changes in functional richness (Fig. 2), the few introduced species prompted moderately high changes in functional composition (Fig. 3).

Drivers of taxonomic and functional change in island bird assemblages
Taxonomic and functional changes were broadly consistent within archipelagos (Fig. 1-3), which is not surprising since islands in the same archipelago typically share similar environmental conditions (e.g., climate, isolation from the mainland), natural histories of colonization and evolution, and thus many of the same native species, which tend to have similar vulnerabilities to extinction (Whittaker et al., 2017). Moreover, islands within the same archipelago are typically also exposed to parallel histories of human colonization and so end up sharing anthropogenic threats, including many of their introduced species (Russell & Kueffer, 2019).

Anthropogenic factors were better at explaining taxonomic and functional change than biogeographic factors (Fig. 4). Human occupation and human connectivity were correlated (Fig. S5) and had similar effects, even if they were not always equally significant. Human population density and the proportion of human-dominated landscapes on an island were positively related to extinction and introduction rates, and taxonomic and functional dissimilarity. This is expected since more densely populated islands tend to have more introduced bird species, which results from their higher connectivity (Blackburn et al., 2008). Additionally, human presence promotes other threats besides introduced species, notably overexploitation (Russell & Kueffer, 2019) and habitat loss, both of which are known to be major drivers of species extinctions (Lees et al., 2022).

Unsurprisingly, islands with more harbours and airports have higher rates of decline in functional richness. Presumably these islands are more connected to international wildlife trade networks, which may result in the introduction of many functionally similar species, including predators and competitors (Seebens et al., 2017) that can promote the extinction of functionally unique birds (Boehm & Cronk, 2021; Russell & Kueffer, 2019).

Biogeographic isolation was, as expected, associated with high extinction rates, associated with the loss of functional richness. Indeed, isolated assemblages (evolved with few predators, competitors, parasites, and diseases) tend to include functionally distinct species (for example, flightless birds) which are particularly sensitive to anthropogenic change such predation by humans or introduced predators (Russell & Kueffer, 2019; Whittaker et al., 2017). Unexpectedly, we found no significant association between isolation and introduction rates (Moser et al., 2018), indicating that anthropogenic pathways of introduction have become dissociated from biogeographic isolation (Blackburn et al., 2008).

Contrary to our prediction, we did not find that arid islands are more resilient to species extinctions, which we had derived from the expectation that forest specialists from humid islands should be more sensitive to habitat transformation than species from more open arid ecosystems. However, we did observe that arid islands have higher rates of species introductions, which may result from a preadaptation of some introduced species associated with anthropogenic landscapes (like urban areas and agricultural fields) to shrubland-dominated arid islands. This, however, does not explain the positive association between island aridity and rates of change in functional richness, which suggest instead that the net effect from extinctions and introductions is resulting in an expansion of the niche space in arid islands.

We found no effect of temperature on any of the measures of change analysed, indicating that when other variables are controlled for, neither tropical nor temperate islands appear to be disproportionately prone to change.

**Implications for oceanic island conservation**

Bird assemblages on oceanic islands are undergoing substantial anthropogenic transformations due to the combined effect of extinctions and introductions. Most oceanic islands larger than 100 km$^2$ lost functional diversity despite gaining species, with some experiencing a near-complete avifaunal turnover. The real magnitude of these changes is likely underestimated since many extinctions have not yet been described (Boehm & Cronk, 2021), and introductions are underestimated (Essl et al., 2018). The pace at which extinctions and introductions occur is likely to increase on oceanic islands in the near future (Russell & Kueffer, 2019; Sax & Gaines, 2008; Seebens et al., 2017), so there is an urgent need to understand their drivers and functional consequences.
Patterns of change were more associated with human presence than with island geography and climate, which has important implications for conservation as the former can be managed to prevent further biodiversity loss whereas the latter are fixed. The Galapagos Islands are a good example of how keeping human occupation relatively low has allowed their native avifauna to remain mostly intact despite high isolation (associated with higher extinction rates) and high aridity (associated with higher competition from introduced species). Islands such as these (whose characteristics make them more susceptible to assemblage turnover) should be prioritized for conservation through the protection of native species and their ecosystems, and by preventing further introductions.

Understanding how the observed taxonomic and functional transformations affect ecosystem functioning on islands is beyond the scope of the present study, but since birds support a wide variety of ecosystem functions (Şekercioğlu et al., 2004), the functional changes described here are likely to have important long-term ecological implications. Understanding how functional changes in bird assemblages impact the provision of ecosystem services is important to guide conservation efforts, including the definition of priorities for protecting and reintroducing native species or functions, as well as for controlling current populations of introduced species and preventing future introductions.

Future assessments of changes in species assemblages need to consider multiple facets of biodiversity, including different temporal and spatial scales. Most assessments of biodiversity change are still based exclusively on taxonomic diversity (Cadotte & Tucker, 2018; Dornelas et al., 2014), even though these can underestimate the magnitude of change. We call for comprehensive assessments of change in taxonomic and functional diversity, focusing on a variety of taxonomic groups and applied at multiple spatial and temporal scales, as a vital effort to predict future changes and propose effective conservation measures that safeguard resilient island ecosystems.

Acknowledgements

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References


**Tables**

**Table 1.** Description of species traits (adapted from Soares et al. 2022a; see Table S2 for details).

<table>
<thead>
<tr>
<th>Trait</th>
<th>Type</th>
<th>Description [value]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diurnal</td>
<td>Dichotomous</td>
<td>Yes [1], No [0]</td>
</tr>
<tr>
<td>Nectivore a</td>
<td>Dichotomous</td>
<td>Yes [1], No [0]</td>
</tr>
<tr>
<td>Water forager b</td>
<td>Dichotomous</td>
<td>Yes [1], No [0]</td>
</tr>
<tr>
<td>Forest specialist</td>
<td>Dichotomous</td>
<td>Yes [1], No [0]</td>
</tr>
<tr>
<td>Wetland specialist</td>
<td>Dichotomous</td>
<td>Yes [1], No [0]</td>
</tr>
<tr>
<td>Diet</td>
<td>Nominal</td>
<td>Granivore, herbivore, frugivore, invertivore, carnivore, omnivore</td>
</tr>
<tr>
<td>Average body mass</td>
<td>Continuous</td>
<td>Natural log-transformed body mass (g)</td>
</tr>
<tr>
<td>Habitat specialization</td>
<td>Ordinal</td>
<td>Number of suitable habitats</td>
</tr>
<tr>
<td>Volancy</td>
<td>Ordinal</td>
<td>Flightless [1], weak flyer [2], volant [3]</td>
</tr>
</tbody>
</table>

**Table 2.** Description of island characteristics and corresponding data sources.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area (km²)*</td>
<td>Island area (Weigelt et al., 2015).</td>
</tr>
<tr>
<td>Isolation from surrounding landmass</td>
<td>Index quantifying the proportion of landmass (other islands and/o...)</td>
</tr>
<tr>
<td>Distance to mainland (km)*</td>
<td>Minimum linear distance from the island coast to the nearest continent</td>
</tr>
<tr>
<td>Elevation range (m)§</td>
<td>Maximum elevation above sea level in each island (proxy to environment)</td>
</tr>
<tr>
<td>Mean annual temperature (°C)</td>
<td>Mean annual temperature (Weigelt et al., 2013).</td>
</tr>
<tr>
<td>Annual precipitation (ml)§</td>
<td>Total annual precipitation (Weigelt et al., 2013).</td>
</tr>
<tr>
<td>Temperature seasonality*</td>
<td>Minimum range of annual temperature in the island (Weigelt et al., 2013).</td>
</tr>
<tr>
<td>Precipitation seasonality*</td>
<td>Coefficient of variation in monthly precipitation (Weigelt et al., 2015)</td>
</tr>
<tr>
<td>Aridity index§</td>
<td>Index obtained by combining precipitation, temperature and reference</td>
</tr>
<tr>
<td>Percentage of forest cover (%)*</td>
<td>Percentage of island area covered by the sum of four classes of land cover</td>
</tr>
<tr>
<td>Percentage of cultivated and managed vegetation (%)§</td>
<td>Percentage of island area covered by land cover class “cultivated and managed vegetation”</td>
</tr>
<tr>
<td>Human population density (persons/km²)*</td>
<td>Estimated average human population density in 2015. Calculated from...</td>
</tr>
<tr>
<td>Percentage of roadless areas (%)</td>
<td>Percentage of island area that is more than 1km away from a road.</td>
</tr>
<tr>
<td>Harbour capacity*</td>
<td>Index corresponding to the weighted number of harbours on the island.</td>
</tr>
<tr>
<td>Airport capacity*</td>
<td>Index corresponding to the weighted number of airports, with weight</td>
</tr>
</tbody>
</table>

*Log transformed; § Square root transformed
Figures

Figure 1. Patterns of extinction and introduction rates across 64 oceanic islands in 11 archipelagos. Rates are the number of extinctions or introductions per island divided by the original species richness. The dashed black circle marks 100% species change: a similar-sized red circle indicates 100% extinction of the original avifauna; a similar-sized blue circle means that the number of introduced species equals the original richness. The West Indies are illustrated across three insets (3a, 3b, 3c). All insets are at the same scale as the Hawaiian Islands.

Figure 2. Patterns of change in functional richness associated with bird extinctions and introductions. The dashed black circle corresponds to a 100% change in functional richness: equal-sized pink circles indicate a 100% loss in original functional richness, and equal-sized green circles correspond to a 100% increase.
(doubling). The West Indies are illustrated across three insets (3a, 3b, 3c). All insets are at the same scale as the Hawaiian Islands.

**Figure 3.** Patterns of taxonomic and functional dissimilarity. The dashed black circle indicates 100% dissimilarity, either taxonomic (if equal-sized yellow circle; if no species in common between original and present bird assemblages) or functional (if equal-sized green circle; if no overlap between spatial trait spaces of original and present assemblages). The West Indies are illustrated across three insets (3a, 3b, 3c). All insets are at the same scale as the Hawaiian Islands.

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**Figure 4.** Drivers of taxonomic or functional diversity. Each panel represents the conditional model-averaged coefficients of a GLMM, the x-axis indicating the effect of each explanatory variable on the corresponding index of change. All GLMMs included 64 islands, except for b (n = 55), where the introduction hotspots of the Hawaiian Islands and the Mascarenes were removed because they strongly affected the overall pattern by over-predicting small values and under-predicting large response values (Fig. S8 and S9). Explanatory variables not shown were not included in the model because of VIF > 2. Points indicate model-average coefficients, horizontal lines represent standard errors, and values on the right are the Relative Variable Importance (RVI). RVI values larger than 0.50 are highlighted in bold, and the corresponding points and lines are in black.