

A global analysis of avian island diversity-area relationships in the Anthropocene

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1 A global analysis of avian island diversity–area relationships in the

2 Anthropocene

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67 DATA AVAILABILITY STATEMENT

All code and data are available on GitHub (txm676/DARs) and archived on Zenodo

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70

71 AUTHORSHIP STATEMENT

- 72 TJM formulated the original idea; TJM, JPW, FS, TEM, BB, PAVB, YK, LdA, FCS, XS,
- 73 PD, YCKS, FER, KAT, DMW, LB, CB and OC sourced and provided bird distribution data,
- 74 JAT, FS, JPH, KAT and TJM sourced trait data; TJM, FR, PC and KP led the analyses; TJM
- vrote the first draft of the manuscript; all authors contributed to writing, editing and
- 76 discussion of ideas.
- 77

78 ABSTRACT

79 Research on island species-area relationships (ISAR) has expanded to incorporate functional (IFDAR) and phylogenetic (IPDAR) diversity. However, relative to the ISAR, we know little 80 about IFDARs and IPDARs, and lack synthetic global analyses of variation in form of these 81 three categories of island diversity-area relationship (IDAR). Here, we undertake the first 82 comparative evaluation of IDARs at the global scale using 51 avian archipelagic datasets 83 representing true and habitat islands. Using null models, we explore how richness-corrected 84 functional and phylogenetic diversity scale with island area. We also provide the largest 85 global assessment of the impacts of species introductions and extinctions on the IDAR. 86 Results show that increasing richness with area is the primary driver of the (non-richness 87 88 corrected) IPDAR and IFDAR for many datasets. However, for several archipelagos, richness-corrected functional and phylogenetic diversity changes linearly with island area, 89 suggesting that the dominant community assembly processes shift along the island area 90 91 gradient. We also find that archipelagos with the steepest ISARs exhibit the biggest differences in slope between IDARs, indicating increased functional and phylogenetic 92 redundancy on larger islands in these archipelagos. In several cases introduced species seem 93 94 to have 're-calibrated' the IDARs such that they resemble the historic period prior to recent 95 extinctions.

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105 INTRODUCTION

The island species-area relationship (ISAR) is a well-established global ecological pattern 106 (MacArthur & Wilson, 1967; Rosenzweig, 1995; Lomolino, 2000; Triantis et al., 2012; 107 Whittaker & Matthews, 2014; Matthews et al., 2019a, 2021). Following the increasing 108 recognition in ecology that species richness only represents one dimension of diversity, ISAR 109 research has expanded to incorporate functional (the island functional diversity-area 110 relationship; IFDAR) and phylogenetic (the island phylogenetic diversity-area relationship; 111 IPDAR) diversity (e.g., Ding et al., 2013; Whittaker et al., 2014; Si et al., 2016, 2017, 2022; 112 113 Ross et al., 2019; Mazel & Thuiller, 2021; Dias et al., 2020; Zhao et al., 2020; Schrader et al., 114 2021; Leclerc et al., 2022; Wang et al., 2023).

Functional diversity (FD) measures the combination of functional traits expressed by 115 116 a set of species in a community and can provide a link between species composition and ecosystem function (Petchey & Gaston, 2006). Phylogenetic diversity (PD) incorporates the 117 118 evolutionary relationships among species in an assemblage and measures the amount of evolutionary history those species represent (Faith, 1992). Collectively, the ISAR, IFDAR, 119 and IPDAR have been termed island diversity-area relationships (herein IDARs), and 120 121 together their analysis aids in generating a more comprehensive understanding of the mechanisms driving the scaling of diversity (Ding et al., 2013; Mazel & Thuiller, 2021; 122 Leclerc et al., 2022; Wang et al., 2023). However, in comparison to the ISAR, we know 123 relatively little about IFDARs and IPDARs, and we lack synthetic comparative global 124 analyses of variation in the form of these three categories of IDAR. 125

A wide range of metrics has been proposed for measuring FD and PD. To construct 126 127 IFDARs and IPDARs that compare easily with standard ISARs, FD and PD are often expressed as metrics that sum the branch lengths (e.g., of a functional dendrogram or 128 129 phylogenetic tree) connecting all species co-occurring on an island (Morlon et al., 2011; Dias et al., 2020; Mammola et al., 2021; Si et al., 2022). While the use of tree/dendrogram-based 130 131 FD and PD metrics ensures the ISAR, IFDAR and IPDAR are comparable, such metrics are generally correlated with species richness. For this reason, the calculation of FD and PD 132 using tree metrics is often combined with a null model to generate (standardised) effect sizes 133 (ES) that are independent of richness (Tucker et al., 2017; Mazel & Thuiller, 2021). In 134 135 addition, the analysis of ES values has been argued to provide insights into the community assembly processes involved (e.g., neutral dynamics vs. competition vs. habitat filtering) and 136

how these may change with island area (Matthews et al., 2020; Münkemüller et al., 2020; 137

Mazel & Thuiller, 2021; Schrader et al., 2021). Herein, we refer to the emergent FD.ES and 138 PD.ES patterns (random, overdispersed, clustered) as assembly patterns, and the potential 139

mechanisms underlying these patterns (neutral dynamics, competition, habitat filtering) as 140

assembly processes. However, we know very little about how FD.ES and PD.ES values scale

142 with island area (rather than across continuous scales; see Kraft & Ackerly, 2010), and

141

previous authors have called for a greater focus on scaling patterns in order to better 143

understand community assembly processes on islands (Leibold & Chase, 2018; Dias et al., 144

145 2020; Münkemüller et al., 2020; Zhao et al., 2020; Schrader et al., 2021; Si et al., 2022).

146 Analysing variation in IDARs among archipelagos can emphasise the (i) form / shape of the relationship (e.g., Mazel et al., 2014), and (ii) slope of the curve. The former is 147 148 important as different relationship forms (e.g., asymptotic vs. non-asymptotic or convex vs. sigmoidal) have different theoretical and conservation implications (Lomolino, 2000; Triantis 149 150 et al., 2012). The latter tends to be undertaken using the power model, of the form $S = c^*A^z$, where S and A are richness and area, respectively, and c and z are fitted parameters 151 (Rosenzweig, 1995; Matthews et al., 2021). Several studies have tested for systematic 152 variation in ISAR slopes (e.g., Rosenzweig, 1995; Triantis et al., 2012; Matthews et al., 153 2019a, 2021). However, there have been no comparable analyses of variation in the z-values 154 (slopes) of IFDARs and IPDARs. 155

156 Many island systems have been particularly affected by extinctions and the introduction of non-native species (herein 'introduced species') (Whittaker & Fernández-157 Palacios, 2007; Boyer & Jetz, 2014; Blackburn et al., 2016; Hume, 2017; Matthews & 158 159 Triantis, 2021; Matthews et al., 2022). Recent work on the impacts of humans on island biogeographic patterns has illustrated how the exclusion of extinct species and the inclusion 160 161 of introduced species can affect the form of ISARs (Cardoso et al., 2010; Helmus et al., 2014; Baiser & Li, 2018), but how these decisions affect other types of IDAR is less understood 162 (Whittaker et al., 2014; Li et al., 2018). 163

Here, we undertake the first comparative synthetic evaluation of IDARs at the global 164 scale using a collection of 51 avian archipelago datasets representing different island types 165 (true and habitat), encompassing 1,051 individual islands and 2,111 species. True islands are 166 those surrounded by water (i.e., oceanic, continental-shelf, continental fragments, and lake 167 islands), while habitat islands are those surrounded by contrasting terrestrial matrices (e.g., 168

169 forest fragments surrounded by pasture; Matthews, 2021). True island datasets were further

- 170 split into volcanic oceanic archipelagos, a subset of true island datasets comprising
- archipelagos of mainly volcanic origin never connected to continental land masses (all
- 172 currently isolated from the mainland by >100km), and other true island archipelagos (e.g.
- 173 continental-shelf islands, inland islands). For all bird species (extant [native and introduced]
- and extinct), we collected nine continuous trait measurements. In combination with
- 175 phylogenetic data, we constructed the ISAR, IFDAR and IPDAR for all datasets. We used
- null models to generate FD.ES and PD.ES values and explore how these scale with island
- area. We also provide the largest global assessment of the impacts of species introductions
- and extinctions on the IDAR, thus furthering our understanding of the 'island biogeography
- 179 of the Anthropocene' (Helmus et al., 2014). Figure 1 provides an overview of the
- 180 methodological framework employed. We used this framework to answer four primary
- 181 questions:
- Q1: Do richness, FD and PD scale with area in different ways (i.e., do different modelsprovide the best fit to the ISAR, IFDAR and IPDAR)?
- Q2: Does the power model slope differ between the ISAR, IFDAR and IPDAR for a givenarchipelago, and what are the archipelago characteristics that determine such variation?
- 186 Q3: To what extent does island functional and phylogenetic community assembly depart from 187 random expectation, and do assembly processes vary with island area in a systematic fashion?
- Q4: To what extent does the inclusion or exclusion of extinct and introduced species affectdifferent IDAR properties?

190 Theoretical expectations

191 For each of the four primary questions above, we developed a theoretical expectation based192 on previous research on IDARs:

193 Q1: We expect asymptotic models to provide relatively better fits to IFDAR and IPDAR data,

- 194 compared with ISAR data, due to the previously reported finding of increasing functional and
- 195 phylogenetic similarity between species (often interpreted as redundancy) with increasing
- 196 area (e.g., Mazel et al., 2014; Dias et al., 2020).
- 197 Q2: For the same reason as in Q1, we expect IFDAR and IPDAR power model slopes to be198 systematically less steep than ISARs.

Q3: The Equilibrium Theory of Island Biogeography (MacArthur & Wilson, 1967) assumes 199 in its simplest form that species are functionally equivalent and thus represents a null model 200 of island assembly. By extension, there should be no relationship between richness-corrected 201 FD and PD (ES) values and island area (Si et al., 2017; Ross et al., 2019), the increase in FD 202 and PD with area being simply a function of richness. However, MacArthur & Wilson (1967) 203 204 recognized entirely random assembly to be simplistic and subsequent work suggests that the 205 relative importance of different traits and assembly processes could potentially vary along the island area gradient, thus influencing the scaling of FD.ES and PD.ES values with island 206 207 area.

208 In theory, community assembly may depart from random towards either clustering or overdispersion of traits. Considering true islands, small islands tend to contain a limited and 209 210 simpler array of habitat types and more extreme abiotic conditions (Sfenthourakis & Triantis, 2009; Ross et al., 2019; Chen et al., 2020). As a result, only a subset of closely related taxa 211 212 with specific traits are adapted to these conditions and can persist (Si et al., 2017; Liu et al., 2020; Schrader et al., 2021). This should lead to a degree of functional and phylogenetic 213 clustering on small true islands, consistent with some recent empirical analyses (e.g., Si et al., 214 2017; Ross et al., 2019; Matthews et al., 2020; Zhao et al., 2020; Schrader et al., 2021). 215

Conversely, larger true islands will often support a broader range of habitats and 216 potential niches (Whittaker & Fernández-Palacios, 2007), allowing a wider set of species to 217 218 be able to colonise and persist, leading to neutral or overdispersed patterns (Matthews et al., 219 2020). Should it be general that island assembly patterns shift from clustering to random / 220 overdispersion along the area gradient, we should then expect a positive relationship between 221 FD.ES and PD.ES and area for true islands. A similar logic applies to habitat islands, where high habitat heterogeneity in large fragments (e.g., due to topographical variation or the 222 223 presence of environmental gradients; dos Anjos et al., 2022) can support a broader range of bird guilds (e.g., Willrich et al., 2019). However, we predict less consistent patterns for 224 habitat islands in general, which tend to be much noisier systems (Matthews, 2021). 225

Q4: Regarding the inclusion of extinct species in oceanic true island datasets, we predict that
IDAR slope will increase from the historic period to the current period. This prediction is
based on the conceptual model of Franklin & Steadman (2008; see also Steadman, 2006) that
was developed in the context of land birds on tropical oceanic islands, whereby, within an
archipelago, most species are predicted to have occurred on each high elevation island above

a minimum size prior to human colonisation, and contemporary positive ISARs are mostly 231 the result of species being harder to drive to extinction on larger islands (e.g., due to larger 232 population sizes and more refugia). We predict the slope of contemporary IDARs should 233 increase with the addition of introduced species, as larger islands are known to experience 234 more introductions (Blackburn et al., 2021). We also predict that extinctions and 235 236 introductions will have dampened the theoretically expected slope of the ES-area relationships (Q3). This is because extinction and introduction are typically non-random 237 processes, involving species with particular traits (e.g., large body size in regard to extinct 238 239 species) and from certain taxonomic groups (Boyer, 2008; Fromm & Meiri, 2021; Matthews et al., 2022), which together would act to reduce FD.ES and PD.ES values (i.e., reduce 240

241 overdispersion and increase clustering), particularly on the larger islands.

242 **METHODS**

243 Data collection

244 We sourced true and habitat island bird datasets from the literature. For most datasets, we used previous synthetic ISAR analyses (e.g., Triantis et al., 2012; Matthews et al., 2021) to 245 locate potential datasets, and returned to the source papers (and subsequent papers by the 246 247 source paper authors) to obtain the species lists for each island. True island datasets were also supplemented using Baiser et al. (2017) and Sin et al. (2022), and habitat islands using Chase 248 249 et al. (2019). For the former, we updated some of the datasets using a range of literature sources (see Appendix S1). For a number of true island cases (the Ryukyus Islands, the 250 251 Azores, Canaries, New Zealand) we created new datasets through comprehensive literature 252 and database searches (Appendix S1). For inclusion, datasets needed to contain at least seven 253 islands (to enable the calculation of AIC_c, discussed below) and possess an accessible bird species list for each island. An exception was made for a Hawaiian dataset (Baiser et al., 254 2017) which only had six islands, as its extreme isolation means it has particular value in 255 representing isolated oceanic archipelagos. Note that two datasets sourced from Baiser et al. 256 (Society Islands and Cook Islands) classify atolls (collections of small islets connected by 257 sand banks) as individual islands (Appendix S1). All island areas were converted to km². For 258 the analyses, it was necessary to impose a criterion of a minimum of one species on an island, 259 260 leading to the removal of a small number of islands with zero species (these were only present in a handful of datasets). 261

As a first step, for each dataset and using either data provided by the source paper 262 authors or using species range maps provided by the IUCN Red List (IUCN, 2021), we 263 classified all species as native or introduced to that archipelago (or region for habitat islands). 264 We then excluded from analysis all introduced species (but for some datasets created 265 alternative versions with introduced species included; see below). Otherwise, we used the 266 267 datasets as originally published in the source papers, meaning that the exact types of species included varied slightly between datasets due to the decisions of the original source paper 268 269 authors (e.g., including / excluding marine and nocturnal species). However, to roughly 270 standardise the datasets, we also created an alternative version of each by removing the marine, coastal, wetland and riverine species to produce a land birds only version, for which 271 we re-ran the analyses (see Appendix S2 for details). This standardisation process involved 272 removing two datasets when analysing just land birds as it resulted in several islands in these 273 archipelagos having no or very few species (Appendix S2). We removed extinct species 274 (when present) from the datasets, but also created alternative versions of certain datasets with 275 extinct species included (discussed below). For each dataset, we formatted all species names, 276 277 including extinct species (see Appendix S2), to match the nomenclature in the phylogenies provided by Jetz et al. (2012) (see Appendix S1). 278

279 Dataset characteristics

For each dataset (archipelago), and using only the islands / species present in the dataset, we 280 281 recorded a number of variables predicted to affect IDAR form (see Triantis et al., 2012; Matthews et al., 2019a, 2021): (1) number of islands (Ni), (2) the ratio between the area of 282 the largest and smallest island (AreaScale), (3) archipelago species richness (Gamma), (4) 283 284 total archipelago land area (ArchArea), (5) annual mean temperature, and (6) maximum island elevation. FD and PD Gamma were calculated as the total FD or PD of an archipelago. 285 286 For each true island dataset, we also calculated (7) isolation (distance) from the mainland and (8) intra-archipelago isolation (MeanDist). Appendix S2 details how these variables were 287 288 sourced and calculated.

289 Functional traits

For functional traits, we sourced data for all of the world's 9993 species (BirdTree taxonomy)

from the AVONET trait dataset (Tobias et al., 2022), allowing us to build a functional space

- using all of the world's birds and ensure distances between species in functional space
- represented the best estimates of the true distances. We used eight continuous morphological

measurements: (1) total beak length (from the tip to the skull), (2) beak length to the nares, 294 (3) beak width and (4) depth (at the nares), (5) wing length, (6) secondary length, (7) tail 295 length, and (8) tarsus length. These measurements have been shown to provide accurate 296 information on the functional role and trophic status of birds at the global scale (Pigot et al., 297 2020). We also sourced body mass estimates (g) for each species from AVONET (Tobias et 298 299 al., 2022). The four kiwi species (Apteryx) represent extreme outliers in terms of the wing 300 length, secondary and tail length traits (e.g., for wing length, the kiwis had values 267 times 301 smaller than the species with the next smallest wing length). To avoid these species affecting 302 the functional space to an extreme degree (which occurred even when log-transforming the traits), for these three traits, we replaced the trait values for the four kiwi species with the 303 mean values across all extant species excluding the kiwis. This approach was preferred to the 304 option of simply removing the kiwis, as one of our analysed datasets comprised islands in 305 New Zealand. 306

Four of the extinct species in our datasets were also in BirdTree and AVONET. For the remaining 154 extinct species in our datasets, we sourced data for the same set of traits (described below). Our final trait dataset comprised 10,147 species. All nine traits were logtransformed and then scaled to have a mean of zero and unit variance.

Because the eight morphological traits are correlated with body mass, we also re-ran the analyses using body-size corrected traits, generated by running eight simple linear regressions with body mass as the predictor and a given morphological trait as the response (both log-transformed). Here, the scaled residuals from each model were then used as the new trait along with log-transformed and scaled body mass.

316 Calculating FD, PD and Effect Sizes

We used FD and PD metrics based on summing branch lengths to ensure our diversity 317 metrics shared the same mathematical framework and are thus directly comparable (i.e., they 318 319 incorporate the sum of the differences in diversity accumulated between species; Tucker et 320 al., 2017; Dias et al., 2020; Mammola et al., 2021). In addition, the use of trees allowed us to include islands with few species (e.g., one or two), which is not possible with FD metrics 321 such as convex hulls when multiple traits are used (Petchey & Gaston, 2006; Jarzyna et al., 322 2021). For FD, we built a global dendrogram comprising all 10,147 species. A Euclidean 323 distance matrix was generated using all species and the nine trait axes. We then transformed 324 this distance matrix into a dendrogram using the agglomerative hierarchical clustering 325

method UPGMA (Petchey & Gaston, 2006). We checked the dendrogram quality using the *tree.quality* function in the 'BAT' R package (Cardoso et al., 2015). The values for our
dendrograms were relatively high (0.70 and 0.95 for the dendrogram using the uncorrected
and body-size corrected traits, respectively; one corresponding to maximum quality of the
functional representation). For each island, we used the global dendrogram to calculate
Petchey & Gaston's (2006) FD metric (including the tree root) using the 'picante' R package
(Kembel et al., 2010).

333 For PD, we based our analyses on the BirdTree phylogenetic trees from Jetz et al. (2012) using the Ericson backbone tree with 9,993 species. We obtained a posterior 334 335 distribution of 3,000 trees from BirdTree and created a maximum clade credibility tree (node heights = median heights) including all bird species, using the TreeAnnotator program 336 337 (v1.10.4, Drummond & Rambaut, 2007). The resultant consensus tree had a small number of negative branch lengths which we resolved by converting negative branch lengths to zero, 338 339 while shortening only the two branches immediately below by the same absolute amount to ensure the tree remained ultrametric and there were no polytomies (we have added this 340 functionality to the 'BAT' R package; tree.zero function). The PD values generated using the 341 original consensus tree and the consensus tree with the negative branches removed were 342 highly correlated (Pearson's r = 0.999). The 154 extinct species not in BirdTree were grafted 343 on to this consensus tree (detailed below). We used this global maximum clade credibility 344 tree to calculate Faith's PD metric (including the tree root; Faith, 1992) for all islands in a 345 dataset as outlined for FD. As a sensitivity check, we re-ran the analyses using a randomly 346 selected tree from the 3,000 (grafting the extinct species onto this selected tree). 347

348 As both FD and PD can be correlated with species richness, to calculate standardised FD and PD values we created a variant of the 'taxa.labels' null model (999 iterations) and the 349 350 ses.pd function in the 'picante' R package. This null model worked by only shuffling the names of species found in a given dataset on the global tree / dendrogram (i.e., the null 351 352 model, for a given dataset, uses the archipelagic species pool, not the global species pool, but does not prune the tree). We did this to ensure a consistent tree (i.e., the global tree) was used 353 354 for calculating FD/PD across datasets, given that pruning the tree was found to affect DAR slopes in a small number of cases (full details provided in Appendix S2). 355

Generally, standardised values of FD and PD are calculated using standardized effect
sizes (SES). However, SES assume a normal distribution of null values, an assumption that is

often violated, particularly where some samples contain most, or very few, of the species in
the pool. Thus, we instead used the effect size (ES) approach used in Matthews et al. (2020).
This works by calculating the empirical probability (P) that the observed value is less than
expected using the formula:

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P = (length(null < obs) + (length(null = obs)) / 2)/(n + 1),

where null is the vector of null distribution values, obs is the observed value and n is 363 the number of null model iterations (here n = 999). This probability was then probit 364 365 transformed to obtain the ES value (see Appendix S2 for further details). This process was done using both FD and PD, resulting in FD.ES and PD.ES values for each island in each 366 367 dataset. Positive ES values > 1.96 were considered to represent cases of significant functional / phylogenetic overdispersion, and negative ES values < -1.96 were taken to represent 368 369 significant clustering. Non-significant ES values (-1.96 < ES < 1.96) were considered to 370 represent random community structure.

371 IDAR multimodel comparison

For each dataset, we fitted twenty SAR models (see Table S2 in Appendix S2) to our three diversity variables (species richness, FD, and PD) using least squares non-linear regression and the 'sars' R package (Matthews et al., 2019b). These models represent a range of curve shapes (linear, convex-upward, sigmoidal), number of model parameters (2–4) and properties (asymptotic and non-asymptotic) (see Triantis et al., 2012 for a review).

We designed a grid search method for selecting model starting parameter values to be 377 used in the non-linear regressions; this method has now been added to the 'sars' package 378 (version 1.3.5; available from CRAN) (see Appendix S2 for details). For each twenty-model 379 set, models were compared and ranked using Akaike's information criterion corrected for 380 small sample size (AIC_c) (Burnham & Anderson, 2002). As the denominator in AIC_c must 381 not be negative, for the Hawaii dataset (with only six islands) it was necessary to exclude the 382 383 two four-parameter models from the model set. For each dataset and diversity metric, we stored the model ranks, and a multi-model curve was constructed using the AIC_c weights 384 385 from all converged model fits (see Matthews et al., 2019b). In each case, we also extracted 386 the z-value and c-value from the non-linear power model fit; this model converged in all 387 cases. To ensure the same models were fitted in all cases, we did not remove model fits based on residual assumptions checks (e.g., normality). However, given that the least square 388 389 parameter estimates equal the maximum likelihood estimates only under the assumption of

normal errors with constant variance (see discussion in 'sars' package vignette), and given we are using AIC_c , we re-ran the model selection including checks for both these properties. As an additional sensitivity test, we also re-ran the various power model z-value analyses using the z-value from the $log_{10}-log_{10}$ (linear) power model.

The majority of these twenty models were originally chosen to fit SAR data (Triantis 394 et al., 2012; Matthews et al., 2021) based on the expected shape of the SAR (e.g., convex-395 upward or sigmoidal). However, the work on island FD.ES-area and PD.ES-area 396 397 relationships to date (e.g., Diaz et al., 2020; Matthews et al., 2020; Schrader et al., 2021) has 398 shown that they are not well characterised by such model shapes and thus it is not necessarily 399 appropriate to fit the same set of models to these data. Instead, based on our theoretical expectations, we compared the fit of a linear regression model with an intercept-only null 400 401 model in semi-log space (i.e., log area but not richness) using AIC_c. We used a semi-log transformation (log₁₀) as there is no *a priori* reason to log-transform ES values and it has 402 403 previously been shown to be an effective method for assessing ES-area relationships (Matthews et al., 2020; Schrader et al., 2021). 404

405 *Exploratory modelling of IDAR slope variation*

406 First, we tested whether there were significant differences between the z-values of the ISAR, IFDAR and IPDAR. As the IDAR z-values within a dataset were not independent, we 407 compared the z-values between datasets using a generalised linear mixed effects model (beta 408 409 family and logit link; fit using restricted maximum likelihood) and the 'glmmTMB' R 410 package (Brooks et al., 2017), with diversity type (i.e., richness, FD, PD) as a categorical fixed effect, and the dataset as a random effect. We used the same approach to compare the 411 412 slopes from the FD.ES and PD.ES-area relationships, except here we used the Gaussian family as many of these slopes were negative. 413

414 Second, we assessed what archipelago characteristics drove variation between datasets in the (i) z-value of the ISAR, IFDAR and IPDAR, and (ii) slope of the ES-area 415 416 relationships. Following Marx et al. (2017), we undertook an exploratory modelling approach using Pearson's correlations, which were preferred over regression analyses due to the 417 relatively small size of our dataset. The z-values of one of the ISAR, IFDAR or IPDAR were 418 correlated against each of our archipelago-level predictor variables in turn, using log-419 transformations when necessary to meet assumptions. As the IFDAR and IPDAR z-values 420 were correlated with the ISAR z-value, we also ran a series of partial correlations with these 421

- 422 two variables, allowing us to control for the ISAR z-value. We ran the modelling using all
- 423 datasets (i.e., true and habitat islands) and using as predictor variables: Ni, Gamma (or FD /
- 424 PD Gamma), AreaScale, ArchArea, (maximum) elevation, temperature, and the power model
- 425 c-value. We then re-ran the modelling using just the true island datasets and adding in as
- 426 predictors both MeanDist and isolation from the mainland. We then re-ran these correlation
- 427 tests but instead used the slope of the linear model fitted to the FD.ES-area and PD.ES-area
- 428 relationships as variables.

429 The effect of including extinct and introduced species on diversity scaling relationships

For ten true island datasets (Canaries, Cook Islands, Hawaii, Lesser Antilles, Marianas, 430 Society Islands, Cape Verde, New Zealand, Azores, and Ryukyu Islands), there were a 431 relatively large number of species introduced to each archipelago (ranging from 11 to 60% 432 433 [median = 19%] of the total contemporary archipelago bird fauna). For these datasets, we also 434 created alternative versions representing the current faunas with introduced species included (we only considered currently established introduced species; see Appendix S1). For the first 435 eight of those, we were also able to build datasets representing the historic fauna, i.e., the 436 island composition around 1500 CE, including extinct species and extirpated extant species. 437 For five datasets where (coarse) data were available (Hawaii, Marianas, Cook Islands, New 438 Zealand, Canaries), we also built datasets representing the prehistoric fauna (i.e., prior to 439 human colonisation of the islands; including all species known to have gone extinct in the last 440 441 ~125,000 years) excluding marine species (Appendix S2). For the Marianas and Cook Island prehistoric datasets, we removed a number of islands as we decided to focus on islands where 442 more fossil data were available. 443

444 The historic and pre-historic datasets (i.e., including extinct species) were built using a range of literature sources (see Appendix S2 for details). The functional traits of extinct 445 species were initially sourced through measurements made on specimens in various museums 446 and literature searches. For 135 of the 158 species, we were able to acquire at least one 447 measurement from skin or skeleton (or both) specimens in museums, with body mass being 448 estimated for the remaining species (see Appendix S2). All gaps were then imputed using 449 450 Bayesian Hierarchical Probabilistic Matrix Factorization (Schrodt et al., 2015). We ran the imputation ten times, averaging the imputed values across the ten runs. As a sensitivity test, 451 we re-ran the analyses using a randomly selected individual imputation run rather than 452 averaging. Extinct species were also grafted onto our consensus phylogeny. Appendix S2 453

454 provides a detailed description of the extinct species data collection, trait inference and455 phylogeny grafting.

We then re-ran the power and linear model fitting for the historic and introduced species datasets, storing the power model z-values for the ISAR, IFDAR, IPDAR, and the slopes (of the linear model) of the two ES–area relationships. We compared the values with those from our main analyses (i.e., current fauna excluding introduced species) using paired Wilcoxon signed-rank sum tests. We also re-fitted the models using the prehistoric datasets.

Unless otherwise stated, all analyses were undertaken in R (Version 4.2.0; R Core
Team, 2019), and the analyses were run on a 500GB cluster using 51 cores (~2,000 corehours).

464

465 **RESULTS**

466 In total, we sourced 51 datasets (26 true island and 25 habitat island archipelagos),

467 incorporating 1,051 islands and 2,111 species (1,953 extant and 158 extinct species)

468 (Appendix S1). The size of habitat islands ranged from 0.004 km^2 to 1592 km^2 , and true

469 islands from 0.001 km² to 150,437 km². A map of the locations of these datasets is provided

470 as Figure S1 in Appendix S3. All best fit models, and the power and linear model parameters,

471 for all five relationships across all datasets are provided in Table S3 in Appendix S3.

472 Q1 and Q2: ISAR, IFDAR and IPDAR model form

473 The non-asymptotic convex-upward Kobayashi, power and logarithmic models were always the three models with the highest mean AIC_c weight values for the ISAR, IFDAR and IPDAR 474 475 (but not always in the same order), across the 51 datasets (Fig. 2). Inspecting the plots of 476 model fits provided further evidence for the convex-upward nature of most of the ISARs, IFDARs and IPDARs (e.g., Fig. 3). In terms of the number of best fits (i.e., cases of lowest 477 AIC_c for a given IDAR and dataset), the top model was always the power model, with the 478 479 linear, logarithmic and Kobayashi models alternating in second and third position (Fig. S2). The results were similar when looking at true and habitat islands separately (Figs. S3-S6 in 480 Appendix S3). 481

The power model provided a reasonable approximation of the form of the three IDARs (mean R^2 across all datasets and the three IDARs = 0.62). In general, for a given dataset, the z-value of the ISAR was larger than that of the IPDAR, which was slightly larger than that of the IFDAR, and these differences became more pronounced the steeper the ISAR
was (Fig. 4). Using a mixed-effect model with the diversity type as a fixed effect and the

- 487 dataset as a random effect revealed that the z-values significantly differed between the ISAR
- 488 (mean z = 0.19), IFDAR (mean z = 0.14) and IPDAR (mean z = 0.16) (Type II Wald χ^2 test
- for the categorical fixed effect, $\chi^2 = 163.5$, P < 0.001). This was also the case when
- 490 considering only true islands or only habitat island datasets.

Figure 5 provides the results of the exploratory modelling of correlations between 491 IDAR slopes and archipelago features. When considering all datasets, ISAR, IFDAR and 492 493 IPDAR slopes were significantly positively correlated with Ni (number of islands), and 494 significantly negatively correlated with (maximum) elevation and temperature. When considering only the true island datasets, there was still a significant negative correlation 495 496 between elevation and the slopes of the three IDARs. There were also negative correlations with ArchArea, although for the ISAR this was not significant. When controlling for ISAR 497 498 slope, there were no significant correlations, either for all datasets or just true island datasets.

499 Q3: Avifaunal community assembly: FD and PD effect sizes and their scaling relationships

The avifauna of most islands (87% for FD, and 79% for PD) exhibited random structure 500 regarding FD.ES and PD.ES values, with a small proportion being characterised as 501 significantly clustered (11% for FD, and 19% for PD). Very few island avifaunas were 502 significantly overdispersed (2% for both metrics). Mean ES values were -0.51 for FD and -503 504 0.89 for PD, indicating a slight tendency toward clustering (Fig. S7a). FD.ES and PD.ES 505 significance results were equivalent for most islands, but there were notable exceptions (Fig. 6); for example, 126 of the islands had significantly negative PD.ES values, but non-506 507 significant FD.ES values (Fig. 6).

Across all datasets, the intercept-only model had the higher mean AIC_c weight, and provided the best fitting candidate model the most times, for both the FD.ES and PD.ES–area relationships (i.e., lowest AIC_c in 34 and 37 out of 51 datasets, respectively). However, there were notable exceptions, with some FD.ES and PD.ES–area relationships exhibiting positive and negative linear relationships (Fig. 3). When looking at true and habitat islands separately (Figs. S3-S6 in Appendix S3), it was apparent that, for true islands, the relative performance of the linear model, regarding both ES–area relationships (but particularly PD.ES), improved.

515 Considering cases where the linear model provided the best fit, there were nine 516 positive and eight negative relationships for the FD.ES–area, and eight and six respectively 517 for the PD.ES-area relationship. The majority of significant linear cases were true island

- 518datasets (11 cases for both the FD.ES and PD.ES relationships) (see Appendix S3). The
- median slope of the linear model across all datasets was 0.02 (-0.03 and 0.03 for true and
- habitat island datasets, respectively) for the FD.ES–area and 0.15 (0.13 and 0.15) for the
- 521 PD.ES-area relationship (Fig. S7b). Interestingly, when only focusing on the ten volcanic
- 522 oceanic island datasets, the median linear slope values were higher: 0.35 and 0.55 for the
- 523 FD.ES and PD.ES-area relationships, respectively (see Fig. S8 in Appendix S3).

The slope values from the FD.ES and PD.ES–area relationships significantly differed according to a mixed-effects model when considering all datasets together ($\chi 2 = 4.5$, P = 0.03), but not true and habitat islands separately. Considering all datasets, there were significant positive correlations between the FD.ES and PD.ES–area relationship slopes and (maximum) elevation (Fig. 5). Considering only the true island datasets, there were significant positive correlations between both slopes and MeanDist, isolation, and elevation, and a significant negative correlation between PD.ES–area slope and AreaScale (Fig. 5).

531 *Q4: The effect of including extinct and introduced species on diversity scaling*532 *relationships*

533 The power model z-value for the ISAR, IFDAR and IPDAR followed an interesting and relatively consistent pattern across the three dataset types: historic fauna (A), current fauna 534 excluding introduced species (B) and current fauna including introduced species (C) (Fig. 7). 535 536 For these three IDAR types, z decreased or remained roughly constant between A and B, and 537 then generally increased between B and C. This pattern was stronger for certain datasets (e.g., Society Islands, Marianas) compared to others (Fig. 7). The (paired) Wilcoxon signed-rank 538 tests indicated that the differences between A and B were significant for the ISAR (P = 0.03), 539 IFDAR (P = 0.02) and IPDAR (P = 0.02). The differences between B and C were also 540 541 significant for all three IDAR types (P = 0.02, 0.02 and 0.04 for the ISAR, IFDAR and IPDAR, respectively), while the differences between A and C were non-significant. For the 542 FD.ES-area and PD.ES-area relationship slopes, there were significant decreases in slopes 543 between A and B (P = 0.01 and 0.04) and A and C (P = 0.04 and 0.01), but the differences 544 545 between B and C were not significant (P > 0.05) (Fig. 7).

546 Comparing models for the prehistoric and current avifaunas (excluding introduced 547 and marine species) for five datasets, the z-values decreased or remained relatively constant 548 for the ISAR, IFDAR and IPDARs, with the exception of Hawaii, for which z-values 549 increased (Fig. 8). For the FD.ES and PD.ES–area relationships, with two exceptions

550 (Marianas for FD.ES and New Zealand for PD.ES) the slope of the relationships decreased

between the two time periods (Fig. 8).

552 Sensitivity analyses

The full results of all sensitivity analyses are presented in Appendices S4-S7. First, re-553 554 running the analyses using body-size corrected traits to construct the functional dendrogram resulted in very similar findings (Appendix S4). Second, re-running the analyses after 555 556 subsetting the datasets to only include land birds also generated mostly similar results (Appendix S5). The main differences here related to the exploratory correlations (e.g., no 557 significant associations involving the number of islands or isolation), and the introduced and 558 extinct species analysis: while some datasets followed the same pattern as the main results, 559 560 the general pattern was less clear and none of the ISAR, IFDAR or IPDAR paired Wilcoxon 561 tests were significant, although this is perhaps expected given the smaller number of datasets involved (Appendix S5). Third, undertaking the model selection using residual assumption 562 checks resulted in very similar results (Appendix S6). The power model passed the 563 assumption checks for 41, 41 and 45 datasets for the ISAR, IFDAR and IPDAR, respectively. 564 Using the z-values from the linear $(log_{10}-log_{10})$ power model also generated similar results 565 (Appendix S6). Fourth, using a randomly selected trait imputation run in combination with an 566 individual Jetz et al. (2012) phylogeny resulted in very similar findings (Appendix S7). 567

568

569 **DISCUSSION**

570

571 Q1 and Q2: The form of island diversity–area relationships

In general, and in contrast to our prediction (Q1) that asymptotic models would provide a 572 better relative fit to the IFDAR and IPDAR, the three island diversity-area relationships 573 (IDARs; i.e., the island species-area relationship [ISAR], the island functional diversity-area 574 relationship [IFDAR], and the island phylogenetic diversity-area relationship [IPDAR]) were 575 best modelled by non-asymptotic convex-upward models, although the linear model provided 576 the best fit in certain cases (see also Triantis et al., 2012). Inspection of the model fit plots 577 578 (Fig. 3) also showed that the form of the three primary IDARs was generally convex-upward. 579 This matches the recent findings of a study on habitat islands by Dias et al. (2020), but for a much larger number of datasets and broader range of island types. 580

As expected (Q2), we observed that, for a given dataset, the ISAR was generally 581 steeper than the IPDAR, which was in turn steeper than the IFDAR. These results indicate 582 that as island area increases, more species are sampled from the archipelagic pool. These 583 additional species initially add novel traits and phylogenetic branches to the island 584 communities, but this process slows down with increasing richness as an increasing 585 586 proportion of these species are functionally, and to a slightly lesser extent phylogenetically, redundant (see also discussion in Karadimou et al., 2016; Schrader et al., 2021; Ferreira-587 Arruda et al., 2022). 588

589 Our exploratory correlation modelling indicated that IDAR slope was significantly 590 negatively associated with elevation, when focusing on all datasets and true islands datasets separately. For true islands, this may seem counterintuitive as many of the relatively isolated 591 592 (mostly oceanic) archipelagos (e.g., Hawaii, Cape Verde, New Zealand) have high elevation, and previous studies have theorised and shown that ISAR slope *increases* with isolation 593 594 (Whittaker et al., 2017). This pattern could be specific to birds: due to their relatively high dispersal ability and the fact that many of the oceanic archipelago datasets are lacking very 595 small islands, it is possible that many bird species are present on most islands, thus lowering 596 IDAR slope. There could also be an effect of anthropogenic extinctions given that these 597 archipelagos are also those that have likely experienced the most extinctions, and our results 598 599 indicate that in many cases (when excluding introduced species) these extinctions have lowered IDAR slope. For the true island dataset correlations, while few associations were 600 significant, OLS regression models including all predictors explained a relatively large 601 proportion of the variation in the slope of the ISAR, IFDAR and IPDAR (R^2 values: 0.72 -602 0.76; adjusted R^2 values: 0.56–0.63). This matches the results of previous studies (e.g. 603 Triantis et al., 2012; Matthews et al., 2019a) and suggests that the lack of significant 604 605 correlations here may be due to smaller sample sizes and thus a lack of power.

606 Q3: Island community assembly patterns and processes

Overall, we found that the majority of island avifaunas were classified as being randomly
assembled in terms of functional diversity (FD) and phylogenetic diversity (PD), although a
sizable minority were significantly clustered (11-19%). This could indicate that neutral
dynamics predominate on most islands, as assumed within the core model of island
biogeography (MacArthur & Wilson, 1967). It should be noted that our null model used the
archipelago species list as the pool rather than a wider (mainland) species pool, as we were

not focused on testing for the effects of mainland to island filters (see Triantis et al., 2022). 613 Nonetheless, if these results were viewed in isolation, it would be tempting to conclude that 614 there were no patterns of interest beyond the 'null' observation that most islands had random 615 functional and phylogenetic structure. However, analysis of the scaling of these assembly 616 patterns (effect size [ES] values) reveals a more complex picture, at least in certain cases. For 617 618 many datasets, the relationships between ES values (assembly patterns) and island area are indeed relatively flat. This indicates that, for these datasets, the convex-upward scaling of 619 unstandardized FD and PD with area was primarily a result of increasing richness with island 620 621 area, rather than changes in the dominant community assembly processes. However, there 622 were numerous exceptions to this pattern, particularly regarding the FD.ES-area relationship, where the linear model provided a better fit for a third of the 51 datasets. 623

624 Based on previous work (e.g., Chen et al., 2020; Matthews et al., 2020), we had hypothesised that, owing to limited habitat availability, smaller true islands would be 625 626 characterised by functional and phylogenetic clustering. In contrast, larger true islands, with a wider range of habitat types, were expected to display functional and phylogenetic neutrality 627 or overdispersion (Carvajal-Endara et al., 2017; Matthews et al., 2020). Together, this would 628 629 result in a positive linear relationship between richness-corrected FD and PD and island area (i.e., less clustering with increasing area). However, approaching half of the datasets where 630 the linear model provided the best fit exhibited a negative relationship (i.e., more clustering 631 with increasing area). This is the opposite of our theoretical prediction (Fig. 3), but has been 632 observed previously, such as for exotic plants in US National Parks (Li et al., 2018) and 633 mammals on oceanic islands (Si et al., 2022). One explanation for this pattern can be found in 634 Diamond's (e.g., 1975; for a review see Whittaker & Fernández-Palacios, 2007) work on 635 assembly rules, which argues that very small islands can only support one bird species per 636 guild (e.g., one fruit pigeon) due to limited niche space and increased interspecific 637 competition. As island area increases, the number of species per guild or habitat type (which 638 639 will be relatively functionally redundant) able to coexist on an island also increases. If the amount of niche space and number of guilds increases with area at a slower rate than for the 640 number of species, this will increase the amount of functional and to a lesser extent 641 phylogenetic redundancy on islands. Following this logic, smaller island assemblages would 642 be expected to be overdispersed, with clustering increasing with island size, ultimately 643 resulting in a negative relationship between richness-corrected FD and PD and island area 644 645 (see also Si et al., 2017). Future research could test this theory by analysing the density of

species per guild or habitat type for archipelagos that have negative ES-area relationships.
The scaling of speciation rate with island area (see Whittaker & Fernández-Palacios, 2007)
could theoretically also result in this pattern, at least for archipelagos where speciation is a
source of new bird species. Specifically, if a small number of colonizers radiate on the larger
islands into numerous closely related species without substantial trait disparification, this
could result in increased clustering on the larger islands.

Interestingly, boxplots of the linear slope values across island types indicate that the 652 653 average slope of both the FD.ES and PD.ES-area relationships was larger on oceanic islands 654 (relative to other true islands and habitat islands; Fig. S8), particularly for PD.ES, and, in our 655 exploratory correlations restricted to true islands, isolation, elevation and MeanDist had positive correlations with the slope. Thus, it could be the case that our theoretical prediction 656 657 is more applicable to large isolated oceanic island systems, than to other island types. However, it should be noted that, while the median slope was relatively high, for most of the 658 659 oceanic dataset ES-area relationships the best model was in fact the intercept-only model. This could partly be because most of these datasets have relatively few data points (a 660 characteristic of many oceanic archipelagos), reducing the power of the test and increasing 661 the effect of noise in the data (e.g., due to anthropogenic impacts). For habitat islands, there 662 was a larger proportion of cases where the intercept-only model provided the best fit. This 663 likely reflects the fact that they are often relatively noisy systems (Matthews, 2021), and can 664 vary substantially in terms of various properties. For example, large forest fragments may 665 666 contain a range of habitat types or be relatively homogenous (e.g., see Fig. 1 in Willrich et al., 2019; dos Anjos et al., 2022). 667

668 It is important to note that there are several limitations associated with the community assembly framework used here (see Münkemüller et al., 2020, for a review). These include (i) 669 670 a focus on specific patterns ignores the reality that a given FD / PD pattern can be produced by multiple processes (Mayfield & Levine, 2010); and (ii) that, as mentioned above, defining 671 672 the species pool as the archipelago species list can only underestimate filtering by excluding species unable to reach or persist on the archipelago (Carvajal-Endara et al., 2017; Si et al., 673 674 2022), but (iii) also underestimates competition by ignoring 'dark diversity' (i.e., species excluded from the archipelago due to past competition will not be present in the pool; 675 676 Münkemüller et al., 2020).

677 Q4: The effect of anthropogenic introductions and extinctions on IDARs

Humans have introduced hundreds of species to islands (Blackburn et al., 2021). Our results
supported our prediction (Q4) that the inclusion of introduced species would generally lead to
steeper IDARs. These increases in z-values were relatively modest in absolute terms but were
statistically significant. It is known that larger islands tend to have higher rates of
anthropogenic colonisation pressure and thus experience more introductions (Baiser & Li,
2018; Blackburn et al., 2021), which will, all else being equal, have the effect of steepening
the ISAR.

685 Particularly on certain oceanic island archipelagos, human colonisation precipitated a 686 wave of avian extinctions (Whittaker & Fernández-Palacios, 2007; Boyer, 2008; Boyer & 687 Jetz, 2014; Sayol et al., 2021; Matthews et al., 2022; Triantis et al., 2022). However, while recent work has started to look at the effects of species extinctions on island diversity and FD 688 689 (e.g., Boyer & Jetz, 2014; Sobral et al., 2016; Matthews et al., 2022; Si et al., 2022; Triantis et al., 2022), how these extinctions have affected IDARs has not been fully evaluated. 690 691 Interestingly, and in contrast to our theoretical prediction (Q4), we found that the slopes of the ISAR, IFDAR and IPDAR significantly decreased between the historic and current period 692 (excluding introduced species). This could indicate (i) that extinctions were more prevalent 693 694 on the larger islands due to greater human impact, or (ii) that there is a bias resulting from greater knowledge of the historic fauna on larger islands. One other caveat is that Franklin & 695 Steadman's (2008) conceptual model was based on all extinctions, but for most archipelagos 696 we lack adequate data at the island-level for species that went extinct prior to 1500 CE. 697 698 However, many archipelagos are known to have suffered numerous extinctions prior to 1500 CE (Steadman, 2006; Hume, 2017; Sayol et al., 2021). Our analysis of five datasets that did 699 include pre-1500 extinct species (Fig. 8) broadly confirmed the decrease in the ISAR, IFDAR 700 701 and IPDAR slope between the pre-human colonisation avifauna and the current avifauna 702 excluding introduced species, although Hawaii was an exception (Fig. 8).

Taking both the above findings together, it appears in several cases that introduced 703 704 species have 're-calibrated' the IDARs such that the slopes are more like the historic period 705 including extinct species; indeed, there were no significant differences in the z-values 706 between the historic and current (with introduced species) assemblages. A similar pattern is observed with the power model R^2 values, with higher values observed for the historic 707 (average R^2 of power model across ISAR, IFDAR and IPDAR = 0.66) and introduced 708 709 datasets (0.63), with lower values for the current fauna without introduced species (0.53), for all three IDARs. Interestingly, Hawaii again provides an exception to this pattern, with the 710

inclusion of introduced species lowering or not changing IDAR slopes. This could indicate
that introductions to that archipelago (or at least the islands in the archipelago that comprise
our dataset) are occurring more independently of island area.

We also observed that extinctions resulted in a statistically significant decrease in slope for the FD.ES and PD.ES–area relationships (Fig. 7), a pattern also apparent in the analysis of the five pre-1500 datasets (Fig. 8). One interpretation of this is that anthropogenic extinctions are leading to more random patterns of community assembly, or even greater clustering due to the selective extinction of certain types of species (e.g., large-bodied; Boyer, 2008; Boyer & Jetz, 2014; Hume, 2017; Matthews et al., 2022).

720 A notable caveat is that the prehistoric and historic datasets analysed here likely underestimate the true island composition at these time periods. First, there are known biases 721 722 in the (sub)fossil record, such as large-bodied species being more likely to leave material 723 evidence than small-bodied species. Second, the fossil record is likely incomplete for almost all islands. Third, several studies present data on which islands extinct species occurred on, 724 with fewer presenting data on the past distributions of extant species. Finally, the trait 725 estimation and imputation, and phylogeny grafting, procedures obviously involve a certain 726 degree of uncertainty. Appendix S2 provides a more detailed discussion of these issues. 727

728 Concluding remarks

729 Overall, we have shown that increasing richness with island size is the main driver of the IPDAR and IFDAR for most datasets, although there are numerous exceptions to this pattern. 730 We also find that archipelagos with the steepest ISARs exhibit the biggest differences 731 between ISARs and the IFDAR / IPDAR. These results indicate that, within a given 732 archipelago, there is an increasing amount of functional and phylogenetic redundancy on 733 larger islands. As a next step, it is necessary to test whether the patterns observed here are 734 consistent across taxonomic groups, particularly those with lower dispersal ability compared 735 736 to birds, given that ISAR slope has been shown to vary between taxa (Triantis et al., 2012). In 737 addition, as more data on extinct island species distributions become available, it will be necessary to evaluate further how anthropogenic extinctions, in combination with 738 introductions, have affected IDAR form and slope, and whether this re-calibration effect is a 739 general pattern. This will ultimately improve our knowledge of the 'island biogeography of 740 the Anthropocene'. 741

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751 FIGURES

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Figure 1. The analytical workflow followed, linked to the four primary research questions. Top row:
we used the full presence-absence matrix for a given dataset (used to calculate island species richness,
S), alongside a functional dendrogram (used to calculate island functional diversity, FD) and a

- phylogeny (used to calculate island phylogenetic diversity, PD). Second row: we fit a set of 20
- diversity-area relationship (IDAR) models to the island area, SR, FD and PD data (here the coloured
- ⁷⁹² lines represent the fit of the power model; blue = ISAR, red = IPDAR, and yellow = IFDAR), and
- assessed variation in the slope of the power model. Third row: for each dataset, we used a null model
- to calculate island FD and PD effect sizes (ES) independent of richness. For each dataset, we fitted a
- linear model to the log₁₀(Area)–ES relationships, comparing it with an intercept model. We used the
 ES values to test the association between FD.ES significance and PD.ES significance at the island
- level (+ = significantly positive ES value; = significantly negative ES value; NS = non-significant
- ES value). Bottom row: for subsets of datasets, we ran the analyses three times the historic fauna
- including extinct species (A), and the current fauna excluding (B) or including (C) introduced species.
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Figure 2. Generally, the shape of IDARs consistently had a convex-upward nature with some variation in exact model shape between the ISAR, IFDAR, and IPDAR. Regarding the ES– area relationships, the intercept model had the higher mean AICc weight for both FD and PD, meaning a lack of relationship between FD.ES and PD.ES and area for many datasets. The bar charts show the mean model AIC_c weights across all datasets in which a model fit converged, for the five IDARs. The total number of datasets is 51. Full model names can be found in Table S2. For the FD.ES–area and PD.ES–area relationships, the two models were

812 fitted in semi-log space, for the other IDARs in untransformed space.

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Figure 3. Some island systems exhibited positive FD.ES and PD.ES-area relationships, and 817 others negative relationships. The top two rows show the IDARs of a dataset of birds 818 (number of species = 54) in 11 true islands in the Galápagos, generated using five diversity 819 metrics: species richness (ISAR), functional diversity (IFDAR), phylogenetic diversity 820 (IPDAR), and the FD (FD.ES-area) and PD (PD.ES-area) effect sizes. The bottom row 821 shows the two ES-area relationships for a dataset of birds (number of species = 101) in 77 822 true islands in the Aegean (Simaiakis et al., 2012). In the top row plots, the different coloured 823 lines represent the fits of up to twenty competing models, and the thick black line represents a 824 multi-model averaged curve generated using the AIC_c weights of the individual model fits. In 825 the middle and bottom row plots (left and middle), the dark green line is the fit of a standard 826 linear model, while the light grey line is the fit of an intercept-only model. For the FD.ES-827

- area and PD.ES–area relationships, the two models were fitted in semi-log₁₀ space, for the
- 829 other IDARs in untransformed space. Increasing ES values from zero denote greater
- 830 overdispersion, while decreasing values from zero denote greater clustering. The two bird
- 831 photos show example species from each archipelago: the middle right plot shows a lava gull
- 832 (*Larus fuliginosus*), the rarest gull in the world and a species endemic to the archipelago, and
- the bottom right plot shows a Rüppell's warbler (*Sylvia rueppelli*), a species that breeds in
- 834 Greece, Turkey and the Aegean Islands. Middle row photo by Andy Morffew and under
- 835 license (https://creativecommons.org/licenses/by/2.0/); bottom row photo by Mick Sway and
- under license (https://creativecommons.org/licenses/by-nd/2.0/).
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Figure 4. The difference between the ISAR z-value and the IPDAR and IFDAR z-values
increases with increasing ISAR z-value. The figure shows the relationships between the zvalues of three IDARs, plotted as a function of the ISAR z-value rank (higher rank = steeper
ISAR): the ISAR (black lines and points), the IPDAR (blue lines and points), and the IFDAR
(red lines and points). Different symbols are used for habitat (circles) and true island
(triangles) systems. The z-values were generated from fitting the non-linear power model to
the bird IDARs of 51 island datasets.



Figure 5. Some characteristics of archipelagos are correlated with IDAR slopes. The figures 851 show Pearson's rank correlation heatmaps, with IDAR slope on the x-axis and various 852 archipelago-level predictors on the y-axis. For the ISAR, IFDAR and IPDAR, slope was 853 measured as the power model z-value. Correlations for IFDAR and IPDAR z-values were 854 also undertaken using partial correlation using ISAR z-values as a covariate. For the ES-area 855 856 relationships, the slope was the slope of a linear model fitted in semi- log_{10} space. Correlations 857 were undertaken twice, once using all 51 datasets (A), and once using only the 26 true island datasets (B). Significant coefficient values (P < 0.05) are indicated using black circles. Cell 858 colour indicates correlation strength. Grey cells indicate a correlation was not undertaken for 859 860 that variable combination. Predictor acronyms are GA = Gamma, C = power model c-value, AA = ArchArea, AS = AreaScale, NI = number of islands, MD = MeanDist, IS = isolation, 861 EL = elevation, and TP = temperature. Note that for the IFDAR and IPDAR correlations, 862 Gamma was the total functional or phylogenetic richness. 863

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Figure 6. The relationship between FD.ES values and PD.ES values for 1,051 islands varied from a 1:1 relationship, but most values were not significantly different from the null expectation. ES values were generated using a null model (999 iterations; see main text for details). The thick black line is the fit of a standard linear model, while the thin line is a line with intercept of zero and slope of one. Points are coloured based on a pairwise comparison of significance for FD.ES and PD.ES values and match the inset grid. Within the inset grid, a '-' sign indicates significantly negative ES values, and '+' indicates significantly positive values; NS = non-significant values.

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Figure 7. Species extinctions and introductions change IDAR slopes in a variety of ways across different island systems. The figure shows the effects of including vs. excluding extinct and introduced species on the power model slope of the ISAR, IFDAR and IPDAR (top row), and on the slope of the linear model fitted to the (semi-log₁₀) FD.ES and PD.ES-area relationships (bottom row), for ten true island datasets. Each trio of the same-coloured circles joined by the same-coloured line represents three different datasets for the same archipelago: (A) historic fauna including extinct species, (B) current fauna excluding introduced species, and (C) current fauna including introduced species. For two datasets (Azores and Ryukyu Islands) there is no historic dataset (i.e., period A). Note the different y-axis scales in the different plots.





Figure 8. The figure shows the effect of including vs. excluding all known extinct species 907 (prehistoric and historic extinctions) on the power model slope of the ISAR, IFDAR and 908 IPDAR (top row), and on the slope of the linear model fitted to the FD.ES and PD.ES-area 909 relationships (bottom row), for five true island datasets (Mar. = Marianas, NZ = New 910 Zealand; Haw. = Hawaii; Cook = Cook Islands; Can. = Canaries). Each pair of coloured 911 912 circles joined by a black line represents two different datasets for the same archipelago: pre-913 historic fauna including extinct species, and current fauna excluding introduced species. In this analysis, all marine species were removed from the datasets prior to model fitting and 914 915 some islands were removed due to a lack of fossil data (i.e. the Modern z-values may differ 916 from those in Figure 7). Note the different y-axis scales in the different plots.

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