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Combined effects of bird extinctions and introductions in oceanic islands: decreased functional diversity despite increased species richness

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ABSTRACT

Aim: We analyze the consequences of species extinctions and introductions on the functional diversity and composition of island bird assemblages. Specifically, we ask if introduced species have compensated the functional loss resulting from species extinctions.

Location: Seventy-four oceanic islands (>100 km²) in the Atlantic, Pacific and Indian Oceans.

Time period: Late Holocene.

Major taxa studied: Terrestrial and freshwater bird species.

Methods: We compiled a species list per island (extinct and extant, native and introduced), and then compiled traits per species. We used single-trait analyses to assess the effects of past species extinctions and introductions on functional composition. Then, we used probabilistic hypervolumes in trait space to calculate functional richness and evenness of original versus present avifaunas of each island (and net change), and to estimate how functional unique are extinct and introduced species.

Results: The net effects of extinctions and introductions were: an increase in average species richness per island (alpha diversity), yet a decline in diversity across all islands (gamma diversity); an average increase in

the prevalence of most functional traits, yet an average decline in functional richness and evenness, associated with the fact that extinct species were functionally more unique (when compared to extant natives) than introduced species.

Main conclusions: Introduced species are on average offsetting (and even surpassing) the losses of extinct species per island in terms of species richness, and they are increasing the prevalence of most functional traits. However, they are not compensating for the loss of functional richness due to extinctions. Current island bird assemblages are becoming functionally poorer, having lost unique species and being composed of functionally more redundant species. This is likely to have cascading repercussions on the functioning of island ecosystems. We highlight that taxonomic and functional biodiversity should be assessed simultaneously to understand the global impacts of human activities.

KEYWORDS

Biotic homogenization, birds, compositional turnover, exotic species, extinctions, functional composition, functional diversity, introductions, oceanic islands, probabilistic hypervolume

1 | INTRODUCTION

Human activities are profoundly changing the distribution of species worldwide at an alarming pace: the composition of communities is being altered both through the local or global disappearance of some species and the introduction and expansion of others (McKinney & Lockwood, 1999). Oceanic islands are among the most threatened ecosystems and their assemblages have been largely shaped by the history of human occupation: compared to continents, islands tend to have higher extinction rates by being more sensitive to habitat modification and biological invasion (Loehle & Eschenbach, 2011; Whittaker et al., 2017; Russell & Kueffer, 2019). Their discreteness, small size, simplified communities, unique biodiversity, and often recent human influence have transformed them into living laboratories remarkably useful to study the impacts of human activities and explore promising conservation strategies (Whittaker et al., 2017; Russell & Kueffer, 2019). In particular, birds have suffered a high proportion of extinctions on islands (Sax & Gaines, 2008), which affected mostly large, flightless and ground-nesting species with specialized diets (e.g. nectivores and insectivores; Boyer & Jetz, 2014). Consequently, on many islands, these non-random extinctions led to a disproportionate loss of functional diversity (Boyer, 2008; Boyer & Jetz, 2014; Sobral et al., 2016; Sayol et al., 2021), potentially causing a sharp decline in the variety of ecological functions provided by birds (e.g. Heinen et al., 2018) and ultimately affecting ecosystem functioning (Şekercioğlu et al., 2004; Sax & Gaines, 2008; Luck et al., 2012).

Although having been recently considered a fundamental question in ecology, conservation and island biogeography, it is yet unclear if introduced species can functionally replace the loss of natives (Patiño et al., 2017). Extinct and introduced bird species can have distinct functional roles, and therefore some functions once performed by extinct birds may have disappeared from some islands (Sobral et al., 2016). A recent study found that the loss of functional diversity through bird extinctions is not offset by the gain of functional diversity through bird introductions (Sayol et al., 2021). The authors showed that although introduced birds often equal or exceed the number of extinct birds, these appear to perform a narrower set of functional roles on oceanic islands. However, it remains uncertain how changes in functional diversity due to species extinctions and introductions translate into changes in function at the assemblage level. For example, while

the decline in the diversity of morphological traits associated with resource use (e.g. beak size and shape) implies a loss of overall function, it is not clear if it means the loss of specific functions (e.g. pollination or insect predation) because of the complexity of mapping functions across the trait space (Pigot et al., 2020).

Functional diversity is usually measured using species traits, under the assumption that these correlate to the species function in the ecosystem (Cadotte et al., 2011). A simple but seldom used measurement of functional diversity change is to assess the changes in functional composition. These changes can be calculated as the difference between the species lost and gained for each individual trait, and measured as absolute changes for categorical (number of species belonging to each trait class – e.g. nectivore class of trait diet) and quantitative traits (average value of all species - e.g. body mass), or as relative changes for categorical traits alone (proportion of species belonging to each trait class; Boyer & Jetz, 2014; Mouillot et al., 2014). In the past two decades, a multitude of mathematical approaches have been developed to estimate and visualize the functional diversity of assemblages as a measure of trait variation or multivariate trait differences within an assemblage (Cadotte et al., 2011; Mammola et al., 2021). These often follow the Hutchinsonian niche concept, relying on the position of species or individuals within a multidimensional space. Among these, the convex hull hypervolume is one of the most used despite some important limitations, such as the assumption that the multidimensional space is homogeneously occupied, making it extremely sensitive to outliers (Mammola & Cardoso, 2021; Mammola et al., 2021). To overcome this limitation, new methods have used probabilistic hypervolumes (Blonder et al., 2018), of which the most popular uses high-dimensional kernel density estimations to delineate the shape and volume of the multidimensional space (Carvalho & Cardoso 2020; Mammola & Cardoso, 2021). This density-based approach assumes a heterogeneous trait space, representing variations in point density within the multidimensional space and better reflecting the concept of niche by Hutchinson (Mammola et al., 2021). Point density is higher where more functionally similar species exist and are closer together within the multidimensional space. Thus, contrarily to other approaches where adding a species can only increase or maintain the occupied volume, in kernel density hypervolumes, adding a species may decrease the volume (i.e. functional richness), namely if the species is added to an area of the hypervolume already filled with other species (decreasing the average distance between points within the cloud).

Because many introduced birds are functionally redundant and most extinct birds were functionally unique (Sobral et al., 2016), many of the functional consequences of extinctions and introductions affect not only the overall volume and boundaries of the multidimensional space but also deeply reorganize its internal structure. Consequently, we expect that both functional richness and evenness will decrease in most oceanic islands following extinctions and introductions, and also that functional originality of extinct species will be higher than that of natives, whereas functional originality of introduced species will be lower. Moreover, as previously shown, both bird extinctions and introductions are non-random events (Boyer & Jetz, 2014), so we expect a severe decline, or even loss, of some important ecological functions provided by birds (e.g. seed dispersal; Heinen et al., 2018), which will most likely translate into drastic consequences for ecosystem functioning (e.g. regeneration of insular native forests; Şekercioğlu et al., 2004; Anderson et al., 2011).

Taking all this into account, our study aims to quantify the consequences of species extinctions and introductions on the functional diversity and composition of island bird assemblages. Focusing on 74 oceanic islands, we explore the changes in functional composition by analysing the species lost and gained in each individual trait, and calculate the changes in functional richness and evenness, as well as the functional originality of each species, using kernel density hypervolumes. Functional richness can show whether

introductions compensate for the amount of functional richness lost following extinctions, whereas functional evenness can show how extinctions and introductions reshape the distribution of species within the multidimensional space. Functional originality of species can show how unique is the position of a species within the multidimensional space. We expect to provide new insights on the link between the changes in taxonomic and functional diversity by evaluating the changes of each individual trait after species extinctions and introductions. By studying the changes of each individual trait, we provide clues on which traits appear to promote extinctions or introductions, shedding a light on how ecosystem functions could be affected in the future. For example, the loss of nectivore species and their replacement by granivores (i.e. seed predators) can disrupt well-established mutualistic plant-animal interactions, particularly through reduced pollination and seed dispersal (Caves et al., 2013; Carpenter et al., 2020), drastically impairing the future of insular native forests (Şekercioğlu et al., 2004). With this functional perspective, we aim to gain valuable insights into the ecology of island bird assemblages and thus understand how to maintain their remaining functional diversity.

2 | METHODS

2.1 | Island selection

We focused on the world's largest oceanic islands with more than 100 km², including single islands and also those belonging to archipelagos. 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 below and Table S1.1).

2.2 | Bird species database

We compiled a list of known breeding bird species for each island, including extinct, extirpated and established introduced species, following the taxonomy used by BirdLife International (Handbook of the Birds of the World & BirdLife International, 2018). Given our focus on the temporal changes in species composition within islands, we also included island-level extirpations. For simplicity, we use the terms 'extinction' and 'extinct' for both global and local extinctions.

We excluded marine birds, non-breeding migrants, occasional breeders, vagrant and accidental species, and focus on regularly breeding terrestrial and freshwater species, since these are the most dependent on island resources and also have particularly high rates of extinction and introduction on oceanic islands (del Hoyo et al., 2014). To obtain a complete list of bird species for each island, we identified extant breeding species, including introduced species, from Avibase (Lepage, 2018), HBW Alive (del Hoyo et al., 2014), IUCN Red List of Threatened Species (IUCN, 2020; Fig. S3.1) and regional field guides (Table S2.2). In particular, for introductions, we also used the Global Avian Invasions Atlas (Dyer et al., 2017a) and specific literature (Table S3.3).

We considered as extinct the native species classified as Extinct and Extinct in the Wild in the *IUCN Red List of Threatened Species* (IUCN, 2020), and as Extinct or Extirpated in *Avibase* (Lepage, 2018). To improve the list of extinct species and capture extinctions prior to 1500 AD, we analysed specific literature (Hume, 2017; Paleobiology Database, 2018; Fig. S3.2), and thoroughly reviewed extinction records for each target island (Table S3.4). Species classified as Probably Extinct in the literature (especially in Hume, 2017) and Critically

Endangered – Probably Extinct in the *IUCN Red List of Threatened Species* were carefully analysed and considered extinct only when the *IUCN Red List of Threatened Species* supported this claim. We only included extinct taxa if these had been identified to species level, which is often not possible from fossil or historical records. The final database comprised 759 species, including 214 extinct, 172 introduced and 445 extant natives (Table S1.1).

2.3 | Bird species traits

For each species, we gathered information on body mass, foraging time, diet, foraging strata, volancy and habitat (Table S3.5). These traits are commonly used in studies evaluating bird functional diversity and summarising the effects of species on ecological processes and on responses of communities to environmental change (Boyer, 2008; Luck et al., 2012; Sobral et al., 2016; Sayol et al., 2021).

For extant species, our main source of information regarding average body mass, foraging time ('diurnal' or 'nocturnal'), diet and foraging strata was the EltonTraits database (Wilman et al., 2014). For the 40 (out of 617) species missing from this database, we inferred traits from the closest species in the genus (Table S3.6). We treated average body mass both as a continuous variable, and as an ordinal trait, based on the 5-quantiles categories: 'very small', 'small', 'medium', 'large', and 'very large'. Regarding diet, we converted the information on the relative importance of each diet class in EltonTraits into six mutually exclusive binary classes: 'granivore', 'herbivore', 'frugivore', 'invertivore', 'carnivore', and 'omnivore'. In addition, to capture the unique nectar-feeding strategy, we created one binary class, 'nectivore', identifying all species dependent on nectar from Mohoidae, Meliphagidae, Trochilidae and Nectariniidae families. For foraging strata, we adapted the information on prevalence (i.e. time spent) from EltonTraits into seven binary classes: 'ground', 'understory', 'midhigh', 'canopy', 'aerial', 'water', and 'nonspecialized'. Information about flight ability (volancy) was extracted directly from Sayol et al. (2020). Information about habitat was obtained from the first level of classification of the IUCN Habitats Classification Scheme (IUCN, 2020), combined into 10 non-mutually exclusive binary classes: 'forest', 'savannah', 'shrubland', 'grassland', 'wetlands', 'desert', 'artificial aquatic habitats', 'marine habitats', 'artificial terrestrial habitats', and 'rocky and subterranean habitats'. The last three habitat classes combined IUCN habitat categories that had few and ecologically similar species, which we assumed to have similar responses to environmental variables.

For extinct bird species, we also used mostly EltonTraits to collect information on body mass, foraging time, diet and foraging strata (Wilman et al., 2014; Fig. S3.3). For missing species (96 out of 214) and traits, we explored additional references (Boyer, 2008; Sobral et al., 2016; Heinen et al., 2018; Crouch & Mason-Gamer, 2019; Case & Tarwater, 2020; IUCN, 2020; Sayol et al., 2020) (Fig. S3.3). Lastly, whenever information on a trait for a given species was still missing, we first attempted to derive it from descriptions of the species, or (if not possible) inferred it from the traits of the closest species in the genus (Appendix 4).

2.4 | Data analysis

Data processing and statistical analyses were done in R (v.4.0.4; R Core Team, 2021).

2.4.1 | Species compositional changes

We used species richness (alpha taxonomic diversity) to quantify the changes in species composition associated with bird species extinctions and introductions in each island. Then, we calculated: average loss, as the average number of extinctions per island; average gain, as the average number of introductions per island; and net change, as the difference between gains and losses (including 95% confidence intervals based on all 74 studied islands). We also calculated changes in the overall number of extinct and introduced species (gamma diversity), and the net change across all islands.

2.4.2 | Effects of bird extinctions and introductions on functional composition

For each island and for each categorical trait (body mass, foraging time, diet, foraging strata, volancy and habitat), we assessed how extinctions and introductions affected functional composition, i.e. the prevalence of species associated with each trait class at the assemblage level. We did this by calculating, for each trait class in each island: 'loss', as the number of extinct species; 'gain', as the number of introduced species; and 'net change', as the difference between gain and loss. We then averaged results across islands, to obtain the average gain, loss and net change of species per island for each trait class, as well as the respective 95% confidence intervals. We calculated averages by considering only islands where the trait class was represented by at least one species, either extant or extinct. The average values were considered to be statistically significant if the 95% confidence interval did not comprise zero.

The calculations described above were done using both the absolute number of species gained and lost, and their percentages to account for differences in the number of species between island. Thus, for each island, we divided the number of species lost or gained associated with each trait class by the total number of species in the original avifauna (i.e. pre-extinctions, including extant native and extinct species, but not introduced species). This allowed us to verify if gain and loss were affected by island species richness.

For analysis of body mass as a continuous trait, we estimated, for each island, loss as the average body mass of extinct species, gain as the average body mass of introduced species, and net change as the difference between gain and loss. We then obtained average results and respective 95% confidence intervals by averaging losses, gains and net changes across islands.

To understand if extinct and introduced species are a random subset of all analysed species, we ran a series of null model analyses, each one based on 9,999 iterations. We used a null model approach for all traits (categorical and continuous) to ensure consistency. The null distributions were slightly skewed (i.e., non-normal), so we followed a non-parametric method to estimate the standardised effect size, using `ses` function in 'BAT' package (Mammola & Cardoso, 2021). We ran a separate null model for body mass and each of the six categorical traits, by randomly sampling the number of extinct species ($n = 214$) from a species pool considering extinct and extant bird species ($n = 621$), and the number of introduced species ($n = 172$) from a species pool considering introduced and extant bird species ($n = 582$), and calculated either the number of species in the different trait classes or the mean body mass of species in this sample. We recognize that the species pool used for introduced species only includes island bird species which is a limitation, however, we are simply trying to understand if there is a bias in introduced species and not if there is an introduction filter. As such, the extinct or introduced species pool allows us to test if the observed losses or gains, respectively,

are different from what would be expected considering the extant species occurring on islands. For example, considering the categorical trait diet, if the standardised effect size for carnivore species is positive and statistically significant, it indicates that more carnivore species went extinct than would be expected considering the number of carnivore species across islands. Accordingly, the overall negative net change would be reflecting the proneness of carnivore birds to extinction.

2.4.3 | Effects of bird extinctions and introductions on functional diversity

For each island, we analysed how bird species extinctions and introductions affected functional diversity, using three measures based on probabilistic hypervolumes: functional richness (alpha functional diversity), functional originality of species (i.e. uniqueness within the assemblage) and functional evenness (Fig. S3.4). To calculate these measures, we built a trait space from a matrix composed of all analysed species and 10 traits derived from those used in previous analyses (Table 1 - more details on trait selectivity can be found in Appendix 5).

Table 1. Description of the 10 traits used to build the trait space.

Trait	Type	Description
Diurnal	Dichotomous	Diurnal (1), nocturnal (0)
Nectivore	Dichotomous	Nectivore (1), non-nectivore (0)
Water forager^a	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	Quantitative	Natural log-transformed body mass
Habitat specialization	Quantitative	Number of suitable habitats listed by IUCN
Volancy	Ordinal	Flightless (1), weak flyer (2), volant (3)
Terrestrial foraging strata^b	Ordinal	Ground (1), understory (2), midhigh (3), nonspecialized (3.5), canopy (4), aerial (5)

Abbreviation: IUCN, International Union for Conservation of Nature.

^aWater forager and terrestrial foraging strata are not mutually exclusive, meaning that a species can be considered, for example, both water forager (1) and ground (1), as with most Anatidae species.

^bWe considered nonspecialized birds, species that forage in most strata between ground and aerial, and thus attributed them the average value of 3.5.

We computed the pairwise functional distances between each pair of species using the Gower dissimilarity index, giving the same weight to each trait (range: 0 – 0.887), and then calculated the contribution of each trait to the resulting distance matrix, using respectively `dist.ktab` and `kdist.cor` in ‘ade4’ package (Table S3.7; Dray & Dufour, 2007). We analysed the distance matrix through a principal coordinate analysis (PCoA) with the Cailliez correction for negative eigenvalues to extract orthogonal axes for the hypervolume delineations, using the `pcoa` function in the ‘ape’ package (Paradis et al., 2004). To construct the trait space, we retained the first eight PCoA axes, which cumulatively explained 81.3% of the total variation (Fig. S3.5).

The trait space was constructed using a Gaussian kernel density estimator with a 95% bandwidth (Blonder et al., 2018). These kernel density hypervolumes were approximated to a cloud of species-based stochastic

points, which were positioned according to their traits in the multidimensional space. The 95% bandwidth means that hypervolumes represent 95% of this cloud density. The functional richness of the assemblage is estimated as the volume of the hypervolume delineated by the cloud of stochastic points (Fig. S3.4; Mammola et al., 2021). This approach assumes a heterogeneous trait space, representing variations in point density within the multidimensional space. Point density is higher where more functionally similar species exist and are closer together within the multidimensional space. Thus, adding a species may decrease functional richness, namely if the species is added to an area of the hypervolume already filled with other species, decreasing the average distance between points within the cloud.

Likewise to the taxonomic approach, we calculated the overall functional richness at two points in time: originally (i.e. including all native species, both extant and extinct); and presently (i.e. including extant native and introduced species) considering all islands (gamma diversity). For this purpose, we used the kernel.alpha function in the 'BAT' package (Cardoso et al., 2015; Mammola & Cardoso, 2021). The net change in functional richness was calculated as the difference between present and original functional richness. Then, we estimated the functional richness for each island, considering original and present avifaunas, using the kernel.alpha function in the 'BAT' package (Cardoso et al., 2015; Mammola & Cardoso, 2021). Also for each island, we calculated net change in functional richness as the difference between present and original functional richness.

Similarly, we evaluated the evenness of the total trait space for each island, considering original and present avifaunas, using kernel.evenness in 'BAT' package (Fig. S3.4; Mammola & Cardoso, 2021), and calculated net change as the difference between the two. Functional evenness of the assemblage is estimated as the overlap between the observed hypervolume and a theoretical, perfectly even hypervolume (Fig. S3.4). A high functional evenness indicates that the species are evenly distributed within the hypervolume. We then calculated average values of functional richness and evenness across islands, and respective 95% confidence intervals, for the original and the present avifaunas, and for the net change.

Finally, we evaluated the functional originality of each species (comparable to functional uniqueness) for each island, considering original and present avifaunas. Functional originality is the average dissimilarity between the species and a sample of random points within the boundaries of the hypervolume. Within each island, the sum of values across all species is equal to one. We estimated originality based on a 0.01 fraction of random points, using the kernel.originality function in the 'BAT' package (Fig. S3.4; Mammola & Cardoso, 2021). It is important to note that for each native species, we obtained two values of functional originality, one considering the original avifauna and another considering the present avifauna. For each island, we calculated the average functional originality of all extinct species and of all native species in the original avifauna, and the average functional originality of all introduced species and of all native species in the present avifauna. From these values, we estimated average values of originality for extinct and native species, and for introduced and native species across all islands, and respective 95% confidence intervals.

3 | RESULTS

Our database included 759 species in 2709 island populations, distributed across 74 oceanic islands (10 single islands and 64 belonging to 11 archipelagos; Table S1.1 and Fig. S3.6). Of these, 214 species and 280 populations were extinct, 172 species and 801 populations were introduced, and the remaining (445 species

and 1628 populations) were extant natives. Some species were introduced to an island but native to another, or extinct from one island while extant on another.

3.1 | Species compositional changes revealed by species richness

There was a net decrease in the total number of species (gamma diversity) across all islands, as there were more extinct than introduced species (Fig. S3.7). However, average species richness per island (alpha diversity) experienced a positive net change, since the average number of introduced species on each island was higher than the number of extinct species (Fig. S3.7 and S3.9, Table S3.8).

3.2 | Effects of species compositional changes on functional composition

We found a positive average net change in the prevalence of 23 out of 34 trait classes (Fig. 1 and Table S3.9 and S3.10), meaning that, for each of those trait classes, the average number of introduced species per island associated with the trait class was higher than that of extinct species. Conversely, net change was negative for seven traits classes and non-significant for five. Qualitatively similar results were obtained when correcting for islands' species richness (using percentages of species gained and lost), with only three additional traits classes having a non-significant net change (nocturnal, invertivore and nectivore; Fig. S3.8). We thus focus on absolute numbers of introduced/extinct species.

We observed a positive net change across all classes of body mass (Fig. 1), meaning that more species were introduced than extinct in each size category. However, the average body mass of extinct species was higher than that of introduced species (natural log-transformed average body mass = $5.241g \pm 0.284 > 4.513g \pm 0.125$, calculated across 52 and 73 islands, respectively), and there was a decrease in average body mass (-0.785 ± 0.348 , calculated across 74 islands; Table S3.9).

We also found a positive net change in the prevalence of diurnal species, granivores, herbivores, invertivores, omnivores, volant species, ground, understory, nonspecialized foragers, and in species that occur in each habitat class, except marine habitats. In contrast, we found a negative net change in the prevalence of carnivores, nectivores, canopy foragers, weak flyers, and flightless species. The only introduced nocturnal bird species was the barn owl, *Tyto alba*, in all the Hawaiian Islands.

Within 4 out of 6 groups of traits, the class with the highest net change (very large body mass, diurnal foraging, ground foraging and volant species) had both the largest loss and the largest gain (Fig. 1), suggesting that these classes are, overall, the most susceptible to changes in species composition. In contrast, the class with the highest net change for both diet and habitat (granivore and occurring in artificial terrestrial habitats) had the greatest gain but not the greatest loss.

Introductions added on average more novel trait classes than those that had been lost by extinctions. Indeed, for 19 trait classes, introduced species added novel trait classes to between 1 and 18 islands (column "+" in Fig. 1), while extinctions removed 12 trait classes between 1 and 22 islands, (column "-" in Fig. 1). Weak flyers and flightless birds were particularly prone to extinction and have disappeared from almost all islands where they used to occur (weak flyers: 9/9 islands, flightless: 22/23 islands - only species, the Campbell teal *Anas nesiotis*, remains in Campbell Island).

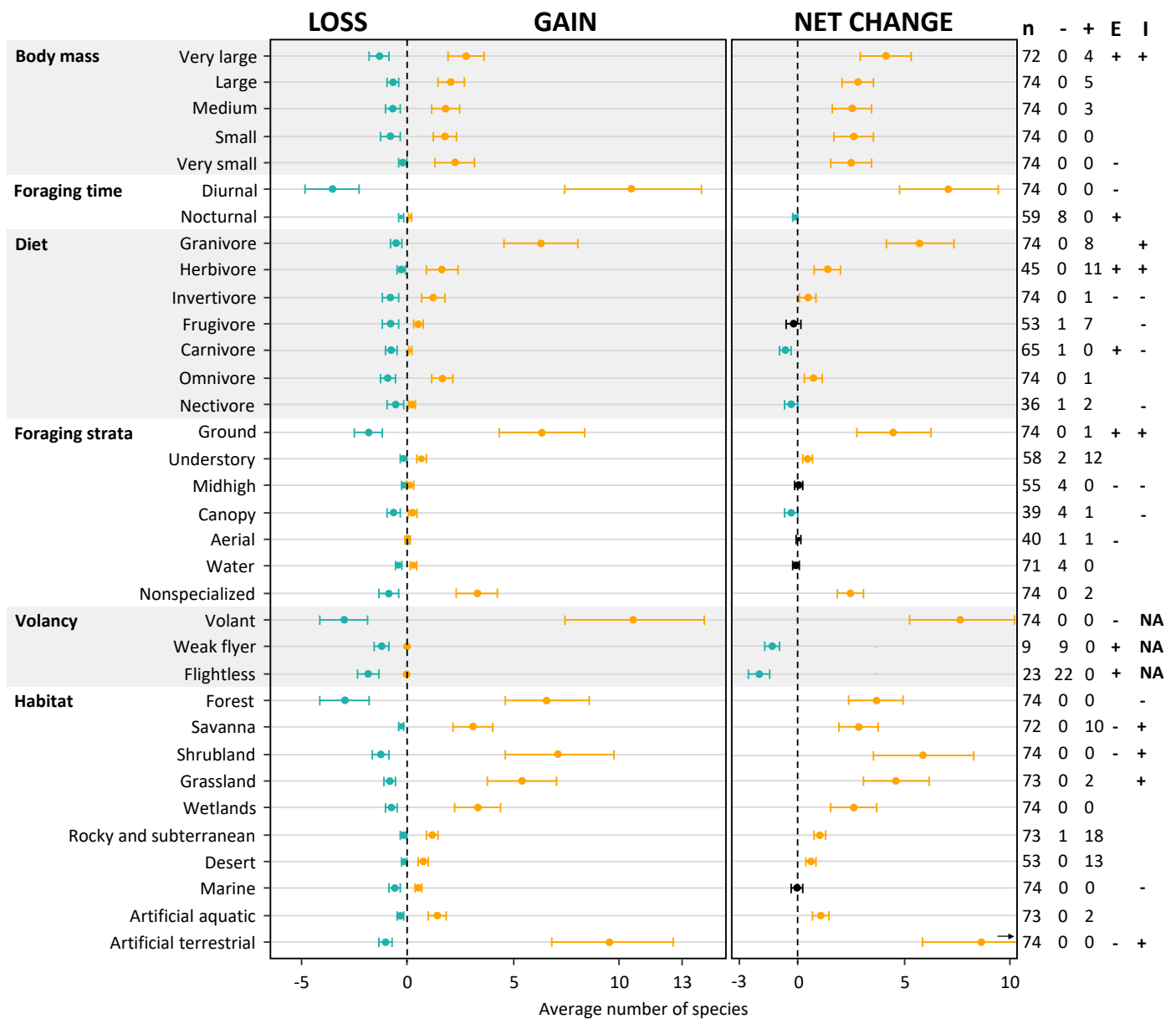


Figure 1. Effects of species compositional changes on island functional composition. For each trait class, we present the average number of species associated with the trait that were lost per island through extinctions (loss), gained through introductions (gain) and the difference between gain and loss (net change). Circles represent average values across islands, the horizontal bars the 95% confidence intervals. Non-significant values of net change (p -value > 0.05) are represented in black, whereas significant negative and positive values are represented in blue and yellow, respectively. Column 'n' represents the number of islands used in the calculations (i.e. with at least one species in the corresponding trait class), whereas columns '-' and '+' show respectively the number of islands that lost and gained species with a given trait. Columns 'E' and 'I' show only the significant results of the null models performed for each trait class for extinct and introduced species, respectively, where (+) and (-) indicate respectively if the standardized effect size was significantly larger or smaller than expected (NA shows that null models for volancy traits were not performed for introduced species). The arrow in the net change panel for the artificial terrestrial habitats indicates that the upper 95% confidence interval goes beyond the limits of the plot.

3.3 | Effects of species compositional changes on functional diversity

There was a net decrease in the overall functional richness (gamma diversity) considering all islands (before extinctions and introductions = 4.349×10^{-6} > after extinctions and introductions = 2.440×10^{-6}). Moreover, despite the net positive change in average species richness per island, we found a net negative change in average functional richness (Fig. 2a and S3.9, Table S3.8). The overall trends of taxonomic and functional richness only coincided (both decreasing or increasing) in 10 out of 74 islands (13.5% - Fig. S3.8). In 57 islands (77%), functional richness decreased despite increased species richness, while in three islands (Socorro, Floreana and San Cristóbal) there was an increase of functional richness despite a decrease in species richness (4.1%). Introduced species with traits mostly similar to extant natives were responsible for a reduced functional richness on 19 islands that had no extinctions.

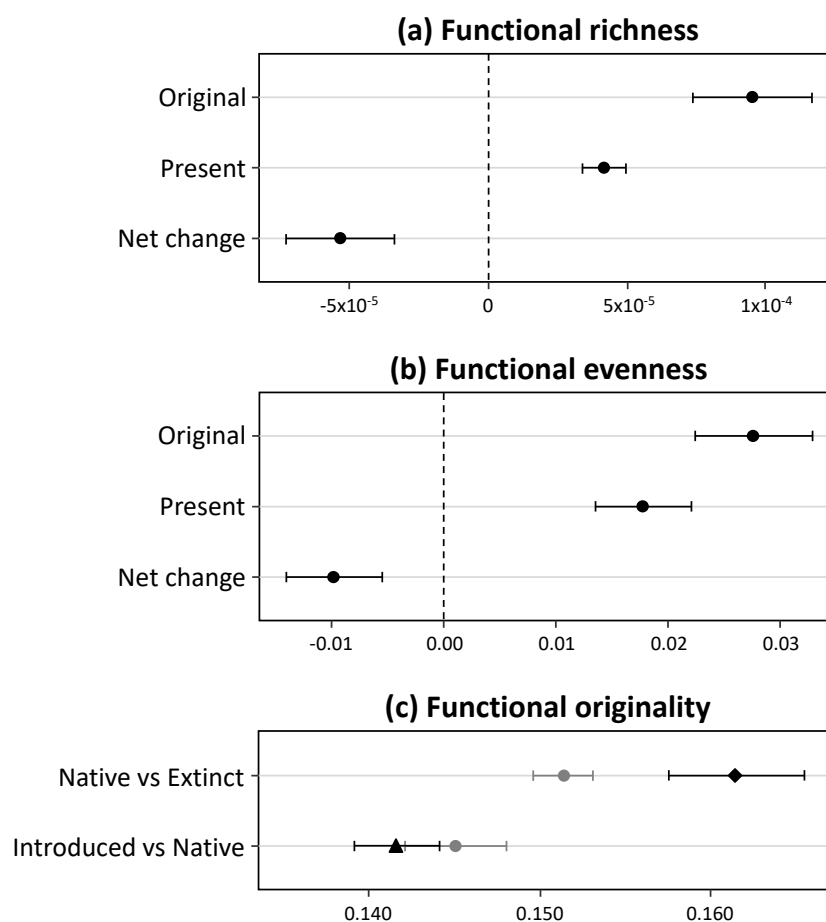


Figure 2. Effects of changes in the species composition of islands on three measures of functional diversity: (a) functional richness; (b) functional evenness; and (c) functional originality. Values presented are averages (circles) and 95% interval confidence estimates (horizontal bars) across islands. In (a) and (b), values correspond to the average volume of the trait space obtained from two probabilistic hypervolumes built for each of the 74 islands: one built with the species in original avifauna (extant native and extinct species), and another derived from the present avifauna (extant native and introduced species); net changes are the difference in volume between present and original: negative indicating a net loss in functional diversity; positive the opposite). In (c), we contrast the average functional originality of extant (circle) versus extinct (diamond) native species in the context of the original assemblages, and of introduced (triangle) versus extant native (circle) species in the context of the present assemblages. Average values were calculated, respectively, for the 52 islands with extinct species, the 73 with introduced species and the 74 with extant native species.

The species compositional changes also led to a negative net change in average functional evenness per island, indicating that the original avifauna was, on average, more evenly distributed across the trait space than the present avifauna (Fig. 2b and S3.9).

Compared with extant native species, the average functional originality of extinct species was significantly higher, whereas that of introduced species did not differ significantly (Fig. 2c and S3.10), meaning that extinct species have a more unique position within the trait space than either extant natives or introduced species.

4 | DISCUSSION

4.1 | Increase in local species richness despite net losses across islands

We found an increase in the average number of bird species per oceanic island (alpha diversity), even though overall species richness decreased across all islands (gamma diversity; Fig. S3.7). This apparent paradox reflects the fact that a smaller overall number of species were introduced, but to multiple islands (Blackburn et al., 2009; Dyer et al., 2017b), than those that went extinct, often endemic to single islands (Boyer, 2008; Boyer & Jetz, 2014). This turnover in community composition associated with extinctions and introductions is likely to increase the similarity between island bird assemblages (i.e., lowering beta diversity, promoting biotic homogenization; McKinney & Lockwood, 1999). These findings are in line with previous studies (e.g. Sobral et al., 2016; Sayol et al., 2021).

An incomplete knowledge of original island avifaunas creates uncertainty around these estimates of the magnitude of species compositional change. First, we are likely to underestimate the number of extinct species (Boehm & Cronk, 2021), given that new extinct species are still being described (e.g. Rheindt et al., 2020). Second, it is not always clear which species are native or introduced (Essl et al., 2018). It is important to keep in mind that these results are a snapshot in time; the number of introduced species is likely to continue to increase in many islands (Seebens et al., 2017). The total number of introductions may thus eventually surpass the total number of extinctions on islands.

4.2 | Changes in species composition lead to changes in functional composition

We found evidence of significant changes in the ecological and morphological traits of island bird assemblages, consistent with previous studies (e.g. Sax & Gaines, 2008). The higher average island species richness was accompanied by an increased prevalence of most traits (Fig. 1 and Table S3.10).

Very large bird species were the most unstable populations in oceanic islands, having simultaneously the greatest number of extinct and introduced species than expected by chance (Table S3.10). Moreover, the average body mass of island bird assemblages decreased because the average body mass of extinct species was higher than that of introduced species. This finding provides further support that large species are particularly prone to extinction (Boyer, 2008; Fromm & Meiri, 2021).

Regarding diet classes, the largest positive net gains in prevalence were by far of granivores, followed by herbivores, omnivores and invertivores. There was no significant net change for frugivores, while for carnivores and nectivores the changes were negative. Similar trends have been described before, especially

about the higher than expected number of granivore and herbivore introduced birds (Blackburn et al., 2009; Soares et al., 2021), and reflect a simplification of ecological networks; favouring lower positions in the trophic chain and unspecialized species, which are often better adapted to simplified anthropogenic landscapes, while hampering species that rely on more complex relationships, such as top positions in the trophic chain and nectarivory. These changes to island bird assemblages might disrupt well-established mutualistic plant-animal interactions and affect native plants, particularly through reduced pollination and seed dispersal (e.g. Caves et al., 2013; Carpenter et al., 2020). Herbivore birds introduced to islands that had no native browsers or grazers can greatly affect ecosystems, including by reducing food resources for pollinators and ultimately changing the phenotypic traits of plants related to pollination (e.g. flowering phenology, flower production, quantity and quality of nectar and pollen; Traveset & Richardson, 2006). Although having gained more species than lost, more herbivore species went extinct than expected, which corroborates recent studies that considered herbivore birds to be at high risk of extinction (Atwood et al., 2020). Conversely, carnivore birds have lost more species than expected by chance, having long been recognized as more extinct-prone due to their high diet specificity (Şekercioğlu et al., 2004). Their loss can have serious negative consequences to ecosystems (Şekercioğlu, 2006), such as the increase of undesirable species and disease outbreaks if predators and scavengers disappear, or the decline of guano and associated nutrients input if piscivores are lost (Şekercioğlu et al., 2004). Nectivore birds, which had a higher loss than expected, can also play a critical ecological role in the ecosystem, and their disappearance can have serious impacts on plant-bird mutualistic interactions, potentially impairing the future of insular native forests (Şekercioğlu et al., 2004; Boyer, 2008). This is particularly important in some island ecosystems that have few pollinators and many flowering plant species that depend exclusively on birds (Anderson et al., 2011).

Flightless and weak flying birds can have important and sometimes irreplaceable ecological roles in key ecosystem functions (Boyer & Jetz, 2014), such as seed dispersal, pollination and herbivory (e.g. Carpenter et al., 2020), but they have been completely eradicated from almost all islands (Sayol et al., 2020; Fromm & Meiri, 2021). This proneness to extinction was corroborated by their bigger loss than expected and is mostly a consequence of the high vulnerability to introduced mammalian predators, as most of these birds evolved in their absence (Milberg & Tyrberg, 1993; Russell & Kueffer, 2019). Competition with introduced mammals may also be important, as some of them occupy niches similar to those of flightless birds.

The prevalence of ground, understory, nonspecialized forager species and of species associated with all habitat classes (except marine) increased, while that the prevalence of canopy foragers decreased. Even though there was a clear net gain in the prevalence of forest species, even more than expected by chance, they were also the ones most subject to extinctions. The loss of forest-dependent birds is likely a direct consequence of the extreme anthropogenic deforestation that occurred on many oceanic islands (Pimm et al., 2006; Hume, 2017; Russell & Kueffer, 2019). In the Hawaiian Islands, for example, hunting and destruction of lowland forest by Polynesians extinguished many endemic forest birds, long before European arrival (Olson & James, 1982). Conversely, this replacement of island native forests by humanized habitats favoured the establishment of bird species that prefer open areas, which often have ground or unspecialized foraging strategies (Blackburn et al., 2009; Soares et al., 2021).

Overall, although islands have gained more bird species than they have lost, the functional composition of their avifaunas has changed markedly, potentially with important consequences to ecosystem functioning (e.g. Heinen et al., 2018).

4.3 | More species but with common traits, resulting in decreased functional diversity

The combined effect of bird extinctions and introductions resulted in a higher average island species richness (Fig. S3.7) and an increased prevalence of most traits (Fig. 1). However, this decreased average island functional richness (Fig. 2a), indicating that introduced species tend to be functionally closer to remaining native species than what extinct species were, resulting in a more compact cloud of points in the multidimensional trait space. In a hypothetical island assemblage with two species of birds, one frugivore and one granivore, the extinction of the frugivore would decrease functional richness, whereas the introduction of several granivore species would increase the prevalence of this trait class, but not functional diversity. The net result of extinctions and introductions in such an island would be a functionally impoverished assemblage, despite the higher prevalence of granivores. Accordingly, we also observed a decrease of assemblage functional evenness (Fig. 2b) and found that, whereas extinct species were functionally more unique than those that persist, introduced species were by contrast functionally less unique (Fig. 2c). The non-random extinction and introduction of bird species was already known to impair the functional diversity of island bird assemblages (Boyer & Jetz, 2014), since introduced species do not compensate for the functional roles of extinct species (Sobral et al., 2016; Sayol et al., 2021). Moreover, the overall decrease in functional richness considering all islands also suggests that island bird assemblages might be becoming functionally homogenized (lower functional beta diversity). Recent studies have shown that the introduction of functionally similar species is promoting functional homogenization of native bird assemblages on oceanic archipelagos (Sobral et al., 2016; Sayol et al., 2021).

Islands are well-known for their high levels of endemism, unique functional traits and peculiar evolutionary patterns (Whittaker et al., 2017; Russel & Kueffer, 2019). Unfortunately, this uniqueness also makes insular species prone to anthropogenic extinctions (Hume, 2017), and their functions more difficult to replace (Boyer & Jetz, 2014). Introduced species tend to have specific ecological niches and prefer human-modified landscapes (Lee et al., 2010; Soares et al., 2021), thus it should not come as a surprise that they do not compensate for the lost functional diversity. However, more species with similar traits to the native bird species are being introduced to islands as a result of new sources in the bird trade market (more Neotropical bird species; Dyer et al., 2017b). These novel introductions appear to be better functional substitutes of extinct species and, most likely, have a great potential to outcompete native species and further push these assemblages towards a functional collapse (Soares et al., 2021).

4.4 | Preserving the original functional diversity

We showed that a gain of species does not necessarily imply a gain in functional diversity, illustrating why these two facets of biodiversity should be assessed simultaneously to understand the impacts of human activities on biodiversity and ecosystem functioning. This mismatch between taxonomic, functional and even phylogenetic diversity has been observed across multiple different taxa (Brum et al., 2017), and has challenged the use of taxonomic diversity as a surrogate of functional diversity (Devictor et al., 2010). Traditionally, global conservation efforts focused on protecting species or sites that have high species richness, inadvertently underrepresenting other facets of biodiversity, such as functional diversity (Cadotte & Tucker, 2018). The non-linear and often negative relationship, as in oceanic island birds, between taxonomic and functional diversity calls for the prioritized protection of functionally unique species to maintain functional diversity. Such a line

of action is also key to ensure that functional redundancy is kept, since it allows preserving ecosystem functions under further, and unfortunate, species loss.

In order to maintain functional diversity, we must prevent further loss of native ecosystems because their functioning depends on complex and irreplaceable ecological interactions (Aslan et al., 2013; Carpenter et al., 2020; Carmona et al., 2021). We also must avoid new introductions, especially of species that might affect species that perform unique functional roles, either through predation (Milberg & Tyrberg, 1993; Sax & Gaines, 2008; Loehle & Eschenbach, 2011), competition (Soares et al. 2021), or the disruption of mutualistic interactions (Caves et al., 2013; Carpenter et al., 2020). Lastly, we need to protect native species, giving particular attention to those that have unique functional traits. Many insular bird species often have characteristics considered to be adaptations to island life, such as body size changes (gigantism and dwarfism), loss of predator avoidance, flightlessness and loss of dispersal powers, naïveté toward predators and diminished clutch size (Whittaker et al., 2017; Russell & Kueffer, 2019; Sayol et al., 2020). We found that some of these characteristics have already disappeared from most islands where the species used to occur (e.g. weak flyers and flightless birds), or have drastically decreased (e.g. carnivores, nectivores, very large-bodied birds, forest and canopy foragers, and birds occurring in forests). Protecting these species known to be unique to islands is key to preserve the original functional diversity of island bird assemblages.

Functionally unique species have recently been considered key for effective conservation because they represent distinct ecological strategies and often have a disproportionately high extinction risk (Griffin et al., 2020; Carmona et al., 2021). However, in order to preserve the global diversity of ecological strategies, conservation efforts have to integrate complementary metrics, such as functional richness and functional uniqueness at multiple scales (Cooke et al., 2020). Many shortcomings still impair this integration, notably the lack of traits and distribution data for most taxa. Our work provides a framework using a density-based approach that allows capturing changes in functional diversity that do not only affect the overall volume and boundaries of the multidimensional space but also its internal structure. This framework involves the estimation of three well-known indices, functional richness, functional evenness and species functional originality (comparable to functional uniqueness), which can be explored at multiple scales, and can be applied to other taxa and other drivers of biodiversity change.

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DATA AVAILABILITY STATEMENT All data supporting the results present in the paper are archived in figshare and should be available after the acceptance of the paper. These data include the species per trait matrix and the sites per species matrix. The current link to the figshare repository is the following: <https://doi.org/10.6084/m9.figshare.16782697.v1>

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website (<https://doi.org/10.1111/geb.13494>).

Appendix S1: [geb13494-sup-0001-AppendixS1.xlsx](#) - Excel 2007 spreadsheet , 24.1 KB

- Table S1.1 List of the 74 oceanic islands considered for analyses.

Appendix S2: [geb13494-sup-0002-AppendixS2.xlsx](#) - Excel 2007 spreadsheet , 22 KB

- Table S2.2 List of the regional field guides used to curate the bird species database.

Appendix S3: [geb13494-sup-0003-AppendixS3.docx](#) - Word 2007 document , 1.6 MB

- Table S3.3 Species that were reclassified as native or introduced in our database.
- Table S3.4 List of references of scientific papers used to find extinct and extirpated bird species.
- Table S3.5 Traits used to evaluate changes in functional composition.
- Table S3.6 Extant bird species absent from the EltonTraits database and corresponding sister species.
- Table S3.7 Contribution of each trait to the global distance matrix.
- Table S3.8 Global change in island bird assemblages: total number of species, species richness and functional diversity metrics based on hypervolumes - functional richness, average functional originality and functional evenness.
- Table S3.9 Average number of species belonging to each trait class and average body mass are represented for loss (extinct species), gain (introduced species) and net change (difference between gain and loss).
- Table S3.10 Standard effective sizes and *p*-values from the null model analyses based on functional traits for extinct and introduced species.
- Figure S3.1. Flow chart describing the decisions made to compile information on extant island bird species.

- Figure S3.2 Flow chart describing the decisions made to compile information on extinct island bird species.
- Figure S3.3 Flow chart describing the decisions made to compile information on the traits of the extinct species.
- Figure S3.4 Graphical representation of (a) functional richness, (b) functional originality of each species and (c) functional evenness based on the probabilistic hypervolume approach (Adapted from Mammola & Cardoso, 2021).
- Figure S3.5 Response variables projected as in PCA with scaling 1.
- Figure S3.6 Location of all analysed islands that after bird extinctions and introductions had a positive net change in species richness, a negative net change and no net change.
- Figure S.7 Total number of extinct and introduced species, and net change (introduced minus extinct) when considering (a) the total number of species across all islands and (b) the average number of species per island.
- Figure S3.8 Effects of species compositional changes on island functional composition.
- Figure S3.9 Net change values per island: species richness, functional richness and functional evenness.
- Figure S3.10 Functional originality of extinct and extant native species in the original assemblage of each island, and of extant native and introduced species in the present assemblage of each island.

Appendix S4: [geb13494-sup-0004-AppendixS4.docx](#) - Word 2007 document , 128.4 KB

- Traits of extinct bird species

Appendix S5: [geb13494-sup-0005-AppendixS5.docx](#) - Word 2007 document , 61 KB

- Best combination of traits
- Principal Component Analysis