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Deterministic assembly and anthropogenic extinctions drive convergence of island bird communities

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1	Type of Article: Research Papers
2	
3	Deterministic assembly and anthropogenic extinctions drive convergence of
4	island bird communities
5	
6	Short running title: Community convergence in island avifaunas
7	
8	ABSTRACT
9	Aim: Whether entire communities of organisms converge toward predictable structural
10	properties under similar environmental conditions remains controversial. We tested for
11	community convergence in birds by comparing the structure of oceanic archipelago assemblages
12	to their respective regional species pools.
13	Location: Eighteen major oceanic archipelagos of volcanic origin with global distribution
14	Major taxa studied: Terrestrial birds
15	Methods: We compiled a comprehensive database of morphological trait and phylogenetic data
16	for 6,579 bird species, including species known to have become extinct due to human activities.
17	We quantified morphological and phylogenetic dissimilarity among species between pairs of
18	archipelagos, using a modified version of the mean nearest taxon distance. We tested for
19	convergence by estimating whether overall mean turnover among archipelagos and pairwise
20	turnover between archipelagos was lower than expected by chance.
21	Results: For all land-birds, we found that turnover in body plan, body mass and phylogeny
22	among archipelagos was significantly lower than expected. Seventeen (of 18) archipelagos
23	showed significant body plan and phylogenetic similarity with at least one other archipelago.
24	Similar convergent patterns of community assembly were detected in different subsamples of the
25	data (extant species, endemics, native non-endemics, and Passeriformes only). Convergence was
26	more pronounced for extant species than for extant and extinct species combined.
27	Main conclusions: Consistent convergence in phylogenetic and morphological structure among
28	archipelagic communities arises through a combination of non-random colonization and <i>in situ</i>
29	adaptation. In addition, by including data from extinct taxa, we show that community

convergence both precedes and is accentuated by the anthropogenic extinction of endemic
 lineages. Our results highlight the potential role of non-random extinction in generating patterns
 of community convergence and also show that convergence existed even prior to anthropogenic
 extinctions as a result of deterministic community assembly in similar environmental settings at

- 34 the global scale.
- 35

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Keywords: birds, community assembly, convergence, determinism, extinct species, historical
 contingency, island biogeography, morphological traits, oceanic archipelagos.

39 INTRODUCTION

Whether spatially isolated ecological communities tend to converge under similar environmental 41 42 conditions towards predictable structural properties, such as traits or functional space occupied, has remained a controversial question for half a century (MacArthur, 1972; Cody & Mooney, 43 1978; Ricklefs & Travis, 1980; Blondel et al., 1984; Samuels & Drake, 1997; Fukami et al., 44 2005; Melville et al., 2006; Winemiller et al. 2015; Moen et al., 2016; Santos et al. 2016; Mazel 45 et al., 2018). Although evolutionary convergence – the emergence of similar species traits or 46 syndromes from divergent evolutionary starting points in geographically distant but 47 environmentally similar locations – is a well-established phenomenon (e.g. Losos et al., 1998; 48 49 Schluter, 2000; Gillespie, 2004; Muschick et al., 2012; Mahler et al., 2013), the question of 50 whether convergence applies to entire communities remains open to debate. For example, historical contingencies (legacies from previous system states) vary across regions and typically 51 generate unpredictable outcomes in the structural properties of local communities (Gould, 1989; 52 see also discussion in Losos & Ricklefs, 2009). 53

A major challenge for the study of community convergence is posed by extinct taxa. In 54 particular, if anthropogenic extinctions are non-random (e.g. Steadman, 2006; Sayol et al., 55 2020) and biased towards outliers, such as the largest and smallest species in an assemblage 56 (e.g. Ripple et al. 2017), then apparent evidence of community convergence may be explained 57 by non-random or clustered extinctions rather than any deterministic process based on 58 59 environmental filtering or evolutionary adaptation (Tobias et al., 2020). Robust tests of community convergence therefore need to account for extinct taxa, particularly in island 60 61 systems where anthropogenic extinctions have often altered native communities (e.g.,

Steadman, 2006; Boyer & Jetz, 2014; Sobral et al., 2016; Sayol et al. 2021). However, previous
 studies of community convergence – most of which have focused on islands – have rarely (if
 ever) accounted for extinctions.

To date, community level convergence has primarily been tested, and in some cases 65 detected, at the level of individual islands (e.g. Gillspie, 2004; Losos, 2011; Mahler et al., 2013), 66 but has never been evaluated at the archipelago level. Yet several filtering processes operate at 67 the scale of archipelagos (Fig. 1), with convergence generated via two primary pathways: 68 (a) the non-random selection of colonists reaching the archipelago from the regional species 69 pool, resulting in greater phylogenetic or morphological similarity than expected by chance, and 70 (b) in situ evolutionary change, including lineage diversification, leading to greater trait 71 similarity among archipelagos than expected by chance (Wiens & Graham, 2005; Emerson & 72 73 Gillespie, 2008; Grant & Grant, 2008; Losos & Ricklefs, 2009; Barnagaud et al., 2014; Weigelt 74 et al., 2015). The relative contribution of these alternative pathways to community convergence is unclear, although they should leave different signatures in the community 75 structure of native non-endemic and endemic lineages, respectively. 76

To test for community convergence in the phylogenetic and morphological structure of 77 oceanic archipelago bird assemblages, in relation to their respective regional species pools, we 78 compiled comprehensive data on species composition, phylogenetic history and 79 morphological traits for birds occurring on volcanic archipelagos across the Pacific, Atlantic 80 and Indian oceans. Since faunal assembly is mostly sourced from larger, older and more 81 complex continental pools, we also collected equivalent data for a far larger number of bird 82 83 species occurring in the continental source pools for each archipelago (see also Graves & Gotelli, 1983; Cardillo et al. 2008; Santos et al. 2016 for previous approaches). We focused 84 on all extant land-bird species, as well as lineages driven to extinction by anthropogenic 85 86 causes. The focal archipelagos share five key features: limited land area, persistent geographical 87 isolation, volcanic origin, tropical/sub-tropical latitude, and oceanic climate (Whittaker & 88 Fernández-Palacios, 2007; Gillespie & Clague, 2009; Weigelt et al., 2013; Triantis et al., 2015).

Volcanic oceanic archipelagos have long been considered ideal systems for exploring
 the processes structuring ecological communities inasmuch as they represent replicated
 natural experiments in faunal assembly (e.g. Whittaker & Fernández-Palacios, 2007; Grant &
 Grant, 2008; Losos & Ricklefs, 2009). At the archipelagic level, island communities respond

to the insular geography on evolutionary time scales, with species undergoing 'taxon cycles', 93 i.e., sequential phases of expansion and contraction across an archipelago (Wilson, 1959; 94 Ricklefs & Bermingham, 2002), and with the divergence of populations in allopatry being 95 arguably the main driving force of diversification (Grant & Grant, 2008; Losos & Ricklefs, 96 2009). Thus, oceanic archipelagos can be seen as macroevolutionary metacommunities, i.e., 97 sets of interacting island communities linked by dispersal. They therefore represent a higher 98 level of hierarchical organization than individual islands and are amenable to framing 99 analyses of large-scale patterns such as community-level convergence (see also Triantis et al., 100 2015; Whittaker et al. 2017; Valente et al. 2020). 101

We developed a novel framework to test for community convergence in both 102 morphological and phylogenetic structure of archipelagic land-bird faunas relative to their 103 respective regional species pools (Fig. 2A). To assess the influence of different assembly or 104 105 disassembly mechanisms, we re-ran our analyses on five subsamples: (i) native non-endemic species, (ii) endemic species (including extinct species), (iii) a subsample with all extinct species 106 removed, and (iv) a monophyletic group (i.e. Passeriformes) that is also the largest order of 107 birds. Our results show that multiple dimensions of archipelagic bird communities are more 108 109 similar than expected by chance, even accounting for the influence of extinction, providing strong support that community convergence arises through deterministic community assembly. 110

111 112

MATERIAL AND METHODS

113 Species lists and regional pools

114 Contemporary biogeographical patterns on islands have been strongly influenced by historic and pre-historic anthropogenic extinctions (Steadman, 2006; Hume, 2017; Valente et al., 2020). 115 Thus, to understand how species' arrivals and subsequent evolutionary dynamics interact to 116 establish patterns of trait diversity, it is important to include species known to have become 117 extinct due to human activities. We collected data on composition and species-level traits for the 118 119 avifaunas of 18 volcanic oceanic archipelagos: Austral islands, Azores, Canaries, Comoros, Cook Islands, Fernando de Noronha, Galápagos, Gulf of Guinea, Hawaii, Juan Fernández, 120 Madeira, Marquesas, Mascarenes, Pitcairn, Revillagigedo, Samoa, Society, and Tristan da Cunha 121 (Tables 1 & S1; Fig. 2). For each archipelago, we collated lists of the endemic and native non-122 endemic species, including all known species extinctions since human colonization (e.g. 123

Steadman, 2006; BirdLife International, 2017; Hume, 2017; Sayol et al., 2020; Valente et al., 124 2020). A list of the data sources is found in Appendix 1 (see also Supporting Information, Data 125 S1). Roughly one-third (157) of the species are extinct (Table S2 & Data S1). To focus our 126 analyses on species strictly relying on terrestrial habitats, we restricted our sample to land-birds, 127 excluding marine and aquatic species. Of 495 species in our sample, 348 (70%) are archipelagic 128 endemics, highlighting the evolutionary independence of many archipelagic avifaunas. However, 129 there are cases of non-endemic archipelagic species that are inferred to have colonized the 130 archipelago in question from a nearby archipelago, such as Anthus berthelotii and Serinus 131 canarius, both endemic to Madeira and the Canary Islands (see Valente et al., 2020). However, 132 only 41 (8%) native non-endemic species are present on more than two archipelagos. 133

To generate regional pools of species as sources for the assembly of each archipelago, we 134 identified the avifaunal regions to which they belong, based on Holt et al. (2013) (Table S3 and 135 136 Fig. 2A). These 10 regions contain 6,231 land-bird species (Data S2). To validate and improve our approach, we compared the zoogeographical region assigned to each archipelago from Holt 137 et al. (2013) with source region reconstructions based on phylogenetic relationships between 138 island and mainland species found in the literature, when available. Despite some discrepancies, 139 140 including a few cases where the species pool was a nearby archipelago rather than the mainland, we found that the zoogeographical regions in Holt et al. (2013) were closely aligned with the 141 source region reconstructions (see Supporting Information). We also tested the sensitivity of our 142 approach to a more spatially restricted definition of species pools by defining a buffer of 100 km 143 width from the nearest coast to each archipelago and only sampling bird species with a 144 145 geographical distribution overlapping with the buffer. Additionally, to remove any biases arising from the way source pools are delimited, we conducted a further set of analyses restricted to 146 archipelagos in the same zoogeographical region, i.e. with a common source pool. This was 147 possible for Macaronesia (Azores, Madeira and Canary Islands archipelagos) and the South 148 Pacific (Austral Islands, Cook Islands, Marquesas, Samoa, Pitcairn and Society), the only two 149 150 regions with more than two archipelagos (see Supporting Information).

Defining an appropriate species pool for archipelagos poses substantial challenges (e.g. Si et al. 2022). The sensitivity analyses described above provide an assessment of species pool selection, but some limitations to our approach should be highlighted: (1) zoogeographical regions were defined using current species distributions, and thus might not accurately represent

- species distributions at the time of colonization; (2) all species in a given pool have the same 155 probability of colonizing and establishing on the focal archipelago, and thus the approach does 156 not account for differences in dispersal ability and niche compatibility (e.g. climate, resource 157 use) between species; and (3) source pools defined at the species level potentially misrepresent 158 the available pool of colonizers, and at least one recent study advocates focusing on higher taxa 159 (genera or families) with geographic distributions overlapping with the focal assemblage (see Si 160 et al. 2022). An additional factor is that extinct species were included in the archipelago species 161 lists, but not for the regional pools, primarily due to the lack of accurate distributional data for 162 extinct continental species. However, this inconsistency seems unlikely to bias our results 163 because recent extinctions have been far more prevalent in island communities than continental 164 source regions. Of all known bird extinctions globally, island endemics comprise 81% (468 of 165 581 species) of extinctions during the last 125,000 years, and 93% of extinctions since 1500 AD 166 (Sayol et al. 2020). 167
- 168

169 Morphological and phylogenetic data

We collated a range of morphometric data for our combined sample of 6,579 species (Data S1, 170 S2). For each extant study species (n = 6,423), we used a global dataset derived from linear 171 measurements of wild birds and museum specimens (Pigot et al. 2020; Tobias et al., 2022) to 172 compile estimates of wing length, tail length, tarsus length, and beak length (mm). These traits 173 were selected because they reflect the overall body plan (bauplan), and correlate with important 174 dimensions of the avian niche, such as habitat use, dispersal and foraging strategy (Pigot et al., 175 176 2020). We also compiled body mass (g) from Wilman et al. (2014). For 36 (23%) of 175 extinct species, measurements were extracted from specialist literature. A list of the data sources is 177 found in Appendix 1, see also Data S1 for sources, including Rothschild, 1907; Amadon, 1950). 178 179 For a further 121 (77%) extinct species with missing data, we inferred morphological and body mass measurements from the most morphologically similar extant species available, selecting 180 181 congeners where possible (Tobias et al., 2022). Extant surrogate species were selected based on key skeletal measurements, including the mandible for beak length, humerus for flight 182 capabilities or flightlessness, and the ratio of femur/tibiotarsus/tarsometatarsus to highlight 183 arboreal or terrestrial modifications (Steadman, 2006). As flightless species tend to be relatively 184 heavy, we estimated the body mass of extinct flightless taxa known only from fossil remains 185

with reference to similar-sized extant flightless species, e.g., flightless rails (J. P. Hume, unpublished data). Since all trait data were calculated as species averages, we do not account for 187 intra-specific variation, although previous analyses have shown this to be negligible compared to 188 inter-specific variation in the same avian traits at global scales (Tobias et al., 2022). 189

All morphological traits were \log_{10} -transformed prior to analyses to avoid the influence 190 of extreme trait values and to linearize data distributions for regressions. To quantify body plan 191 differences between species, we measured morphological dissimilarity using log₁₀-transformed 192 lengths of tail, tarsus, beak, and wing after accounting for differences in body mass. We obtained 193 these size-corrected traits using the residuals from a linear regression of trait size against body 194 mass; i.e., the log₁₀-transformed lengths of tail, tarsus, beak, and wing were regressed separately 195 196 against log₁₀-transformed body mass to calculate the residuals (e.g. Ingram & Kai, 2014; 197 Supporting Information, Fig. S1).

198 We based our analyses on the phylogenetic tree from Jetz et al. (2012), using the Ericson backbone with 9,993 species. We selected this backbone topology because it represents a 199 reasonably well-supported hypothesis of the relationships among extant taxa and has been used 200 in many recent studies of avian macroevolution. From a posterior distribution of 1,000 trees 201 obtained from www.birdtree.org, we generated a single maximum clade credibility tree using 202 TreeAnnotator (Drummond et al., 2012). We grafted all extinct species (157) on to this tree using 203 taxonomic constraints and information from the literature (see Supporting Information). 204

205

Colonization events 206

207 We estimated the number of colonization events for each archipelago according to the following rules. When explicit phylogenetic hypotheses were available (e.g., Valente et al., 2020), we 208 examined whether congeneric endemic species from a particular archipelago formed a 209 monophyletic group, and assumed that such cases were the product of a single colonization event 210 (Cornuault et al., 2013). Thus, for a particular archipelago, the number of colonization events 211 212 generating the current endemic avifauna is equal to the number of clades present (mostly genera). Each native non-endemic species was counted as one colonization event. 213

Molecular data are lacking for most archipelagic extinct species, which can lead to 214 215 phylogenetic uncertainty, so we estimated the minimum and maximum number of colonization events for these species. The minimum number of events was calculated by assuming congeneric 216

extinct endemics of an archipelago were monophyletic, thus representing a single colonization;
the maximum number of events was calculated by assuming that extinct genera were non-

- 219 monophyletic, with each species representing a different colonization event (see sections B3 and
- 220 C3 in Supporting Information). Subsequent analyses were implemented in two ways, first using
- 221 the minimum number of colonization events, and then by randomly selecting a number of
- colonization events between the minimum and the maximum.
- 223

224 Measuring morphological and phylogenetic convergence

We quantified differences in body mass, body plan (using body mass-corrected wing, tail, tarsus, and beak length; Supporting Information, Fig. S1), and phylogenetic dissimilarity among species, between pairs of archipelagos, using a modified version of the mean nearest taxon distance (MNTD). This metric was designed to focus solely on morphological or phylogenetic turnover (replacement of species traits or phylogenetic lineages across archipelagos) and herein we refer to it as MNTD_{TURN} (Webb et al., 2008, Holt et al., 2018). For a pair of archipelagos, A and B, MNTD_{TURN} is computed as follows:

232

$$MNTD_{(TURN) A,B} = min\left[\left(\frac{1}{n}\sum_{i=1}^{n}min(d_{iB})\right), \left(\frac{1}{m}\sum_{j=1}^{m}min(d_{jA})\right)\right]$$

234

where *n* and *m* are the species richness of the archipelagos A and B, respectively, *min* d_{iB} is the 235 distance (either morphological or phylogenetic) between each species *i* of archipelago A and the 236 nearest (in terms of either morphological or phylogenetic distance) species of archipelago B 237 while min d_{iA} is the distance between each species *i* of archipelago B and the nearest species of 238 archipelago A. So, if the least diverse archipelago has no unique species, then MNTD_{TURN} is 239 zero. Moreover, if both archipelagos have completely different species and their species richness 240 is equal, then, MNTD_{TURN} equals MNTD (see Supporting Information). Morphological distances 241 (for both body mass and body plan) between species across archipelagos were measured using 242 Euclidean distances, while pairwise phylogenetic distances between species were quantified 243 using a cophenetic distance matrix (i.e. the phylogenetic branch length distance between 244 species). 245

247 Null model

We tested for a pattern of convergent community structure by estimating whether overall mean 248 turnover (MNTD_{TURN}) among archipelagos, and each pairwise MNTD_{TURN} value between 249 archipelagos, was lower than expected by chance. To do so, we compared observed turnover 250 values to those simulated under a null model with random phylogenetic and morphological 251 differentiation. For each archipelago, we simulated a null morphospace and phylogeny, 252 constraining our model to the same number of species, endemic species, and colonization events 253 as those observed for the archipelago (Tables 1, S2 and S5). To simulate a null morphospace and 254 phylogeny for a given archipelago, we first started by randomly sampling colonizers from the 255 respective regional pool (see above). Once sampled, each colonizer was randomly assigned to a 256 specific trajectory: either it stays unchanged (native non-endemic), or speciates (becomes 257 endemic) via anagenesis or cladogenesis (Fig. S2), with the number of native non-endemic and 258 259 endemic species being constrained to the current totals observed in the archipelago (see Supporting Information and Fig. S2). For instance, if two colonization events have generated 260 current totals of one native non-endemic and five endemic species, respectively, in a particular 261 archipelago, then, in our simulation, one colonizer fails to speciate or evolve new traits, while the 262 other gives birth to a monophyletic clade of five endemic species. 263

For each colonizer that undergoes speciation, morphological features of the resulting 264 endemic species were simulated through a Brownian motion model of evolution (BM) 265 (Freckleton et al., 2002). Under a BM model, a trait value changes as a function of time (t) and 266 rate (σ^2), so that the simulated value is normally distributed with the mean equal to its initial 267 value (x_0) and the variance equal to the product of rate and time. For body mass, simulations 268 were performed using a univariate BM model while for body plan, a multivariate BM framework 269 was used to fit the BM model simultaneously to the four size-corrected traits together, while 270 assuming that traits are correlated (Clavel et al., 2015). The BM model was implemented on a 271 birth-death (BD) tree (Fig. S2), with the number of branches corresponding to the number of 272 273 species in the endemic clade (see details in Supporting information). The time since the most recent common ancestor was fixed for the stem node at the geological age of the archipelago 274 (using the oldest island currently present; Valente et al., 2020; Table S1). 275

276 To simulate the BD tree, we identified the family to which each speciating island-277 colonizer belongs, and then estimated speciation rate (λ) and extinction rate (μ) for that family

using the phylogeny retrieved from 6,231 land-bird species of the 10 avifaunal regions included 278 in our study (the 349 endemic species of 18 archipelagos were excluded from this analyses). For 279 families with fewer than 10 species, we sampled species more widely from the order to which 280 the family belongs (see Supporting information). We then applied a BM model to the branches of 281 the BD tree using the estimated trait value of the speciating colonizer (i.e. the ancestral state x_0) 282 as a starting point, while the σ^2 value was retrieved by fitting a BM model (univariate for body 283 mass; multivariate for body plan) to the phylogeny and the traits of the family members as 284 identified above. Therefore, for a given archipelago A, a species S belonging to the family F is 285 randomly selected from the regional pool of potential colonizers, and is allowed to generate an 286 endemic clade containing N species. We used: (1) the geological age of archipelago A, and λ , μ 287 values estimated for the tree of the family F to create the tree of the endemic clade using the BD 288 tree, and (2) the trait value of S as the ancestral state and σ^2 estimated for the tree and traits of 289 family F, to generate trait values for the N species along the BD tree previously generated. It 290 291 should be noted that, for the colonizers that stayed unchanged (native non-endemic species), the island species was simply assigned the morphological traits of the mainland species. 292

We constructed a null phylogeny for each simulation by retaining the phylogenetic 293 relationships between colonizers randomly selected from the pool as a backbone tree onto which 294 we grafted the associated simulated BD tree(s) of the endemic clade. For each archipelago, the 295 simulation protocol was independently implemented 1,000 times. Simulated data (body mass, 296 body plan and phylogeny) were used to generate 1,000 random values for each pairwise 297 MNTD_{TURN} value and 1,000 average pairwise MNTD_{TURN} values among all pairs of 298 299 archipelagos. To test whether archipelagos overall were convergent in morphological and phylogenetic structure in relation to their respective species pools, we tested whether pairwise 300 turnover and average turnover (measured by MNTD_{TURN}) were less than expected under the null 301 model simulation (one-tailed test). To compare the relative roles of potential influences on 302 community convergence, we also calculated how far the observed overall mean MNTD_{TURN} 303 304 among archipelagos deviated from null expectations using the standardized effect size (SES). SES was calculated as (MNTD_{TURN}- μ sim)/ σ sim, where μ sim is the mean index of the simulated 305 values, and σ sim is the associated standard deviation. Negative SES values indicate lower 306 morphological/phylogenetic MNTD_{TURN} than expected by chance, i.e. negative numbers farther 307 from 0 indicate stronger convergence. 308

Null model approaches that involve sampling from a (larger) species pool may suffer 309 high type I error rates due to differences between the species richness of the focal assemblages 310 and that of the pool (Kraft et al. 2007). To evaluate the type I error of our approach in detecting 311 community convergence, we first designed a set of simulations to test the type I error associated 312 with using the metric MNTD_{TURN} to detect community convergence by using different 313 combinations of community (i.e. archipelago) and pool size (i.e. regional pool). Second, we re-314 ran our convergence analyses by randomly selecting, for each archipelago, a subset of the species 315 in the pool. Two subset sizes were used, corresponding to the number of species where the 316 species richness of an archipelago represented 30% and 60% of the pool (Kraft et al. 2007, see 317 Supporting Information for further details of our approach). 318

319 Assessing mechanisms of convergence

To evaluate the effects of different assembly processes and to exclude the effects of extinction 320 (Fig. 1), we conducted analyses for all land-birds including both extant and extinct species. We 321 separately analyzed archipelagic non-endemic and endemic species to tease apart the roles of 322 colonization and *in situ* adaptation. To assess whether extinction explains patterns of 323 convergence, we excluded extinct species and restricted our dataset to native bird species that 324 have so far survived the filter effect of anthropogenic activities on each archipelago. To reduce 325 the ecological variation in our sample of species, and test if convergence is significant within 326 more homogeneous groups of species, we re-ran all analyses restricted to the monophyletic order 327 of passerines (Passeriformes) (see Supporting Information). 328

We further tested for patterns of non-random colonization by comparing the taxonomic composition of each archipelago with its respective species pool, at the family level. We used two metrics: (1) a simple count of families in each archipelago, and (2) the dissimilarity in family composition (see Supporting Information) and the proportion of shared species per family between the archipelago and its associated species pool. Both the observed number of families and dissimilarity were compared against 1000 null values generated by randomly selecting from the species pool the same number of species as observed in the respective archipelagos.

Further details of all methods are given in the Supporting Information. All statistical analyses were implemented within the R programming environment (R Development Core Team, 2018).

340 **RESULTS**

Simulations showed that our framework for testing community convergence has very low type I
error, and convergence detection was not sensitive to community size or pool size (see
Supporting Information, Fig. S3 and S4).

When all extant and extinct land-bird species are analyzed together, we found that 344 345 turnover in body plan, body mass and phylogeny among the 18 archipelagos was significantly lower than expected by chance (i.e. lower MNTD_{TURN} than expected), indicating convergence in 346 community structure (Fig. 2B, C & D; Table S6). The strongest evidence for convergence was 347 detected in phylogenetic structure. Results were similar when we restricted analyses to 348 Passeriformes only, with the exception of body mass, which did not appear to show a pattern of 349 community convergence (Fig. 2E - J; Table S6). All archipelagos (except Juan Fernández) 350 exhibited significant body plan and phylogenetic similarity (i.e. lower pairwise MNTD_{TURN} than 351 expected) with at least one other archipelago (Fig. 3A-C). For body mass, several archipelagos 352 showed no significant similarity with any other archipelago (Fig. 3B, E and H). The lack of 353 significant findings for Juan Fernández was due to the presence of two hummingbird species 354 (Sephanoides fernandensis and S. sephaniodes, Trochilidae) on the archipelago, the only species 355 in this morphologically distinct family present on any oceanic archipelago included in this study. 356 A reanalysis of the convergence pattern without the two hummingbirds showed convergence of 357 Juan Fernández with at least four archipelagos for body plan and phylogeny, but still no evidence 358 of convergence for body mass (Fig. S5). 359

Sensitivity analyses (Supporting Information) revealed these findings to be generally 360 robust to (i) assumptions regarding species pool definition, and (ii) the estimated number of 361 colonization events; with the analysis based on the number of colonization events randomly 362 selected between the minimum and maximum numbers retrieved from the literature providing 363 similar results to the main analysis (Tables 1 and S7–S9). Our analyses testing for differences in 364 taxonomic composition between archipelagos and their species pools for all land birds revealed 365 that most of the avifauna in each of the 18 archipelagos was dominated by two main orders, 366 passerines (Passeriformes) and pigeons (Columbiformes), with the latter being 367 overrepresented on islands compared to the respective zoogeographic regions (Table S10). In 368 addition, we found a significantly reduced number and different composition of families in 369

most archipelagos compared with null expectations (Table S11), for all land birds and also for
Passeriformes only.

Significant convergence in body plan, body mass and phylogenetic structure was also 372 found for the native non-endemic species subset, suggesting that non-random patterns of 373 colonization (and persistence) play an important role in establishing overall convergence 374 patterns. Significant convergence in body plan and phylogenetic structure was detected for native 375 non-endemic Passeriformes (Table S6) but these results have to be interpreted with caution as 376 they are based on a smaller sample size (seven archipelagos). We also found significant 377 convergence in body plan and phylogenetic structure (but not body mass) in the endemic species 378 subset of all birds and Passeriformes only, indicating that colonization is only part of the story, 379 and that in situ adaptation also contributes to convergence. 380

Significant convergence in each of body plan, body mass and phylogeny was also 381 detected in the extant species subset (post-extinction datasets). In addition, we found that body 382 plan convergence was more pronounced in the sample of extant species (SES = -3.415; P = 383 (0.001) than in the dataset containing extant and extinct species sampled together (SES = -2.364; 384 P = 0.006). This was also true for extant and extinct species: SES = -3.277; P = 0.001) but was 385 less pronounced for Passeriformes (SES = -3.337; P = 0.001 and SES = -3.291; P = 0.001). 386 These findings suggest that community convergence existed prior to human influences on island 387 faunas, and that convergence has been further strengthened by anthropogenic extinctions. 388

389

390 DISCUSSION

391 Our results reveal clear evidence of convergence in both the phylogenetic structure and morphology of archipelagic avifaunas, despite their assembly from distinct mainland source 392 pools. The pattern of convergence was particularly strong for phylogenetic structure, suggesting 393 that archipelagic assemblages are drawn from a non-random set of clades predisposed to over-394 sea dispersal and/or successful establishment in insular environments. The concordance of 395 396 evidence from phylogeny and key aspects of phenotype can be assigned to the fact that morphology is generally phylogenetically conserved in birds and also reflects dispersal 397 propensity (e.g. Ricklefs, 2012; Barnagaud et al., 2014; Jønsson, et al., 2015; Sheard et al., 2020; 398 399 Tobias et al., 2020; Table S4).

Support for community convergence is further strengthened by two observations from 400 our analyses. First, the composition and number of families observed in each archipelago are 401 consistently different from the adjacent mainland avifauna (see also Whittaker & Fernández-402 Palacios, 2007, pp. 50-53). Second, the assemblages of the majority of volcanic archipelagos 403 analyzed here are dominated by two particular clades (pigeons and passerines), which make up a 404 larger proportion of the archipelago land-bird community than predicted as a random draw based 405 on respective continental source pools. The unusual diversity of pigeons on remote islands was 406 noted long ago by Wallace (1876) and highlights the role of clade-specific traits in the assembly 407 of island fauna (Whittaker & Fernández-Palacios, 2007; Emerson & Gillespie, 2008; Warren et 408 al., 2015; Weigelt et al., 2015). Taken together, these aspects of convergent community structure 409 suggest that dispersal and environmental filters strongly constrain which types of species can 410 reach and thrive on oceanic archipelagos (Fig. 1). 411

412 Community convergence is clearly promoted by deterministic colonization and establishment in faunal build-up, but this effect may be augmented by in situ adaptation and 413 diversification, as the colonization of islands by avian lineages is often followed by predictable 414 evolutionary change (e.g. Grant & Grant, 2008; Losos & Ricklefs, 2009; Warren et al., 2015). 415 For example, island-dwelling species tend to become less mobile, resulting in a loss or reduction 416 of flight ability (Wright et al., 2016), whereas brain size tends to increase (Sayol et al., 2018). 417 Similarly, beak size may evolve to increase or decrease after species colonize islands, depending 418 on niche availability (e.g. Clegg et al., 2002; Grant & Grant, 2008). Although this process can 419 lead to in situ morphological divergence when a lineage diversifies during archipelagic radiation, 420 421 the resultant communities may nonetheless be convergent if the same sets of niches are repeatedly filled across different archipelagos. 422

Results from analyses based on endemic and non-endemic species separately confirm the 423 general pattern of convergence, with both subsets structurally more similar than expected by 424 chance. Assuming that non-endemic species are generally more recently derived from mainland 425 426 populations and that endemic species reflect insular speciation events, these findings suggest that non-random patterns of colonization and in situ adaptation both contribute to community 427 convergence. Overall, while our analyses show consistent evidence for convergent patterns in 428 429 body plan and phylogenetic structure, evidence for body mass convergence, although significant for all species, was not detected for passerines, or archipelagic endemics. There are two potential 430

explanations for these findings. First, larger-bodied species may not be able to overcome the 431 dispersal barrier (Fig. 1) and colonize islands. Species belonging to Struthionidae (e.g. Struthio 432 camelus), Rheidae (e.g. Rhea americana), and Casuariidae (e.g. Casuarius casuarius) are 433 missing from island systems, and this may at least partly explain the pattern of body mass 434 convergence when focusing on all species (body mass of archipelago species ranges from 5.17 to 435 22,500 g, and for mainland species from 1.9 to 111,000 g). For passerines the ranges of body 436 mass are very similar between archipelagos and mainland areas (Fig. S6), and so it follows that 437 there is also less community convergence between archipelagos with regard to their respective 438 species pools. Moreover, *in situ* speciation events within these groups (Figs 2, 3) resulted in the 439 presence of several relatively large species, such as the pigeons *Raphus cucullatus* (12,450 g) 440 and Pezophaps solitaria (22,500 g) in the Mascarenes, further diluting community convergence. 441

To examine the potential effect of anthropogenic extinctions in driving convergence of 442 community structure, we compiled data for pre- and post-human arrival communities, and then 443 compared evidence for convergence with and without extinct species. Our results show that the 444 pattern of convergence existed prior to the impact of humans and was subsequently strengthened 445 as a result of anthropogenic extinctions. This finding suggests that anthropogenic extinctions 446 have selectively removed morphologically distinctive species - including endemic lineages with 447 large body size or unusual wing morphology (Steadman, 2006; Boyer & Jetz, 2014; Hume, 2017; 448 Heinen et al., 2018) – thus accentuating the signal of convergence in extant avifaunas. Therefore, 449 our results (i) highlight the risk of testing for convergence without accounting for extinct taxa, 450 and (ii) provide the best evidence to date that patterns of convergence precede the effects of 451 452 anthropogenic extinctions. However, it is worth emphasizing that our knowledge of extinct species remains incomplete (e.g. Steadman, 2006; Hume, 2017; Sayol et al., 2020), with the 453 global number of described extinct species no doubt representing only a partial picture of the 454 original avifaunal diversity driven to extinction by humans. Focusing on oceanic island 455 systems reduces the problem somewhat as many archipelagos have now been relatively well 456 457 studied by paleontologists, yet the inadequate fossil record of some islands suggests that our dataset of extinct taxa may be missing a large number of species that await discovery (e.g. 458 Steadman, 2006; Hume, 2017; Sayol et al., 2020). Nonetheless, community convergence is 459 460 evident even without the extinct species.

Historical contingencies arising from regional factors and chance events have resulted in 461 the assembly of unique biotas on archipelagos worldwide, often featuring multiple narrowly 462 endemic species (Whittaker & Fernández-Palacios, 2007; Gillespie & Clague, 2009). Hence, 463 traditional comparisons of species or clade composition among oceanic archipelagos are not 464 suitable for assessing convergence at the community level. By focusing on phylogenetic 465 relationships and morphological traits in relation to distinct regional species pools, we have 466 shown that avian community assembly on oceanic archipelagos is shaped by non-random, 467 deterministic and therefore predictable process regimes over large temporal scales. Crucially, we 468 show that non-random anthropogenic extinctions contribute to this pattern, yet are insufficient to 469 explain its pervasiveness. These findings clarify that historical contingencies are overridden by a 470 combination of biogeographical assembly, *in situ* evolutionary adaptation, and non-random 471 anthropogenic impacts to generate convergent archipelagic bird communities worldwide. Similar 472 approaches should be extended to other vertebrate groups, as well as plants and invertebrates, to 473 assess the generality of our findings across a wider sample of biodiversity. 474

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658 **DATA AVAILABILITY STATEMENT**:

All data are available in Supporting Information. The code for analyses in R can be download
 from https://github.com/frigal001/Functions-Birds-Convergence.

661

662 SUPPORTING INFORMATION

663 Additional Supporting Information may be found online in the Supporting Information section.

TABLE 1 Species richness, numbers of endemic and extinct species and the retrieved minimum and maximum numbers of colonization events for each of the 18 archipelagos, for all land-birds. For the respective numbers of Passeriformes see Supporting Information.

Archipelago	Species richness	Endemic species	Extinct species	Colonization events (min–max)
Austral	7	6	4	5–7
Azores	20	7	5	17–20
Canary	61	16	4	58–59
Comoros	52	22	0	46
Cook Islands	21	12	9	17–20
Fernando de Noronha	4	3	1	4
Galápagos	30	26	1	13
Gulf of Guinea	60	28	0	53
Hawaii	100	99	68	13–17
Juan Fernández	9	3	0	8
Madeira	32	10	7	29–32
Marquesas	26	22	14	16–20
Mascarenes	49	47	29	32–45
Pitcairn	8	8	3	7
Revillagigedo	16	5	1	15
Samoa	30	12	2	30
Society	24	15	14	21–24
Tristan da Cunha	7	7	0	5



FIGURE 1 Quantifying convergent properties of archipelagic communities. If subsets of bird species from distinctive regional pools reach archipelagos A and B, the constraints of dispersal and environmental filters potentially select species with similar traits from the same regions of the evolutionary tree. In situ cladogenesis (archipelagic speciation) generates endemic lineages, further modifying the morphological and phylogenetic profile of archipelagic communities, theoretically increasing the number of species with combinations of traits adapted to insular environments. Thus, morphological or functional similarity between archipelagos may reflect a combination of a) non-random characteristics of colonizing lineages, and b) subsequent convergent evolution. Species highlighted in red are anthropogenic extinctions, which, if also non-random, can generate or strengthen patterns of convergence. Robust analyses of community convergence therefore need to account for the role of extinctions. Pictograms are courtesy of PhyloPic (www.phylopic.org) and the image of Hawaiian honeycreepers is reproduced, with permission, from Pratt (2005).



724 FIGURE 2 Island avifaunas converge on repeated patterns of morphological and phylogenetic structure. (A) 725 Assignment of 18 archipelagos to nine biogeographical regions (Tables S1-S3). Regions are indicated by colour and archipelagos by abbreviations: Aus = Austral islands; Azo = Azores; Can = Canaries; Com = Comoros; CkI = Cook 726 727 Islands; FdN = Fernando de Noronha; Gal = Galápagos; GoG = Gulf of Guinea; Haw = Hawaii; JFe = Juan 728 Fernández; Mad = Madeira; Mar = Marquesas; Mas = Mascarenes; Pit = Pitcairn; Rev = Revillagigedo; Sam = 729 Samoa; Soc = Society; TdC = Tristan da Cunha. (B-G) Similarity analyses for body plan, body mass, and phylogeny for all land-birds (B-D; n=496 species), and Passeriformes (E-G; n=284 species). Panels provide results 730 731 for all (ALL), native-non-endemic (NAT) and endemic (END) species, including extinct species, as well as a 732 comparison with extant species (NEX), i.e. with all extinct species removed. Dots indicate average turnover between 733 pairs of archipelagos (among archipelago turnover); numbers on dots are sample sizes (number of archipelagos). 734 MNTD_{TURN} for body plan (unitless) and body mass (log₁₀[g]) were calculated using Euclidean distances between 735 species and MNTD_{TURN} for phylogeny was calculated using cophenetic distances (million years) between species. 736 Violin plots show the distribution of average MNTD_{TURN} calculated from 1,000 simulations using a null model with 737 random morphological and phylogenetic structure. Boxes show P-values of one-tailed tests (red = significant; black 738 = non-significant).



741 FIGURE 3 Convergent properties in morphological and phylogenetic structure of archipelagic avifaunas. The 742 networks show convergence properties in body plan, body mass and phylogeny for all land-birds (A-C), and 743 Passeriformes only (D-F). Nodes correspond to the 18 and 15 major oceanic archipelagos for all land-birds and 744 Passeriformes respectively. Red and grey connectors depict convergence and non-convergence, respectively. 745 Convergence was estimated by comparing pairwise morphological and phylogenetic turnover between pairs of 746 archipelagos against the distribution of values calculated from 1,000 simulations using a null model with random morphological and phylogenetic differentiation. A pair of archipelagos was considered convergent when the 747 748 observed dissimilarity was below the lower bound of the 95% of the confidence limits of the null model distribution. Colours indicate the biogeographical region to which each archipelago belongs (see Fig. 2 and Supporting 749 750 Information, Tables S1–S3, for regions and archipelago names).