

## ECOLOGY

# Loss of functional diversity through anthropogenic extinctions of island birds is not offset by biotic invasions

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Human impacts reshape ecological communities through the extinction and introduction of species. The combined impact of these factors depends on whether non-native species fill the functional roles of extinct species, thus buffering the loss of functional diversity. This question has been difficult to address, because comprehensive information about past extinctions and their traits is generally lacking. We combine detailed information about extinct, extant, and established alien birds to quantify historical changes in functional diversity across nine oceanic archipelagos. We found that alien species often equal or exceed the number of anthropogenic extinctions yet apparently perform a narrower set of functional roles as current island assemblages have undergone a substantial and ubiquitous net loss in functional diversity and increased functional similarity among assemblages. Our results reveal that the introduction of alien species has not prevented anthropogenic extinctions from reducing and homogenizing the functional diversity of native bird assemblages on oceanic archipelagos.

## INTRODUCTION

The rapid expansion and intensification of human impacts on the environment have caused hundreds of extinctions (1–3) and alien species introductions worldwide (4, 5). These changes have resulted in substantial turnover of species in ecological communities, with uncertain effects on the functioning of ecosystems. While, on the one hand, it is expected that extinctions of key species will compromise ecosystem functioning (6, 7), the extent to which established alien species can compensate for the loss of extinct species is still a matter of debate (8–10).

Anthropogenic extinctions often represent a disproportionate loss of evolutionary history (11, 12) and can involve selectivity for specific traits (13, 14), causing the loss of some key ecosystem functions, such as seed dispersal (15). However, extinctions can be outnumbered by alien species establishment at a local scale (16), potentially balancing some of the lost functional diversity. According to niche theory, the establishment of introduced species might be facilitated by the availability of vacated niches (17, 18), predicting a high functional overlap between extinct and established species. On the other hand, empty niches might remain unoccupied if both the surviving resident species and alien species represent trait combinations resilient to human impacts or if alien species occupy distinct regions of trait space (19).

Another potential consequence of assemblage turnover can be functional homogenization, where species assemblages become more ecologically similar over time (20). If species driven to extinction tend

to have distinct traits, then we expect that average functional similarity among assemblages will increase following extinctions. In addition, if alien species tend to be more similar to one another in identity and/or function than native species, then we would expect the functional similarity among assemblages to increase further following biotic invasions. While previous work has shown that anthropogenic impacts can cause taxonomic homogenization in species assemblages (21, 22), it is not clear whether this also translates into functional homogenization, especially because the two processes can occur independently (23–25).

Island bird assemblages offer a unique opportunity to test alternative hypotheses on how extinctions and invasions drive functional change. Islands have been disproportionately affected by anthropogenic extinctions (26, 27) and the establishment of alien species (28). In addition, a wealth of information exists about current and extinct bird assemblages, coupled with unparalleled datasets on avian functional traits (29). Anthropogenic impacts have driven the extinction of birds for thousands of years, often involving the loss of distinct functional roles (30, 31). A prominent example is the moa in New Zealand, which likely occupied an ungulate-like niche that has not been replaced by other bird species (32). Other examples of ecosystem effects include the loss of seed dispersal interactions (33) and the disproportionate elimination of particular trophic levels (34). Set against the effects of extinction is accelerating waves of alien bird species introductions to islands worldwide (5). However, these alien bird species are often widespread generalists with identities largely driven by human selectivity for features (e.g., utility as game or pets) (5) that may not result in the replacement of functions lost to extinction.

Although some previous work has identified a disproportionate loss of both phylogenetic (35) and functional (36) diversity in birds following extinctions, other studies accounting for invasions have found that the functional space occupied by extinct and alien bird species is of similar size, albeit with these species occupying different regions of functional space (37), suggesting that some functions might have been lost, while others have been gained. These studies have often been geographically restricted or focused on recent extinction events (after 1500 CE), despite evidence that many anthropogenic

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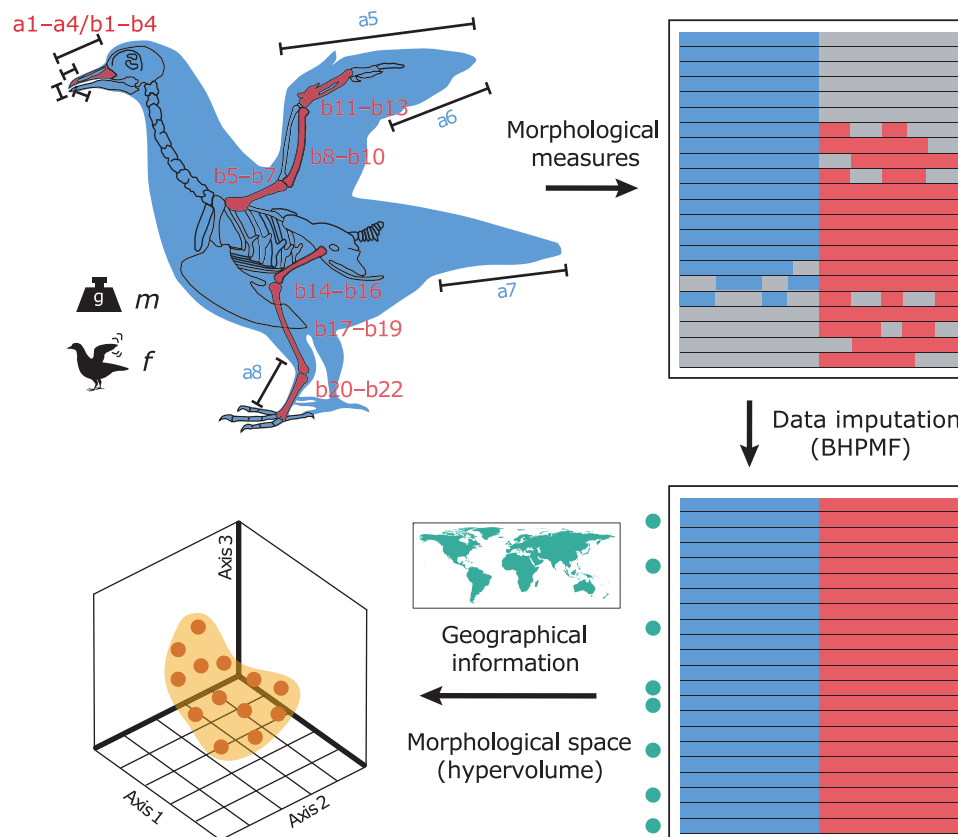
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extinctions happened in the Holocene or Late Pleistocene, much earlier than previously recognized (1). In particular, recent bird extinctions account for only one-third of the total list of known anthropogenic bird extinctions (38).

Given the long history of anthropogenic extinctions, the impacts of humans on functional diversity loss will inevitably be underestimated, unless early extinctions are considered. However, accounting for these historical events remains challenging, particularly because information about the ecological roles of long-extinct species is often missing. Morphological traits provide one way to quantify the impact of humans on the functional diversity of species assemblages. In birds, morphological measurements on preserved bones and skins have been shown to be reliable predictors of species ecology (29, 39–41) and can also be recovered for most known extinct species (42, 43). By combining these measurements with detailed information about the identity of species that have become extinct or invaded different assemblages, changes in morphological diversity can allow us to quantify the effect of anthropogenic extinctions and invasions on the functional space occupied by birds and how this has been altered by human activity.

To achieve this goal, we compiled trait data for bird assemblages in nine well-studied and biogeographically distinct archipelagos,

including all extant native species and species that have either been introduced by humans or driven to extinction since the Late Pleistocene (omitting failed introductions and focusing exclusively on successfully established species). Our dataset consists of eight lineal morphological traits, including measurements of the beak (e.g., beak length) and body (e.g., wing length) (29). We also compiled estimates of body mass (29, 44) and flight ability (38). Because features such as plumage and mandibles are not well preserved in the fossil record, we used additional data on 22 lineal skeleton measurements to infer missing trait data from related extinct or extant species. We use this dataset to assess how species extinctions and introductions have altered the functional diversity (i.e., morphological and behavioral variation) of island bird assemblages (Fig. 1). In particular, we evaluate which regions of functional space are (re)filled by alien species and which regions remain empty. We also evaluate the extent to which functional diversity among archipelagos has been homogenized by human impacts. We do this by comparing three stages on each archipelago: native preextinction, native postextinction (including only extant native species), and postextinction and alien species introductions. The results provide insights into the impacts of anthropogenic extinctions and subsequent species turnover on the ecological functioning of island ecosystems.



**Fig. 1. Pipeline for data collection and quantification of morphological space in each archipelago.** We gathered information about eight morphological traits from skin material (in blue, a1 to a8) and 22 morphological traits from skeleton material (in red, b1 to b22) and information about body mass ( $m$ ) and flight ability ( $f$ ) (see a list of all traits in table S1). The raw data therefore consisted of a matrix of 32 traits for 10,845 species, including some missing values (in gray). A data imputation method [Bayesian hierarchical probabilistic matrix factorization (BHPMF)] was used to infer missing data. Last, the 10 most complete traits (a1 to a8 +  $m$  +  $f$ ) were used to infer the morphological space in each archipelago bird community, selecting the species on each archipelago based on geographical information and estimating the archipelago niche volume in a three-dimensional space using hypervolumes.

## RESULTS

We obtained data for 1302 bird species that have been recorded across the nine archipelagos, including 265 globally or locally extinct and 355 established introductions from 143 separate species (Table 1). Although recent species extinctions (after 1500 CE) have been the main focus of previous studies, we found that these account for only 38% of total species lost in the studied archipelagos. The ratios of extinct to alien species (extinct:alien) varies across archipelagos, from those where alien species outnumber extinctions (Saint Helena = 0.83, Hawaii = 0.84, and Bermuda = 0.85) to those where extinctions slightly (New Zealand = 1.05, Mascarene Islands = 1.24, and Madagascar = 1.36) or greatly (New Caledonia = 1.63, Cuba and Jamaica = 1.71, and Canary Islands = 2.0) outnumber the number of established alien species. However, there is a positive association across archipelagos between the number of extinct and established alien species, showing that archipelagos that have lost more species also tend to have gained more species following invasions ( $R^2 = 0.88$ ,  $P < 0.001$ ; see fig. S1).

We summarized trait diversity using principal components analysis (PCA). The first three PC axes explain 83% of the variance in traits (PC1 = 64.8%, PC2 = 11.1%, and PC3 = 7.4%; see fig. S2 and table S2 for PCA loadings). The PC1 can be interpreted as an index of size, with higher PC1 scores indicating longer linear measurements of each trait. The PC2 captures species flight capacity, with higher PC2 scores indicating shorter wings, shorter tails, and longer tarsi of weak flyers and flightless species. Last, the PC3 captures both variation in flight capacity and relative changes in beak length, with higher scores indicating shorter beaks relative to tail and wings. For example, species with high PC3 scores include several ibises and spoonbills (family Threskiornithidae), whereas examples of species with higher PC3 are the moa-nalo (goose-like ducks) in Hawaii (family Anatidae).

Visualizing this functional trait space for each archipelago (Fig. 2) suggests that many extinct species were morphologically distinctive compared to surviving (extant) native species. Specifically, extinct species tend to have larger body size (i.e., high PC1 scores) and lower flight capacity (i.e., higher PC2 scores). Examples of giant and flightless extinct birds include moa of New Zealand (order Dinornithiformes) and elephant birds of Madagascar (order Aepyornithiformes). Extinct

and flightless species also tended to have relatively short beaks (i.e., higher PC3), with examples including the abovementioned elephant birds, moa, and giant ducks as well as flightless passerines such as the long-legged bunting (*Emberiza alcoveri*) from the Canary Islands. In addition, some extinct species were instead volant and had relatively longer beaks, with examples including the radiation of Hawaiian honeycreepers (family Fringillidae).

To compare functional diversity across archipelagos for different scenarios, we quantified the volume of the three-dimensional functional trait space occupied by all the species present in each scenario, controlling for differences in species numbers (see Materials and Methods). We found that, across all archipelagos, native preextinction functional diversity was greater than the native postextinction functional diversity, even when correcting for the declining number of native species over time (Fig. 3 and table S3). Thus, native island bird communities show a disproportionate loss of functional diversity that is greater than expected on the basis of their loss of taxonomic diversity.

We next examined the effects of alien species on archipelago functional diversity by comparing how the functional diversity of current assemblages (i.e., native postextinction and alien species) compares with that of native preextinction assemblages (Fig. 3). The combined loss of extinct species and gain of established alien species leads to different patterns depending on the archipelago. In some cases (e.g., Hawaii, Canary Islands, and Saint Helena), including alien species leads to a significantly higher functional diversity than when only extant native species are considered (i.e., native postextinction and alien species versus native postextinction assemblages in Fig. 3). However, these gains do not compensate for the loss of functional diversity as a consequence of extinctions (i.e., native postextinction and alien species versus native preextinction assemblages in Fig. 3). These results remained unaltered when comparing the three scenarios at the level of islands rather than archipelagos, indicating that these losses of functional diversity have occurred among co-occurring species rather than simply due to the loss of functionally distinct species occurring on different islands within an archipelago (fig. S3).

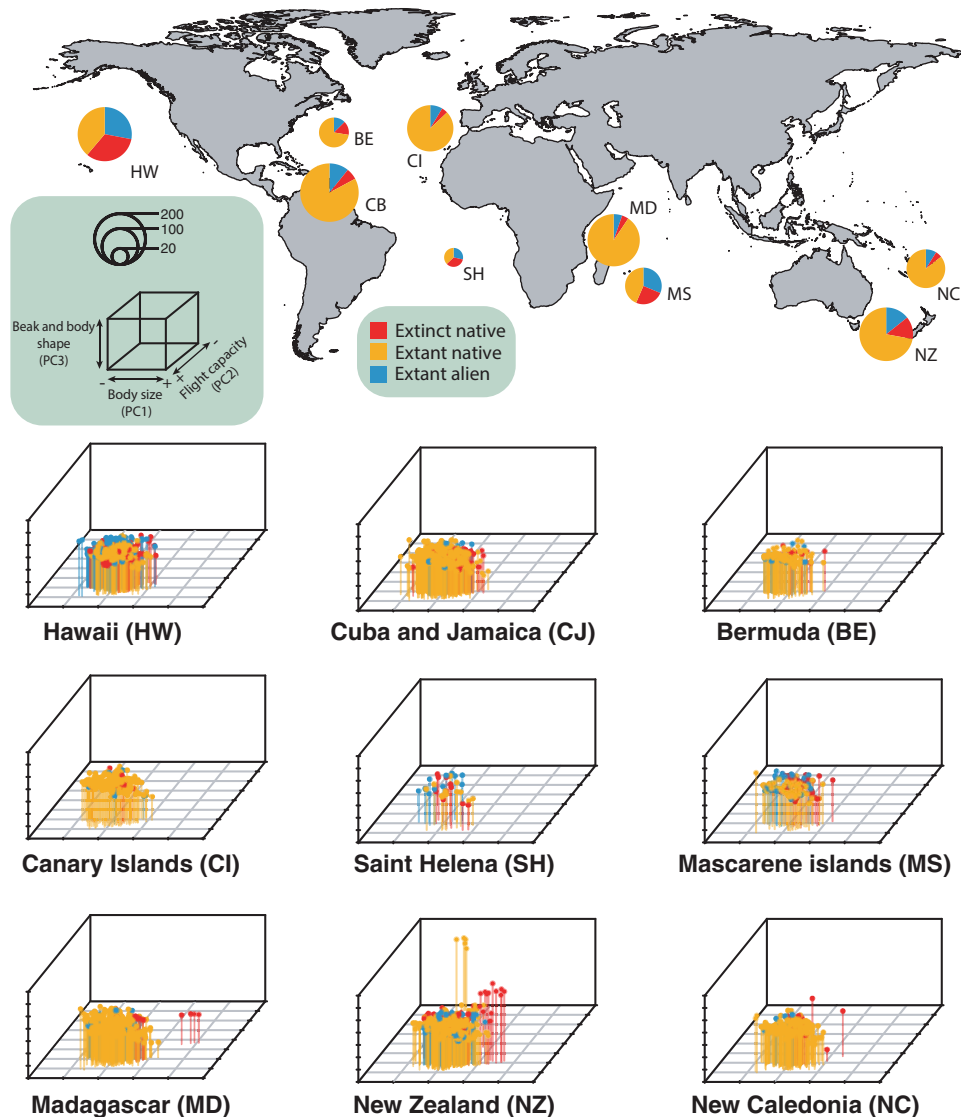
Last, we quantified the overlap among archipelagos to assess whether trait space across archipelagos is currently more similar than it was before extinctions and alien establishments occurred and thus whether archipelagos have become functionally more homogenous over time. Across the nine archipelagos, there is an increase in functional overlap after extinctions (i.e., native postextinction versus native preextinction scenarios), suggesting that each archipelago lost functionally distinct birds compared to the other archipelagos (Fig. 4B and table S4). This functional homogenization becomes even more evident when including established alien species (Fig. 4B and table S4). Despite initial differences in the level of functional overlap between each archipelago and the rest, anthropogenic impacts have consistently driven a strong increase in functional similarity between archipelagos (Fig. 4C and table S4). Results were unchanged when this analysis was rerun at the island level (fig. S4).

## DISCUSSION

Our results show that anthropogenic extinctions have caused a disproportionate loss of functional diversity in oceanic archipelagos. In addition, we found that established alien species have not filled the gap in functional diversity created by extinctions, although the number of extinct species is, in many cases, matched or even exceeded by

**Table 1. Number of reported extinct, extant, and alien species in nine archipelagos.** Native only includes extant native species; alien only includes introduced and successfully established species.

Archipelago	Extinct	Native (extant)	Alien (established)
Hawaii	80	111	95
Cuba and Jamaica	36	276	21
Bermuda	11	63	13
Saint Helena	10	12	12
Canary Islands	18	182	9
Madagascar	16	240	11
Mascarene Islands	41	57	33
New Zealand	40	202	38
New Caledonia	13	118	8



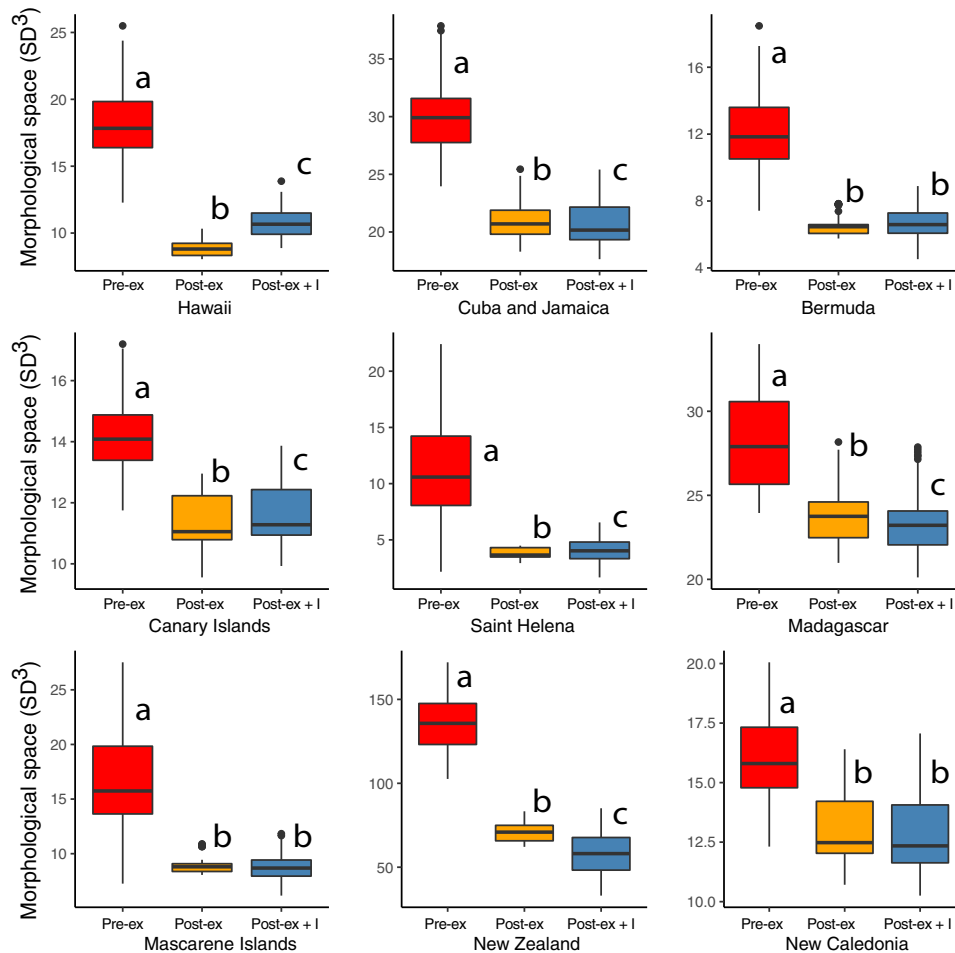
**Fig. 2. Functional space across archipelagos.** The map shows the percentage of species in each archipelago that are extinct (red), extant natives (yellow), and established aliens (blue). Cubes represent three-dimensional plots depicting the three principal morphological axes of variation from a PCA.

the number of alien species. Last, comparisons among archipelagos reveal a general trend of functional homogenization after the combined effects of avian extinctions and successful introductions, indicating that bird assemblages are becoming more functionally similar as a result of human impacts.

The pervasive signature of functional loss and homogenization among oceanic archipelagos reflects a general pattern of the Anthropocene. Similar outcomes have been reported in a range of taxa (24, 45, 46) in the context of recent environmental change, including habitat degradation (47), agricultural intensification (48), and urbanization (49, 50). However, earlier studies generally lacked information from both extinct and introduced taxa, making it difficult to determine the net effects of anthropogenic impacts. By compiling functional trait datasets for extinct, extant, and introduced species in island assemblages, we have clearly shown that anthropogenic

introductions can boost species richness to preextinction levels without compensating for the overall loss of functional diversity.

The role of anthropogenic extinction in reducing functional diversity is clearly linked to the nonrandom nature of these extinctions, with some trait combinations increasing vulnerability to anthropogenic threats such as hunting and habitat loss (11). A classic example is body size selectivity in mammals, where larger species, often termed megafauna, are more prone to extinction (14, 51). In birds, it has also been shown that large body size and flightlessness are associated with a higher extinction risk (38, 52, 53). We detect a similar pattern with many extinct birds in our sample characterized by large body size, low flight capacity (or flightlessness), and a relatively short and wide beak. Examples of this combination include the famous moa, elephant birds, and the radiation of flightless ducks on Hawaii. These features might be adaptations to grazing, as all these species



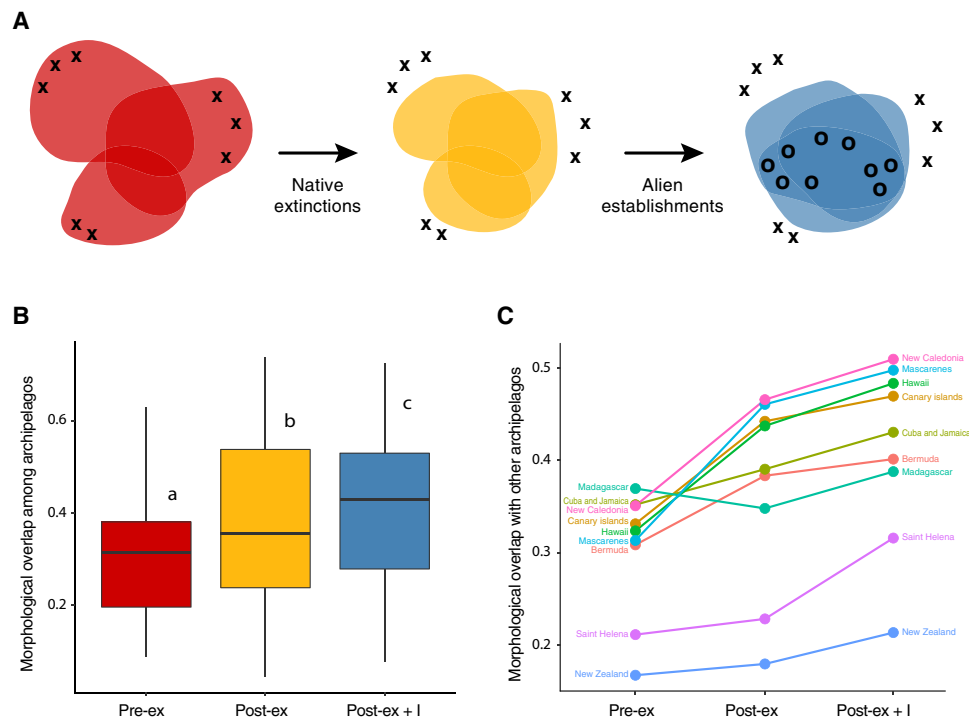
**Fig. 3. Functional diversity changes across archipelagos.** Three scenarios were compared in each archipelago: Native preextinction (Pre-ex), native postextinction (Post-ex), and postextinction and alien species introductions together (Post-ex + I), colored in red, yellow, and blue, respectively. Both Pre-ex and Post-ex + I assemblages were standardized to the sample size of the Post-ex assemblage. Units are shown as  $SD^3$  (according to the number of dimensions). Letters (a to c) indicate whether scenarios differed in a paired samples Wilcoxon tests (at  $P < 0.05$ ), with different letters representing significant differences between scenarios.

may have occupied an ungulate-like niche (32, 54, 55). Our analyses also suggest that other distinct niches were filled by extinct species, which, in total, are morphologically diverse and occupy distinct positions in functional space. Examples include smaller flightless forms, such as Lyall's wren from New Zealand (*Traversia lyalli*) and a flightless bunting from the Canary Islands (*E. alcoveri*). Although the exact ecological niche of these flightless passerines is uncertain, some authors suggest that they had a similar niche to small rodents that are absent from many oceanic islands (56). Flightless passerines on oceanic islands likely suffered from excessive predation after the introduction of invasive small mammals, such as rats and cats (31, 57). On the other hand, there are also some examples of extinct species with good flight ability and relatively long beaks, such as the Hawaiian honeycreepers (family Fringillidae). The loss of these distinct species further erased functional diversity and is in line with previous evidence that more specialized species are less tolerant to anthropogenic threats (58, 59).

In parallel with the extinction process, humans have also caused the introduction and establishment of many alien species on islands (5, 16). Across archipelagos, the number of established alien species

is strongly associated with the number of extinct species, potentially consistent with the idea that vacant niches have facilitated invasions (8) or that alien species have displaced ecologically similar residents (60). However, when comparing the original assemblage (i.e., before anthropogenic extinctions and introductions) with the current assemblage, we found that all archipelagos experienced a net functional diversity loss. These results suggest that some trait combinations of extinct bird species, possibly related to a distinct niche, have not been filled by alien birds (61) and suggest that processes other than niche filling and replacement might drive the association between the number of extinct and alien species. Several studies show that one of the best predictors of establishment success of alien species is the number of introduction attempts and the number of individuals being released (i.e., propagule pressure) (62, 63). Therefore, different degrees of human impacts might be the common cause explaining the association between the number of extinct and alien species. Because alien introductions are a relatively recent phenomenon (64), the different timing of human impacts (i.e., first human colonizations versus recent human impacts) might further explain additional differences in the ratios of extinct versus established alien species.





**Fig. 4. Functional homogenization across archipelagos.** Three scenarios were compared (red, Native preextinction; yellow, native postextinction; blue, postextinction and alien species introductions together). We visualize a representation of morphological space occupation among archipelagos using different polygons (**A**), where crosses (X) represent extinct species and circles (O) represent alien species. For each of these scenarios, we show the morphological overlap among archipelagos, for all pair comparisons (**B**) or for each archipelago compared to the others (**C**). Letters (a to c) indicate whether scenarios differed in a paired samples Wilcoxon tests (at  $P < 0.05$ ), with different letters representing significant differences between scenarios.

The combined effect of extinctions and introductions has led to functional homogenization of island assemblages. That is, species turnover related to anthropogenic impacts is increasing the functional similarity among archipelagos, suggesting that functionally distinct species are more prone to extinction, leading to the loss of taxa with distinct ecologies adapted to local conditions. This finding aligns with previous work showing that more phylogenetically and functionally distinct species tend to be most sensitive to human disturbance (35–37) and at greater potential risk of future extinction (59, 65). The loss and homogenization of functional diversity is concerning, as it may impair the functioning of ecosystems (66–68), particularly on islands where species richness and redundancy are lower and biotic interactions are more easily disrupted [e.g., (69)].

Unexpectedly, when we accounted for alien species established in current island assemblages, we found even stronger evidence of trait similarity and overlap among archipelagos. This is because alien species tend to occupy the center of functional space, where morphological traits are redundant both within and among archipelagos, leading to further functional homogenization in addition to that caused by extinctions. Regarding the debate on the possible contribution of alien species to ecosystem services (9, 10), our results suggest that various ecological roles filled by extinct native bird species seem to have not been replaced by alien species, with potential consequences for ecosystem functions such as frugivory and seed dispersal (70, 71). In addition, these results suggest that alien species may be competing with native extant species for similar resources, with potential future consequences for biodiversity loss (72).

Our analyses suggest that anthropogenic extinctions tend to remove functionally distinctive species from island ecosystems and that the ecological impacts of these losses are only partially offset by anthropogenic species introductions. These findings support calls to focus conservation efforts (36, 73) on preserving functionally distinct threatened species (65, 73), an important step toward minimizing further erosion of unique ecological functions that underpin the diversity and resilience of ecosystems. More generally, our study highlights how emerging global datasets of functional traits offer a tool for assessing the impacts of species turnover in assemblages, particularly when traits can be estimated from living organisms and the fossil record.

## MATERIALS AND METHODS

### Presence data

We selected nine archipelagos with good coverage of extinct species: Hawaii, Cuba and Jamaica, Bermuda, Saint Helena, Canary Islands, Madagascar, Mascarene Islands, New Caledonia, and New Zealand. We grouped archipelagos according to an existing classification (74), with some modifications. Specifically, we aggregated archipelagos that were closely related (e.g., Canary Islands with Madeira) and disaggregated larger archipelagos (i.e., Greater Antilles, where Cuba and Jamaica are treated as an archipelago, also including Cayman Islands). New Caledonia included both Grand Terre, Ile des Pines and Loyalty Islands, whereas New Zealand included North Island, South Island, and Stewart Island. The aggregation and disaggregation of archipelagos

were informed by hierarchical clustering based on a distance matrix between the island centroids and biogeographical (e.g., shared mainland) and ecological (e.g., shared species) similarities.

From these nine archipelagos, we collected a list of all extant species currently present (native and alien) from the *Handbook of the Birds of the World* checklists (75). Vagrant species were excluded from the lists, and we only included native birds (breeding and nonbreeding) and established alien birds. We complemented the information about alien species with the Global Avian Invasions Atlas (GAVIA) (5). We updated a small number of records from GAVIA to reflect more recent information about establishment success. We note that, in some cases, it might be challenging if the species is fully established, so our dataset could marginally overestimate the number of alien species in each archipelago. However, if this is the case, then the functional diversity of extant species (native + alien) might be even lower than the reported estimates, strengthening our claim that lost functional diversity by extinctions is not regained by species introductions. For extinct species, we used the complete list of known extinct birds, from which 251 species are found in the nine archipelagos included here. We also included 14 species that are globally extant but have been extirpated from one or more of the archipelagos. Since we only include anthropogenic extinctions (i.e., during Late Pleistocene and Holocene when the colonization of the various archipelagos took place), we assume that all extant native species were already present at the time of the extinctions and hence have co-occurred with the extinct fauna. The final list includes  $n = 1302$  species of native extinct, native extant, or alien-established species across the nine archipelagos (data file S1). For each archipelago where at least one species is confined to an island not connected to the main island at the last glacial maximum, we recorded species presence at the largest island on each of these archipelagos (i.e., Hawaii big island, Tenerife, Reunión, Cuba, and Grand Terre) (data file S2) to allow us to test whether our predictions hold at the island level. Our final list follows the *Handbook of the Birds of the World* and BirdLife International checklist of the birds of the world (76).

### Trait data

We obtained morphological data for all extant species ( $N = 10,845$  species) based on measurements taken from 63,945 individual birds, including both wild caught and museum specimens (29). To compare with these traits, we collected morphological data for 43 extinct species (data file S3). In both cases, we used measurements (in millimeters) of eight morphological traits, including four beak measurements (depth, width, length from culmen, and length from nares), two wing measurements (total wing chord and Kipp's distance), tarsus length, and tail length [for details of methods, see (29)]. For 212 extinct or extirpated species described from subfossils, we gathered available data for 22 linear skeletal measurements (data file S4), including three measures for each of the long bones (total length, proximal width, and distal width) and four beak measurements (length, depth, width, and length from nares) (see Fig. 1 for more details). These skeleton measurements were either collected from the species descriptions in the literature or measured in museum collections. We also gathered information about body mass (in grams) and scored species according to their flight ability (flightless = 0, weak flyer = 0.5, and volant = 1) based on (38). Last, to inform the imputation of missing data, we took skeletal measurements of 269 museum specimens including 152 extant species from 55 different bird families (data file S5) so that we had complete data for this

sample. The list of specimens measured for this study can be found in data file S6.

### Trait imputations

To complete the missing traits in our species list, we used Bayesian hierarchical probabilistic matrix factorization (BHPMF), implemented in R package BHPMF (77). This method uses a machine learning algorithm to impute missing entries. BHPMF is an extension of PMF that uses the taxonomic hierarchy of the data as a proxy for the phylogenetic signal in the traits. BHPMF has proven a robust approach that simultaneously uses the taxonomic trait signal and the correlation structure of the trait matrix (77). In our case, we used the complete trait matrix including all traits (eight skin measurements, 22 skeletal measures, body mass, and flight ability) of all extant species, as well as the extinct species from the target archipelagos. We then used three levels of taxonomic information (order, family, and genus) to infer trait gaps. As the imputation method requires that each species has at least one trait measure, for 15 species for which there were no data available, we included the average body size from their genus as a proxy of their body size (see table S5). To check whether the imputation technique was able to correctly impute skin measurements from skeleton measurements, we used the complete dataset of all morphological traits and subsequently removed all skin measurements of one species at a time and estimated them using the BHPMF method. For all eight skin measurements, observed versus predicted values had a high correlation ( $R^2 \sim 0.98$  to  $0.99$ ; fig. S5). To include imputation uncertainty in the analysis, we ran the imputation algorithm 10 times and used the 10 different datasets in the following analyses.

### Summarizing the variation in functional space

To quantify the functional diversity of birds in each archipelago, we selected the 10 traits with the lowest percentage of missing data. These were the eight skin measurements, body mass, and flight ability, with a completeness of 84, 80, and 96% of the species included here, respectively. In the case of the skin measurements and body mass, we log-transformed and rescaled to a mean of 0 and an SD of 1 before further analysis. Then, using the complete imputed dataset for the 10 selected traits (data files S7 to S16), we summarized trait variation with a PCA. We selected the first three PC axes, which accounted for more than 80% of variation in traits and allowed us to position each species in a three-dimensional space (fig. S2 and table S2). To better interpret the PC axes, we did a bootstrap test (iterations of sampling of species with replacement) to get significant loadings of PC scores, following Peres-Neto *et al.* (78), running 100 iterations for each of the 10 imputed trait datasets (table S2). Using the PCA loadings for each species and for each archipelago, we computed the volume of occupied trait space for three different assemblage phases and the overlap between these phases. The three phases were “native preextinction” (including extinct and native extant species), “native postextinction” (including only the extant native species), and “postextinction and alien species introductions” (including the extant native and alien species). The traits used for each species across the three scenarios are the same, so we assume that there are no morphological changes between scenarios (i.e., evolutionary shifts due to changes in interspecific competition).

### Functional diversity changes among scenarios

To estimate the volume of functional trait space of each scenario, we modeled the volume occupied by the pool of species formed by

the first three PC axes and computed the volume of functional space using the R package hypervolume, which estimates the shape and volume of high-dimensional objects using a machine learning algorithm (79). Because the occupied volume necessarily increases as new species are added (unless the added species is morphologically identical to an existing species), for each comparison, we standardized the volume to the scenario with the lower number of species (i.e., the native postextinction dataset) by subsampling the two other datasets for 10 permutations. For instance, when comparing the volumes in the native preextinction ( $N = 200$ ) and native postextinction ( $N = 121$ ) assemblages for Hawaii, for each permutation, we quantified the hypervolume of the current assemblage and a subsample of 121 species from the 200 species in the preextinction assemblage. To obtain the volumes, we used the “hypervolume\_svm” function. We repeated the calculations for 10 iterations (i.e., to account for variation in subsampling) and for the 10 different imputed trait datasets (see previous section), resulting in 100 samples for each analyzed metric. Following Pimiento *et al.* (80), we tested for differences between the three different scenarios using a Wilcoxon test, as data in some of the comparisons did not follow a normal distribution.

### Functional diversity overlaps among archipelagos

For each of the three scenarios (native preextinction, native postextinction, and postextinction and alien establishment), we calculated the functional overlap among all pairs of archipelagos, using the “hypervolume\_set” function from R package hypervolume. We then used the “hypervolume\_overlap\_statistics” function from the same package to compute the Jaccard similarity index, which quantifies the similarity between a pair of hypervolumes. This was calculated for all pairs of archipelagos for each of the three scenarios and repeated by each of 10 imputed datasets. Last, we used a paired samples Wilcoxon test to identify differences among scenarios. We used the paired version to incorporate the fact that two scenarios within the same archipelago are expected to be more similar than comparisons between scenarios from different archipelagos.

### SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <https://science.org/doi/10.1126/sciadv.abj5790>

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## Loss of functional diversity through anthropogenic extinctions of island birds is not offset by biotic invasions

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