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

3 Loss of island functional diversity

4 **Abstract**

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

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

9 Time period: Late Holocene.

10 Major taxa studied: Terrestrial and freshwater bird species.

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

17 Results: The net effects of extinctions and introductions were: an increase in average species richness
18 per island (alpha diversity), yet a decline in diversity across all islands (gamma diversity); an average
19 increase in the prevalence of most functional traits, yet an average decline in functional richness and
20 evenness, associated with the fact that extinct species were functionally more unique (when
21 compared to extant natives) than introduced species.

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

29

30 **Keywords**

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

33

34 **1. Introduction**

35 Human activities are profoundly changing the distribution of species worldwide at an alarming pace:
36 the composition of communities is being altered both through the local or global disappearance of
37 some species and the introduction and expansion of others (McKinney & Lockwood, 1999). Oceanic
38 islands are among the most threatened ecosystems and their assemblages have been largely shaped
39 by the history of human occupation: compared to continents, islands tend to have higher extinction
40 rates by being more sensitive to habitat modification and biological invasion (Loehle & Eschenbach,
41 2011; Whittaker et al., 2017; Russell & Kueffer, 2019). Their discreteness, small size, simplified
42 communities, unique biodiversity, and often recent human influence have transformed them into
43 living laboratories remarkably useful to study the impacts of human activities and explore promising
44 conservation strategies (Whittaker et al., 2017; Russell & Kueffer, 2019). In particular, birds have
45 suffered a high proportion of extinctions on islands (Sax & Gaines, 2008), which affected mostly
46 large, flightless and ground-nesting species with specialized diets (e.g. nectivores and insectivores;
47 Boyer & Jetz, 2014). Consequently, on many islands, these non-random extinctions led to a
48 disproportionate loss of functional diversity (Boyer, 2008; Boyer & Jetz, 2014; Sobral et al., 2016;
49 Sayol et al., 2021), potentially causing a sharp decline in the variety of ecological functions provided
50 by birds (e.g. Heinen et al., 2018) and ultimately affecting ecosystem functioning (Şekercioğlu et al.,
51 2004; Sax & Gaines, 2008; Luck et al., 2012).

52 Although having been recently considered a fundamental question in ecology, conservation and
53 island biogeography, it is yet unclear if introduced species can functionally replace the loss of natives
54 (Patiño et al., 2017). Extinct and introduced bird species can have distinct functional roles, and
55 therefore some functions once performed by extinct birds may have disappeared from some islands
56 (Sobral et al., 2016). A recent study found that the loss of functional diversity through bird
57 extinctions is not offset by the gain of functional diversity through bird introductions (Sayol et al.,
58 2021). The authors showed that although introduced birds often equal or exceed the number of
59 extinct birds, these appear to perform a narrower set of functional roles on oceanic islands.
60 However, it remains uncertain how changes in functional diversity due to species extinctions and
61 introductions translate into changes in function at the assemblage level. For example, while the
62 decline in the diversity of morphological traits associated with resource use (e.g. beak size and

63 shape) implies a loss of overall function, it is not clear if it means the loss of specific functions (e.g.
64 pollination or insect predation) because of the complexity of mapping functions across the trait space
65 (Pigot et al., 2020).

66 Functional diversity is usually measured using species traits, under the assumption that these
67 correlate to the species function in the ecosystem (Cadotte et al., 2011). A simple but seldom used
68 measurement of functional diversity change is to assess the changes in functional composition. These
69 changes can be calculated as the difference between the species lost and gained for each individual
70 trait, and measured as absolute changes for categorical (number of species belonging to each trait
71 class – e.g. nectivore class of trait diet) and quantitative traits (average value of all species - e.g. body
72 mass), or as relative changes for categorical traits alone (proportion of species belonging to each trait
73 class; Boyer & Jetz, 2014; Mouillot et al., 2014). In the past two decades, a multitude of mathematical
74 approaches have been developed to estimate and visualize the functional diversity of assemblages as
75 a measure of trait variation or multivariate trait differences within an assemblage (Cadotte et al.,
76 2011; Mammola et al., 2021). These often follow the Hutchinsonian niche concept, relying on the
77 position of species or individuals within a multidimensional space. Among these, the convex hull
78 hypervolume is one of the most used despite some important limitations, such as the assumption
79 that the multidimensional space is homogeneously occupied, making it extremely sensitive to outliers
80 (Mammola & Cardoso, 2021; Mammola et al., 2021). To overcome this limitation, new methods have
81 used probabilistic hypervolumes (Blonder et al., 2018), of which the most popular uses high-
82 dimensional kernel density estimations to delineate the shape and volume of the multidimensional
83 space (Carvalho & Cardoso 2020; Mammola & Cardoso, 2021). This density-based approach assumes
84 a heterogeneous trait space, representing variations in point density within the multidimensional
85 space and better reflecting the concept of niche by Hutchinson (Mammola et al., 2021). Point density
86 is higher where more functionally similar species exist and are closer together within the
87 multidimensional space. Thus, contrarily to other approaches where adding a species can only
88 increase or maintain the occupied volume, in kernel density hypervolumes, adding a species may
89 decrease the volume (i.e. functional richness), namely if the species is added to an area of the
90 hypervolume already filled with other species (decreasing the average distance between points
91 within the cloud).

92 Because many introduced birds are functionally redundant and most extinct birds were functionally
93 unique (Sobral et al., 2016), many of the functional consequences of extinctions and introductions
94 affect not only the overall volume and boundaries of the multidimensional space but also deeply
95 reorganize its internal structure. Consequently, we expect that both functional richness and evenness
96 will decrease in most oceanic islands following extinctions and introductions, and also that functional

97 originality of extinct species will be higher than that of natives, whereas functional originality of
98 introduced species will be lower. Moreover, as previously shown, both bird extinctions and
99 introductions are non-random events (Boyer & Jetz, 2014), so we expect a severe decline, or even
100 loss, of some important ecological functions provided by birds (e.g. seed dispersal; Heinen et al.,
101 2018), which will most likely translate into drastic consequences for ecosystem functioning (e.g.
102 regeneration of insular native forests; Şekercioğlu et al., 2004; Anderson et al., 2011).

103 Taking all this into account, our study aims to quantify the consequences of species extinctions and
104 introductions on the functional diversity and composition of island bird assemblages. Focusing on 74
105 oceanic islands, we explore the changes in functional composition by analysing the species lost and
106 gained in each individual trait, and calculate the changes in functional richness and evenness, as well
107 as the functional originality of each species, using kernel density hypervolumes. Functional richness
108 can show whether introductions compensate for the amount of functional richness lost following
109 extinctions, whereas functional evenness can show how extinctions and introductions reshape the
110 distribution of species within the multidimensional space. Functional originality of species can show
111 how unique is the position of a species within the multidimensional space. We expect to provide new
112 insights on the link between the changes in taxonomic and functional diversity by evaluating the
113 changes of each individual trait after species extinctions and introductions. By studying the changes
114 of each individual trait, we provide clues on which traits appear to promote extinctions or
115 introductions, shedding a light on how ecosystem functions could be affected in the future. For
116 example, the loss of nectivore species and their replacement by granivores (i.e. seed predators) can
117 disrupt well-established mutualistic plant-animal interactions, particularly through reduced
118 pollination and seed dispersal (Caves et al., 2013; Carpenter et al., 2020), drastically impairing the
119 future of insular native forests (Şekercioğlu et al., 2004). With this functional perspective, we aim to
120 gain valuable insights into the ecology of island bird assemblages and thus understand how to
121 maintain their remaining functional diversity.

122 **2. Methods**

123 **2.1. Island selection**

124 We focused on the world's largest oceanic islands with more than 100 km², including single islands
125 and also those belonging to archipelagos. From an initial list of 87 islands (Weigelt et al., 2015), we
126 excluded 13 for which we were unable to obtain a species checklist or that do not have terrestrial or
127 freshwater breeding bird species (see below and Table S1.1).

128 **2.2. Bird species database**

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

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

142 We considered as extinct the native species classified as Extinct and Extinct in the Wild in the *IUCN*
143 *Red List of Threatened Species* (IUCN, 2020), and as Extinct or Extirpated in *Avibase* (Lepage, 2018).
144 To improve the list of extinct species and capture extinctions prior to 1500 AD, we analysed specific
145 literature (Hume, 2017; Paleobiology Database, 2018; Fig. S3.2), and thoroughly reviewed extinction
146 records for each target island (Table S3.4). Species classified as Probably Extinct in the literature
147 (especially in Hume, 2017) and Critically Endangered – Probably Extinct in the *IUCN Red List of*
148 *Threatened Species* were carefully analysed and considered extinct only when the *IUCN Red List of*
149 *Threatened Species* supported this claim. We only included extinct taxa if these had been identified
150 to species level, which is often not possible from fossil or historical records. The final database
151 comprised 759 species, including 214 extinct, 172 introduced and 445 extant natives (Table S1.1).

152 **2.3. Bird species traits**

153 For each species, we gathered information on body mass, foraging time, diet, foraging strata, volancy
154 and habitat (Table S3.5). These traits are commonly used in studies evaluating bird functional
155 diversity and summarising the effects of species on ecological processes and on responses of
156 communities to environmental change (Boyer, 2008; Luck et al., 2012; Sobral et al., 2016; Sayol et al.,
157 2021).

158 For extant species, our main source of information regarding average body mass, foraging time
159 (‘diurnal’ or ‘nocturnal’), diet and foraging strata was the EltonTraits database (Wilman et al., 2014).
160 For the 40 (out of 617) species missing from this database, we inferred traits from the closest species
161 in the genus (Table S3.6). We treated average body mass both as a continuous variable, and as an

162 ordinal trait, based on the 5-quantiles categories: 'very small', 'small', 'medium', 'large', and 'very
163 large'. Regarding diet, we converted the information on the relative importance of each diet class in
164 EltonTraits into six mutually exclusive binary classes: 'granivore', 'herbivore', 'frugivore', 'invertivore',
165 'carnivore', and 'omnivore'. In addition, to capture the unique nectar-feeding strategy, we created
166 one binary class, 'nectivore', identifying all species dependent on nectar from Mohoidae,
167 Meliphagidae, Trochilidae and Nectariniidae families. For foraging strata, we adapted the
168 information on prevalence (i.e. time spent) from EltonTraits into seven binary classes: 'ground',
169 'understory', 'midhigh', 'canopy', 'aerial', 'water', and 'nonspecialized'. Information about flight
170 ability (volancy) was extracted directly from Sayol et al. (2020). Information about habitat was
171 obtained from the first level of classification of the IUCN Habitats Classification Scheme (IUCN, 2020),
172 combined into 10 non-mutually exclusive binary classes: 'forest', 'savannah', 'shrubland', 'grassland',
173 'wetlands', 'desert', 'artificial aquatic habitats', 'marine habitats', 'artificial terrestrial habitats', and
174 'rocky and subterranean habitats'. The last three habitat classes combined IUCN habitat categories
175 that had few and ecologically similar species, which we assumed to have similar responses to
176 environmental variables.

177 For extinct bird species, we also used mostly *EltonTraits* to collect information on body mass,
178 foraging time, diet and foraging strata (Wilman et al., 2014; Fig. S3.3). For missing species (96 out of
179 214) and traits, we explored additional references (Boyer, 2008; Sobral et al., 2016; Heinen et al.,
180 2018; Crouch & Mason-Gamer, 2019; Case & Tarwater, 2020; IUCN, 2020; Sayol et al., 2020) (Fig.
181 S3.3). Lastly, whenever information on a trait for a given species was still missing, we first attempted
182 to derive it from descriptions of the species, or (if not possible) inferred it from the traits of the
183 closest species in the genus (Appendix 4).

184 **2.4. Data analysis**

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

186 **2.4.1. Species compositional changes**

187 We used species richness (alpha taxonomic diversity) to quantify the changes in species composition
188 associated with bird species extinctions and introductions in each island. Then, we calculated:
189 average loss, as the average number of extinctions per island; average gain, as the average number
190 of introductions per island; and net change, as the difference between gains and losses (including
191 95% confidence intervals based on all 74 studied islands). We also calculated changes in the overall
192 number of extinct and introduced species (gamma diversity), and the net change across all islands.

193 **2.4.2. Effects of bird extinctions and introductions on functional composition**

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

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

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

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

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

233 **2.4.3. Effects of bird extinctions and introductions on functional diversity**

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

240 (insert Table 1 here)

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

249 The trait space was constructed using a Gaussian kernel density estimator with a 95% bandwidth
250 (Blonder et al., 2018). These kernel density hypervolumes were approximated to a cloud of species-
251 based stochastic points, which were positioned according to their traits in the multidimensional
252 space. The 95% bandwidth means that hypervolumes represent 95% of this cloud density. The
253 functional richness of the assemblage is estimated as the volume of the hypervolume delineated by
254 the cloud of stochastic points (Fig. S3.4; Mammola et al., 2021). This approach assumes a
255 heterogeneous trait space, representing variations in point density within the multidimensional
256 space. Point density is higher where more functionally similar species exist and are closer together
257 within the multidimensional space. Thus, adding a species may decrease functional richness, namely
258 if the species is added to an area of the hypervolume already filled with other species, decreasing the
259 average distance between points within the cloud.

260 Likewise to the taxonomic approach, we calculated the overall functional richness at two points in
261 time: originally (i.e. including all native species, both extant and extinct); and presently (i.e. including
262 extant native and introduced species) considering all islands (gamma diversity). For this purpose, we
263 used the kernel.alpha function in the 'BAT' package (Cardoso et al., 2015; Mammola & Cardoso,
264 2021). The net change in functional richness was calculated as the difference between present and
265 original functional richness. Then, we estimated the functional richness for each island, considering
266 original and present avifaunas, using the kernel.alpha function in the 'BAT' package (Cardoso et al.,
267 2015; Mammola & Cardoso, 2021). Also for each island, we calculated net change in functional
268 richness as the difference between present and original functional richness.

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

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

289

290 **3. Results**

291 Our database included 759 species in 2709 island populations, distributed across 74 oceanic islands
292 (10 single islands and 64 belonging to 11 archipelagos; Table S1.1 and Fig. S3.6). Of these, 214 species

293 and 280 populations were extinct, 172 species and 801 populations were introduced, and the
294 remaining (445 species and 1628 populations) were extant natives. Some species were introduced to
295 an island but native to another, or extinct from one island while extant on another.

296 **3.1. Species compositional changes revealed by species richness**

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

301 **3.2. Effects of species compositional changes on functional composition**

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

310 (insert Figure 1 here)

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

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

321 Within 4 out of 6 groups of traits, the class with the highest net change (very large body mass, diurnal
322 foraging, ground foraging and volant species) had both the largest loss and the largest gain (Fig. 1),
323 suggesting that these classes are, overall, the most susceptible to changes in species composition. In

324 contrast, the class with the highest net change for both diet and habitat (granivore and occurring in
325 artificial terrestrial habitats) had the greatest gain but not the greatest loss.

326 Introductions added on average more novel trait classes than those that had been lost by extinctions.
327 Indeed, for 19 trait classes, introduced species added novel trait classes to between 1 and 18 islands
328 (column "+" in Fig. 1), while extinctions removed 12 trait classes between 1 and 22 islands, (column
329 "-" in Fig. 1). Weak flyers and flightless birds were particularly prone to extinction and have
330 disappeared from almost all islands where they used to occur (weak flyers: 9/9 islands, flightless:
331 22/23 islands - only species, the Campbell teal *Anas nesiotis*, remains in Campbell Island).

332 **3.3. Effects of species compositional changes on functional diversity**

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

343 (insert Figure 2 here)

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

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

351

352 **4. Discussion**

353 **4.1. Increase in local species richness despite net losses across islands**

354 We found an increase in the average number of bird species per oceanic island (alpha diversity), even
355 though overall species richness decreased across all islands (gamma diversity; Fig. S3.7). This
356 apparent paradox reflects the fact that a smaller overall number of species were introduced, but to
357 multiple islands (Blackburn et al., 2009; Dyer et al., 2017b), than those that went extinct, often
358 endemic to single islands (Boyer, 2008; Boyer & Jetz, 2014). This turnover in community composition
359 associated with extinctions and introductions is likely to increase the similarity between island bird
360 assemblages (i.e., lowering beta diversity, promoting biotic homogenization; McKinney & Lockwood,
361 1999). These findings are in line with previous studies (e.g. Sobral et al., 2016; Sayol et al., 2021).

362 An incomplete knowledge of original island avifaunas creates uncertainty around these estimates of
363 the magnitude of species compositional change. First, we are likely to underestimate the number of
364 extinct species (Boehm & Cronk, 2021), given that new extinct species are still being described (e.g.
365 Rheindt et al., 2020). Second, it is not always clear which species are native or introduced (Essl et al.,
366 2018). It is important to keep in mind that these results are a snapshot in time; the number of
367 introduced species is likely to continue to increase in many islands (Seebens et al., 2017). The total
368 number of introductions may thus eventually surpass the total number of extinctions on islands.

369 **4.2. Changes in species composition lead to changes in functional composition**

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

373 Very large bird species were the most unstable populations in oceanic islands, having simultaneously
374 the greatest number of extinct and introduced species than expected by chance (Table S3.10).

375 Moreover, the average body mass of island bird assemblages decreased because the average body
376 mass of extinct species was higher than that of introduced species. This finding provides further
377 support that large species are particularly prone to extinction (Boyer, 2008; Fromm & Meiri, 2021).

378 Regarding diet classes, the largest positive net gains in prevalence were by far of granivores, followed
379 by herbivores, omnivores and invertivores. There was no significant net change for frugivores, while
380 for carnivores and nectivores the changes were negative. Similar trends have been described before,
381 especially about the higher than expected number of granivore and herbivore introduced birds
382 (Blackburn et al., 2009; Soares et al., 2021), and reflect a simplification of ecological networks;
383 favouring lower positions in the trophic chain and unspecialized species, which are often better
384 adapted to simplified anthropogenic landscapes, while hampering species that rely on more complex
385 relationships, such as top positions in the trophic chain and nectarivory. These changes to island bird
386 assemblages might disrupt well-established mutualistic plant-animal interactions and affect native

387 plants, particularly through reduced pollination and seed dispersal (e.g. Caves et al., 2013; Carpenter
388 et al., 2020). Herbivore birds introduced to islands that had no native browsers or grazers can greatly
389 affect ecosystems, including by reducing food resources for pollinators and ultimately changing the
390 phenotypic traits of plants related to pollination (e.g. flowering phenology, flower production,
391 quantity and quality of nectar and pollen; Traveset & Richardson, 2006). Although having gained
392 more species than lost, more herbivore species went extinct than expected, which corroborates
393 recent studies that considered herbivore birds to be at high risk of extinction (Atwood et al., 2020).
394 Conversely, carnivore birds have lost more species than expected by chance, having long been
395 recognized as more extinct-prone due to their high diet specificity (Şekercioğlu et al., 2004). Their
396 loss can have serious negative consequences to ecosystems (Şekercioğlu, 2006), such as the increase
397 of undesirable species and disease outbreaks if predators and scavengers disappear, or the decline of
398 guano and associated nutrients input if piscivores are lost (Şekercioğlu et al., 2004). Nectivore birds,
399 which had a higher loss than expected, can also play a critical ecological role in the ecosystem, and
400 their disappearance can have serious impacts on plant-bird mutualistic interactions, potentially
401 impairing the future of insular native forests (Şekercioğlu et al., 2004; Boyer, 2008). This is
402 particularly important in some island ecosystems that have few pollinators and many flowering plant
403 species that depend exclusively on birds (Anderson et al., 2011).

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

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

421 open areas, which often have ground or unspecialized foraging strategies (Blackburn et al., 2009;
422 Soares et al., 2021).

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

426 **4.3. More species but with common traits, resulting in decreased functional diversity**

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

446 Islands are well-known for their high levels of endemism, unique functional traits and peculiar
447 evolutionary patterns (Whittaker et al., 2017; Russel & Kueffer, 2019). Unfortunately, this uniqueness
448 also makes insular species prone to anthropogenic extinctions (Hume, 2017), and their functions
449 more difficult to replace (Boyer & Jetz, 2014). Introduced species tend to have specific ecological
450 niches and prefer human-modified landscapes (Lee et al., 2010; Soares et al., 2021), thus it should
451 not come as a surprise that they do not compensate for the lost functional diversity. However, more
452 species with similar traits to the native bird species are being introduced to islands as a result of new
453 sources in the bird trade market (more Neotropical bird species; Dyer et al., 2017b). These novel

454 introductions appear to be better functional substitutes of extinct species and, most likely, have a
455 great potential to outcompete native species and further push these assemblages towards a
456 functional collapse (Soares et al., 2021).

457 **4.4. Preserving the original functional diversity**

458 We showed that a gain of species does not necessarily imply a gain in functional diversity, illustrating
459 why these two facets of biodiversity should be assessed simultaneously to understand the impacts of
460 human activities on biodiversity and ecosystem functioning. This mismatch between taxonomic,
461 functional and even phylogenetic diversity has been observed across multiple different taxa (Brum et
462 al., 2017), and has challenged the use of taxonomic diversity as a surrogate of functional diversity
463 (Devictor et al., 2010). Traditionally, global conservation efforts focused on protecting species or sites
464 that have high species richness, inadvertently underrepresenting other facets of biodiversity, such as
465 functional diversity (Cadotte & Tucker, 2018). The non-linear and often negative relationship, as in
466 oceanic island birds, between taxonomic and functional diversity calls for the prioritized protection
467 of functionally unique species to maintain functional diversity. Such a line of action is also key to
468 ensure that functional redundancy is kept, since it allows preserving ecosystem functions under
469 further, and unfortunate, species loss.

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

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

498

499 5. References

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665 **6. Data accessibility statement**

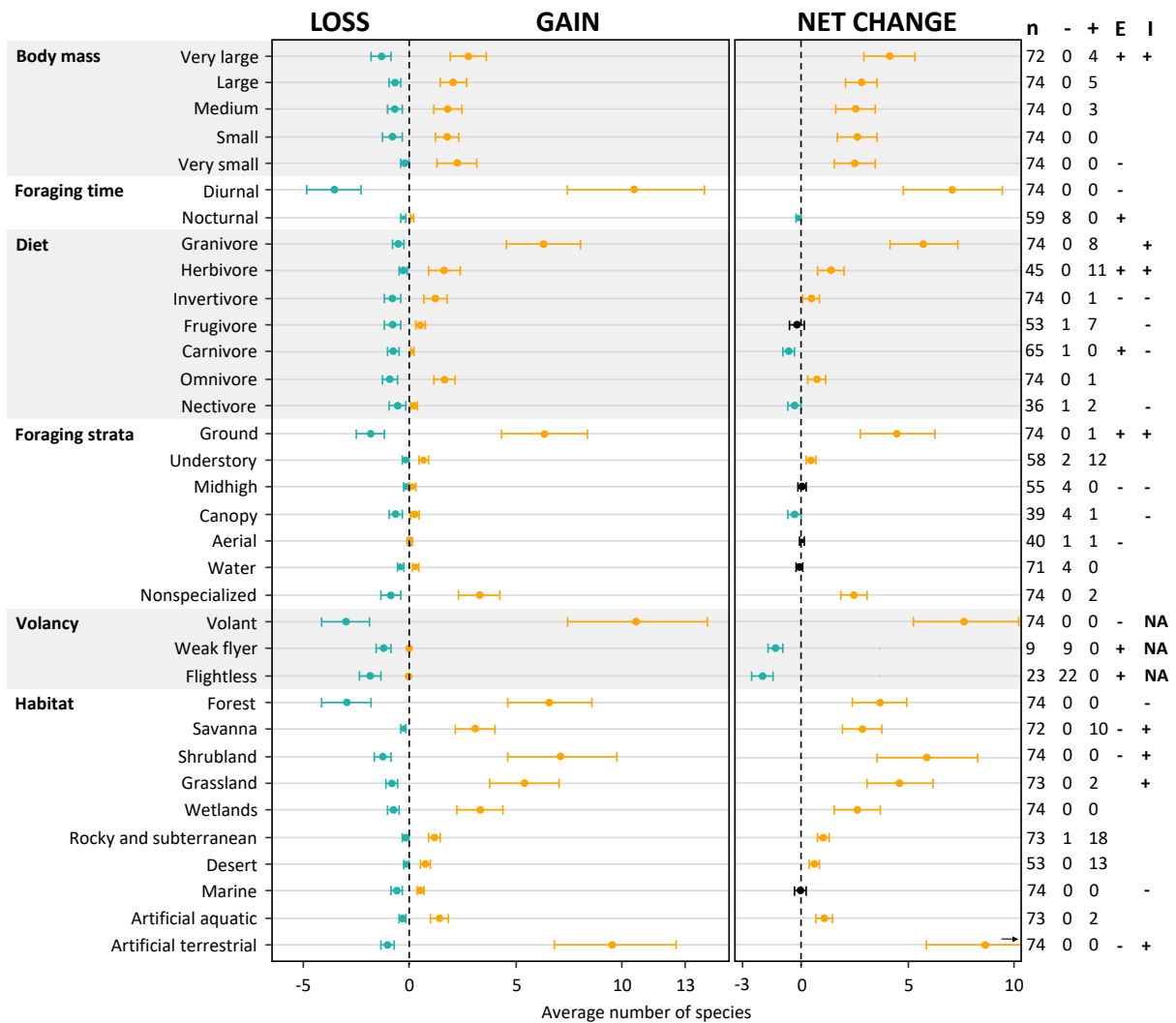
666 All data supporting the results present in the paper are archived in figshare and should be available
667 after the acceptance of the paper. This data includes the species per trait matrix and the sites per
668 species matrix. The current link to figshare repository is the following:

669 <https://doi.org/10.6084/m9.figshare.16782697.v1>

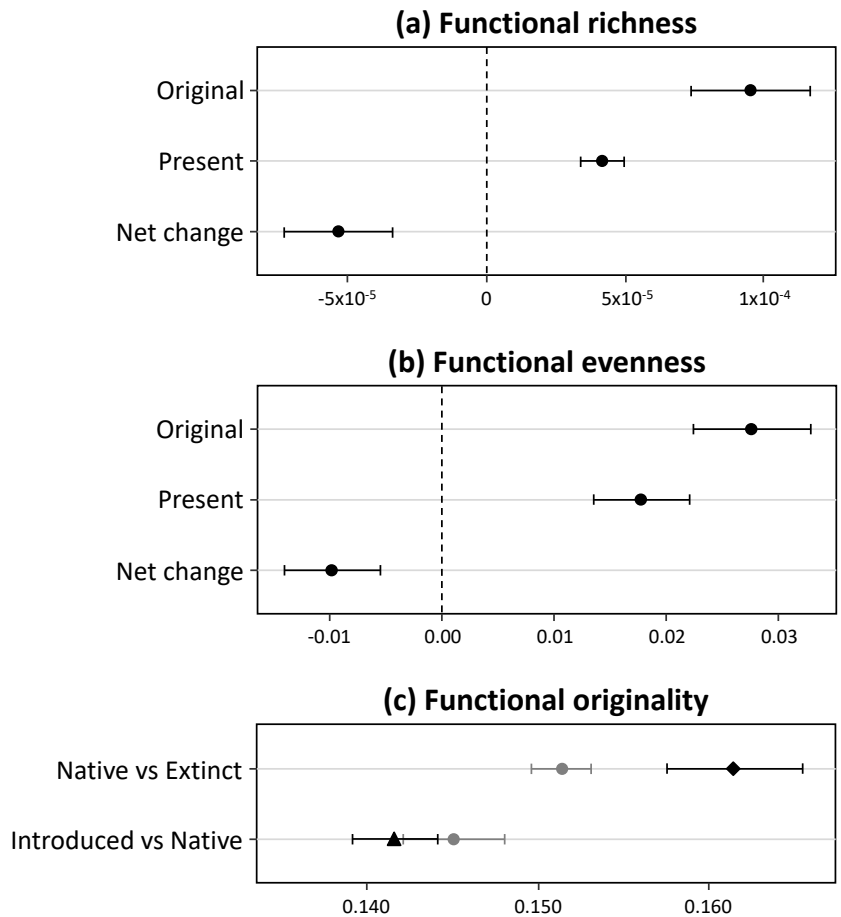
670 **7. Tables**671 **Table 1.** Description of the 10 traits used to build the trait space.

Trait	Type	Description
Diurnal	Dichotomous	Diurnal (1), nocturnal (0)
Nectivore	Dichotomous	Nectivore (1), non-nectivore (0)
Water forager ¹	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 ²	Ordinal	Ground (1), understory (2), midhigh (3), nonspecialized (3.5), canopy (4), aerial (5)

672 **Note:** ¹Water forager and terrestrial foraging strata are not mutually exclusive, meaning that a species can be considered,
673 for example, both water forager (1) and ground (1), as with most Anatidae species. ²We considered nonspecialized birds,
674 species that forage in most strata between ground and aerial, and thus attributed them the average value of 3.5.



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



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

703

704 **9. Supplementary material**

705 **Appendix 1:**

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

707 **Appendix 2:**

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

709 **Appendix 3:**

710 Table S3.3 Species that were reclassified as native or introduced in our database.

711 Table S3.4 List of references of scientific papers used to find extinct and extirpated bird species.

712 Table S3.5 Traits used to evaluate changes in functional composition.

713 Table S3.6 Extant bird species absent from the EltonTraits database and corresponding sister species.

714 Table S3.7 Contribution of each trait to the global distance matrix.

715 Table S3.8 Global change in island bird assemblages: total number of species, species richness and
716 functional diversity metrics based on hypervolumes - functional richness, average functional
717 originality and functional evenness.

718 Table S3.9 Average number of species belonging to each trait class and average body mass are
719 represented for loss (extinct species), gain (introduced species) and net change (difference between
720 gain and loss).

721 Table S3.10 Standard effective sizes and p -values from the null model analyses based on functional
722 traits for extinct and introduced species.

723 Figure S3.1. Flow chart describing the decisions made to compile information on extant island bird
724 species.

725 Figure S3.2 Flow chart describing the decisions made to compile information on extinct island bird
726 species.

727 Figure S3.3 Flow chart describing the decisions made to compile information on the traits of the
728 extinct species.

729 Figure S3.4 Graphical representation of (a) functional richness, (b) functional originality of each
730 species and (c) functional evenness based on the probabilistic hypervolume approach (Adapted from
731 Mammola & Cardoso, 2021).

732 Figure S3.5 Response variables projected as in PCA with scaling 1.

733 Figure S3.6 Location of all analysed islands that after bird extinctions and introductions had a positive
734 net change in species richness, a negative net change and no net change.

735 Figure S.7 Total number of extinct and introduced species, and net change (introduced minus extinct)
736 when considering (a) the total number of species across all islands and (b) the average number of
737 species per island.

738 Figure S3.8 Effects of species compositional changes on island functional composition.

739 Figure S3.9 Net change values per island: species richness, functional richness and functional
740 evenness.

741 Figure S3.10 Functional originality of extinct and extant native species in the original assemblage of
742 each island, and of extant native and introduced species in the present assemblage of each island.

743 **Appendix 4:**

744 Traits of extinct bird species

745 **Appendix 5:**

746 Best combination of traits

747 Principal Component Analysis