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## Deterministic assembly and anthropogenic extinctions drive convergence of island bird communities

Kostas A Triantis, Francois Rigal, Robert J Whittaker, Julian P Hume, Catherine Sheard, Dimitrios Poursanidis, Jonathan Rolland, Spyros Sfenthourakis, Thomas J Matthews, Christophe Thébaud, et al.

### ► To cite this version:

Kostas A Triantis, Francois Rigal, Robert J Whittaker, Julian P Hume, Catherine Sheard, et al.. Deterministic assembly and anthropogenic extinctions drive convergence of island bird communities. *Global Ecology and Biogeography*, 2022, 31 (9), pp.1741-1755. 10.1111/geb.13556 . hal-03799259

**HAL Id: hal-03799259**

**<https://hal.science/hal-03799259v1>**

Submitted on 5 Oct 2022

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1 **Global Ecology and Biogeography**

2  
3 **Type of Article: Research Papers**

4  
5 **Deterministic assembly and anthropogenic extinctions drive convergence of**  
6 **island bird communities**

7  
8 **Short running title:** Community convergence in island avifaunas

9  
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## 51 **ABSTRACT**

52 **Aim:** Whether entire communities of organisms converge toward predictable structural  
53 properties under similar environmental conditions remains controversial. We tested for  
54 community convergence in birds by comparing the structure of oceanic archipelago assemblages  
55 to their respective regional species pools.

56 **Location:** Eighteen major oceanic archipelagos of volcanic origin with global distribution

57 **Major taxa studied:** Terrestrial birds

58 **Methods:** We compiled a comprehensive database of morphological trait and phylogenetic data  
59 for 6,579 bird species, including species known to have become extinct due to human activities.  
60 We quantified morphological and phylogenetic dissimilarity among species between pairs of  
61 archipelagos, using a modified version of the mean nearest taxon distance. We tested for  
62 convergence by estimating whether overall mean turnover among archipelagos and pairwise  
63 turnover between archipelagos was lower than expected by chance.

64 **Results:** For all land-birds, we found that turnover in body plan, body mass and phylogeny  
65 among archipelagos was significantly lower than expected. Seventeen (of 18) archipelagos  
66 showed significant body plan and phylogenetic similarity with at least one other archipelago.  
67 Similar convergent patterns of community assembly were detected in different subsamples of the  
68 data (extant species, endemics, native non-endemics, and Passeriformes only). Convergence was  
69 more pronounced for extant species than for extant and extinct species combined.

70 **Main conclusions:** Consistent convergence in phylogenetic and morphological structure among  
71 archipelagic communities arises through a combination of non-random colonization and *in situ*  
72 adaptation. In addition, by including data from extinct taxa, we show that community  
73 convergence both precedes and is accentuated by the anthropogenic extinction of endemic  
74 lineages. Our results highlight the potential role of non-random extinction in generating patterns  
75 of community convergence and also show that convergence existed even prior to anthropogenic  
76 extinctions as a result of deterministic community assembly in similar environmental settings at  
77 the global scale.

78  
79 **Keywords:** birds, community assembly, convergence, determinism, extinct species, historical  
80 contingency, island biogeography, morphological traits, oceanic archipelagos.

## 81 82 INTRODUCTION

83  
84 Whether spatially isolated ecological communities tend to converge under similar environmental  
85 conditions towards predictable structural properties, such as traits or functional space occupied,  
86 has remained a controversial question for half a century (MacArthur, 1972; Cody & Mooney,  
87 1978; Ricklefs & Travis, 1980; Blondel et al., 1984; Samuels & Drake, 1997; Fukami et al.,

88 2005; Melville et al., 2006; Winemiller et al. 2015; Moen et al., 2016; Santos et al. 2016; Mazel  
89 et al., 2018). Although evolutionary convergence – the emergence of similar species traits or  
90 syndromes from divergent evolutionary starting points in geographically distant but  
91 environmentally similar locations – is a well-established phenomenon (e.g. Losos *et al.*, 1998;  
92 Schluter, 2000; Gillespie, 2004; Muschick et al., 2012; Mahler et al., 2013), the question of  
93 whether convergence applies to entire communities remains open to debate. For example,  
94 historical contingencies (legacies from previous system states) vary across regions and typically  
95 generate unpredictable outcomes in the structural properties of local communities (Gould, 1989;  
96 see also discussion in Losos & Ricklefs, 2009).

97 A major challenge for the study of community convergence is posed by extinct taxa. In  
98 particular, if anthropogenic extinctions are non-random (e.g. Steadman, 2006; Sayol et al.,  
99 2020) and biased towards outliers, such as the largest and smallest species in an assemblage  
100 (e.g. Ripple et al. 2017), then apparent evidence of community convergence may be explained  
101 by non-random or clustered extinctions rather than any deterministic process based on  
102 environmental filtering or evolutionary adaptation (Tobias et al., 2020). Robust tests of  
103 community convergence therefore need to account for extinct taxa, particularly in island  
104 systems where anthropogenic extinctions have often altered native communities (e.g.,  
105 Steadman, 2006; Boyer & Jetz, 2014; Sobral et al., 2016; Sayol et al. 2021). However, previous  
106 studies of community convergence – most of which have focused on islands – have rarely (if  
107 ever) accounted for extinctions.

108 To date, community level convergence has primarily been tested, and in some cases  
109 detected, at the level of individual islands (e.g. Gillespie, 2004; Losos, 2011; Mahler et al., 2013),  
110 but has never been evaluated at the archipelago level. Yet several filtering processes operate at  
111 the scale of archipelagos (Fig. 1), with convergence generated via two primary pathways:  
112 (a) the non-random selection of colonists reaching the archipelago from the regional species  
113 pool, resulting in greater phylogenetic or morphological similarity than expected by chance, and  
114 (b) *in situ* evolutionary change, including lineage diversification, leading to greater trait  
115 similarity among archipelagos than expected by chance (Wiens & Graham, 2005; Emerson &  
116 Gillespie, 2008; Grant & Grant, 2008; Losos & Ricklefs, 2009; Barnagaud et al., 2014; Weigelt  
117 et al., 2015). The relative contribution of these alternative pathways to community

118 convergence is unclear, although they should leave different signatures in the community  
119 structure of native non-endemic and endemic lineages, respectively.

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

132 Volcanic oceanic archipelagos have long been considered ideal systems for exploring  
133 the processes structuring ecological communities inasmuch as they represent replicated  
134 natural experiments in faunal assembly (e.g. Whittaker & Fernández-Palacios, 2007; Grant &  
135 Grant, 2008; Losos & Ricklefs, 2009). At the archipelagic level, island communities respond  
136 to the insular geography on evolutionary time scales, with species undergoing ‘taxon cycles’,  
137 i.e., sequential phases of expansion and contraction across an archipelago (Wilson, 1959;  
138 Ricklefs & Bermingham, 2002), and with the divergence of populations in allopatry being  
139 arguably the main driving force of diversification (Grant & Grant, 2008; Losos & Ricklefs,  
140 2009). Thus, oceanic archipelagos can be seen as macroevolutionary metacommunities, i.e.,  
141 sets of interacting island communities linked by dispersal. They therefore represent a higher  
142 level of hierarchical organization than individual islands and are amenable to framing  
143 analyses of large-scale patterns such as community-level convergence (see also Triantis et al.,  
144 2015; Whittaker et al. 2017; Valente et al. 2020).

145 We developed a novel framework to test for community convergence in both  
146 morphological and phylogenetic structure of archipelagic land-bird faunas relative to their  
147 respective regional species pools (Fig. 2A). To assess the influence of different assembly or  
148 disassembly mechanisms, we re-ran our analyses on five subsamples: (i) native non-endemic

149 species, (ii) endemic species (including extinct species), (iii) a subsample with all extinct species  
150 removed, and (iv) a monophyletic group (i.e. Passeriformes) that is also the largest order of  
151 birds. Our results show that multiple dimensions of archipelagic bird communities are more  
152 similar than expected by chance, even accounting for the influence of extinction, providing  
153 strong support that community convergence arises through deterministic community assembly.

## 154 **MATERIAL AND METHODS**

### 155 **Species lists and regional pools**

156 Contemporary biogeographical patterns on islands have been strongly influenced by historic and  
157 pre-historic anthropogenic extinctions (Steadman, 2006; Hume, 2017; Valente et al., 2020).  
158 Thus, to understand how species' arrivals and subsequent evolutionary dynamics interact to  
159 establish patterns of trait diversity, it is important to include species known to have become  
160 extinct due to human activities. We collected data on composition and species-level traits for the  
161 avifaunas of 18 volcanic oceanic archipelagos: Austral islands, Azores, Canaries, Comoros,  
162 Cook Islands, Fernando de Noronha, Galápagos, Gulf of Guinea, Hawaii, Juan Fernández,  
163 Madeira, Marquesas, Mascarenes, Pitcairn, Revillagigedo, Samoa, Society, and Tristan da Cunha  
164 (Tables 1 & S1; Fig. 2). For each archipelago, we collated lists of the endemic and native non-  
165 endemic species, including all known species extinctions since human colonization (e.g.  
166 Steadman, 2006; BirdLife International, 2017; Hume, 2017; Sayol et al., 2020; Valente et al.,  
167 2020). A list of the data sources is found in Appendix 1 (see also Supporting Information, Data  
168 S1). Roughly one-third (157) of the species are extinct (Table S2 & Data S1). To focus our  
169 analyses on species strictly relying on terrestrial habitats, we restricted our sample to land-birds,  
170 excluding marine and aquatic species. Of 495 species in our sample, 348 (70%) are archipelagic  
171 endemics, highlighting the evolutionary independence of many archipelagic avifaunas. However,  
172 there are cases of non-endemic archipelagic species that are inferred to have colonized the  
173 archipelago in question from a nearby archipelago, such as *Anthus berthelotii* and *Serinus*  
174 *canarius*, both endemic to Madeira and the Canary Islands (see Valente et al., 2020). However,  
175 only 41 (8%) native non-endemic species are present on more than two archipelagos.

176  
177 To generate regional pools of species as sources for the assembly of each archipelago, we  
178 identified the avifaunal regions to which they belong, based on Holt et al. (2013) (Table S3 and  
179 Fig. 2A). These 10 regions contain 6,231 land-bird species (Data S2). To validate and improve

180 our approach, we compared the zoogeographical region assigned to each archipelago from Holt  
181 et al. (2013) with source region reconstructions based on phylogenetic relationships between  
182 island and mainland species found in the literature, when available. Despite some discrepancies,  
183 including a few cases where the species pool was a nearby archipelago rather than the mainland,  
184 we found that the zoogeographical regions in Holt et al. (2013) were closely aligned with the  
185 source region reconstructions (see Supporting Information). We also tested the sensitivity of our  
186 approach to a more spatially restricted definition of species pools by defining a buffer of 100 km  
187 width from the nearest coast to each archipelago and only sampling bird species with a  
188 geographical distribution overlapping with the buffer. Additionally, to remove any biases arising  
189 from the way source pools are delimited, we conducted a further set of analyses restricted to  
190 archipelagos in the same zoogeographical region, i.e. with a common source pool. This was  
191 possible for Macaronesia (Azores, Madeira and Canary Islands archipelagos) and the South  
192 Pacific (Austral Islands, Cook Islands, Marquesas, Samoa, Pitcairn and Society), the only two  
193 regions with more than two archipelagos (see Supporting Information).

194 Defining an appropriate species pool for archipelagos poses substantial challenges (e.g. Si  
195 et al. 2022). The sensitivity analyses described above provide an assessment of species pool  
196 selection, but some limitations to our approach should be highlighted: (1) zoogeographical  
197 regions were defined using current species distributions, and thus might not accurately represent  
198 species distributions at the time of colonization; (2) all species in a given pool have the same  
199 probability of colonizing and establishing on the focal archipelago, and thus the approach does  
200 not account for differences in dispersal ability and niche compatibility (e.g. climate, resource  
201 use) between species; and (3) source pools defined at the species level potentially misrepresent  
202 the available pool of colonizers, and at least one recent study advocates focusing on higher taxa  
203 (genera or families) with geographic distributions overlapping with the focal assemblage (see Si  
204 et al. 2022). An additional factor is that extinct species were included in the archipelago species  
205 lists, but not for the regional pools, primarily due to the lack of accurate distributional data for  
206 extinct continental species. However, this inconsistency seems unlikely to bias our results  
207 because recent extinctions have been far more prevalent in island communities than continental  
208 source regions. Of all known bird extinctions globally, island endemics comprise 81% (468 of  
209 581 species) of extinctions during the last 125,000 years, and 93% of extinctions since 1500 AD  
210 (Sayol et al. 2020).



211

## 212 **Morphological and phylogenetic data**

213 We collated a range of morphometric data for our combined sample of 6,579 species (Data S1,  
214 S2). For each extant study species ( $n = 6,423$ ), we used a global dataset derived from linear  
215 measurements of wild birds and museum specimens (Pigot et al. 2020; Tobias et al., 2022) to  
216 compile estimates of wing length, tail length, tarsus length, and beak length (mm). These traits  
217 were selected because they reflect the overall body plan (bauplan), and correlate with important  
218 dimensions of the avian niche, such as habitat use, dispersal and foraging strategy (Pigot et al.,  
219 2020). We also compiled body mass (g) from Wilman et al. (2014). For 36 (23%) of 175 extinct  
220 species, measurements were extracted from specialist literature. A list of the data sources is  
221 found in Appendix 1, see also Data S1 for sources, including Rothschild, 1907; Amadon, 1950).  
222 For a further 121 (77%) extinct species with missing data, we inferred morphological and body  
223 mass measurements from the most morphologically similar extant species available, selecting  
224 congeners where possible (Tobias et al., 2022). Extant surrogate species were selected based on  
225 key skeletal measurements, including the mandible for beak length, humerus for flight  
226 capabilities or flightlessness, and the ratio of femur/tibiotarsus/tarsometatarsus to highlight  
227 arboreal or terrestrial modifications (Steadman, 2006). As flightless species tend to be relatively  
228 heavy, we estimated the body mass of extinct flightless taxa known only from fossil remains  
229 with reference to similar-sized extant flightless species, e.g., flightless rails (J. P. Hume,  
230 unpublished data). Since all trait data were calculated as species averages, we do not account for  
231 intra-specific variation, although previous analyses have shown this to be negligible compared to  
232 inter-specific variation in the same avian traits at global scales (Tobias et al., 2022).

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

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

### 248 **Colonization events**

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

256 Molecular data are lacking for most archipelagic extinct species, which can lead to  
257 phylogenetic uncertainty, so we estimated the minimum and maximum number of colonization  
258 events for these species. The minimum number of events was calculated by assuming congeneric  
259 extinct endemics of an archipelago were monophyletic, thus representing a single colonization;  
260 the maximum number of events was calculated by assuming that extinct genera were non-  
261 monophyletic, with each species representing a different colonization event (see sections B3 and  
262 C3 in Supporting Information). Subsequent analyses were implemented in two ways, first using  
263 the minimum number of colonization events, and then by randomly selecting a number of  
264 colonization events between the minimum and the maximum.

### 265 **Measuring morphological and phylogenetic convergence**

266 We quantified differences in body mass, body plan (using body mass-corrected wing, tail, tarsus,  
267 and beak length; Supporting Information, Fig. S1), and phylogenetic dissimilarity among  
268 species, between pairs of archipelagos, using a modified version of the mean nearest taxon  
269 distance (MNTD). This metric was designed to focus solely on morphological or phylogenetic  
270 distance (MNTD). This metric was designed to focus solely on morphological or phylogenetic  
271 distance (MNTD).

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:

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

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

### Null model

We tested for a pattern of convergent community structure by estimating whether overall mean turnover ( $MNTD_{TURN}$ ) among archipelagos, and each pairwise  $MNTD_{TURN}$  value between archipelagos, was lower than expected by chance. To do so, we compared observed turnover values to those simulated under a null model with random phylogenetic and morphological differentiation. For each archipelago, we simulated a null morphospace and phylogeny, constraining our model to the same number of species, endemic species, and colonization events as those observed for the archipelago (Tables 1, S2 and S5). To simulate a null morphospace and phylogeny for a given archipelago, we first started by randomly sampling colonizers from the respective regional pool (see above). Once sampled, each colonizer was randomly assigned to a specific trajectory: either it stays unchanged (native non-endemic), or speciates (becomes endemic) via anagenesis or cladogenesis (Fig. S2), with the number of native non-endemic and

302 endemic species being constrained to the current totals observed in the archipelago (see  
303 Supporting Information and Fig. S2). For instance, if two colonization events have generated  
304 current totals of one native non-endemic and five endemic species, respectively, in a particular  
305 archipelago, then, in our simulation, one colonizer fails to speciate or evolve new traits, while the  
306 other gives birth to a monophyletic clade of five endemic species.

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

319 To simulate the BD tree, we identified the family to which each speciating island-  
320 colonizer belongs, and then estimated speciation rate ( $\lambda$ ) and extinction rate ( $\mu$ ) for that family  
321 using the phylogeny retrieved from 6,231 land-bird species of the 10 avifaunal regions included  
322 in our study (the 349 endemic species of 18 archipelagos were excluded from this analyses). For  
323 families with fewer than 10 species, we sampled species more widely from the order to which  
324 the family belongs (see Supporting information). We then applied a BM model to the branches of  
325 the BD tree using the estimated trait value of the speciating colonizer (i.e. the ancestral state  $x_0$ )  
326 as a starting point, while the  $\sigma^2$  value was retrieved by fitting a BM model (univariate for body  
327 mass; multivariate for body plan) to the phylogeny and the traits of the family members as  
328 identified above. Therefore, for a given archipelago A, a species S belonging to the family F is  
329 randomly selected from the regional pool of potential colonizers, and is allowed to generate an  
330 endemic clade containing N species. We used: (1) the geological age of archipelago A, and  $\lambda$ ,  $\mu$   
331 values estimated for the tree of the family F to create the tree of the endemic clade using the BD  
332 tree, and (2) the trait value of S as the ancestral state and  $\sigma^2$  estimated for the tree and traits of

333 family F, to generate trait values for the N species along the BD tree previously generated. It  
334 should be noted that, for the colonizers that stayed unchanged (native non-endemic species), the  
335 island species was simply assigned the morphological traits of the mainland species.

336 We constructed a null phylogeny for each simulation by retaining the phylogenetic  
337 relationships between colonizers randomly selected from the pool as a backbone tree onto which  
338 we grafted the associated simulated BD tree(s) of the endemic clade. For each archipelago, the  
339 simulation protocol was independently implemented 1,000 times. Simulated data (body mass,  
340 body plan and phylogeny) were used to generate 1,000 random values for each pairwise  
341  $MNTD_{TURN}$  value and 1,000 average pairwise  $MNTD_{TURN}$  values among all pairs of  
342 archipelagos. To test whether archipelagos overall were convergent in morphological and  
343 phylogenetic structure in relation to their respective species pools, we tested whether pairwise  
344 turnover and average turnover (measured by  $MNTD_{TURN}$ ) were less than expected under the null  
345 model simulation (one-tailed test). To compare the relative roles of potential influences on  
346 community convergence, we also calculated how far the observed overall mean  $MNTD_{TURN}$   
347 among archipelagos deviated from null expectations using the standardized effect size (SES).  
348 SES was calculated as  $(MNTD_{TURN} - \mu_{sim}) / \sigma_{sim}$ , where  $\mu_{sim}$  is the mean index of the simulated  
349 values, and  $\sigma_{sim}$  is the associated standard deviation. Negative SES values indicate lower  
350 morphological/phylogenetic  $MNTD_{TURN}$  than expected by chance, i.e. negative numbers farther  
351 from 0 indicate stronger convergence.

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

### 362 **Assessing mechanisms of convergence**

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

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

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

382

## 383 **RESULTS**

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

387 When all extant and extinct land-bird species are analyzed together, we found that  
388 turnover in body plan, body mass and phylogeny among the 18 archipelagos was significantly  
389 lower than expected by chance (i.e. lower  $MNTD_{TURN}$  than expected), indicating convergence in  
390 community structure (Fig. 2B, C & D; Table S6). The strongest evidence for convergence was  
391 detected in phylogenetic structure. Results were similar when we restricted analyses to  
392 Passeriformes only, with the exception of body mass, which did not appear to show a pattern of  
393 community convergence (Fig. 2E - J; Table S6). All archipelagos (except Juan Fernández)

394 exhibited significant body plan and phylogenetic similarity (i.e. lower pairwise MNTD<sub>TURN</sub> than  
395 expected) with at least one other archipelago (Fig. 3A–C). For body mass, several archipelagos  
396 showed no significant similarity with any other archipelago (Fig. 3B, E and H). The lack of  
397 significant findings for Juan Fernández was due to the presence of two hummingbird species  
398 (*Sephanoides fernandensis* and *S. sephaniodes*, Trochilidae) on the archipelago, the only species  
399 in this morphologically distinct family present on any oceanic archipelago included in this study.  
400 A reanalysis of the convergence pattern without the two hummingbirds showed convergence of  
401 Juan Fernández with at least four archipelagos for body plan and phylogeny, but still no evidence  
402 of convergence for body mass (Fig. S5).

403         Sensitivity analyses (Supporting Information) revealed these findings to be generally  
404 robust to (i) assumptions regarding species pool definition, and (ii) the estimated number of  
405 colonization events; with the analysis based on the number of colonization events randomly  
406 selected between the minimum and maximum numbers retrieved from the literature providing  
407 similar results to the main analysis (Tables 1 and S7–S9). Our analyses testing for differences in  
408 taxonomic composition between archipelagos and their species pools for all land birds revealed  
409 that most of the avifauna in each of the 18 archipelagos was dominated by two main orders,  
410 passerines (Passeriformes) and pigeons (Columbiformes), with the latter being  
411 overrepresented on islands compared to the respective zoogeographic regions (Table S10). In  
412 addition, we found a significantly reduced number and different composition of families in  
413 most archipelagos compared with null expectations (Table S11), for all land birds and also for  
414 Passeriformes only.

415         Significant convergence in body plan, body mass and phylogenetic structure was also  
416 found for the native non-endemic species subset, suggesting that non-random patterns of  
417 colonization (and persistence) play an important role in establishing overall convergence  
418 patterns. Significant convergence in body plan and phylogenetic structure was detected for native  
419 non-endemic Passeriformes (Table S6) but these results have to be interpreted with caution as  
420 they are based on a smaller sample size (seven archipelagos). We also found significant  
421 convergence in body plan and phylogenetic structure (but not body mass) in the endemic species  
422 subset of all birds and Passeriformes only, indicating that colonization is only part of the story,  
423 and that *in situ* adaptation also contributes to convergence.



424 Significant convergence in each of body plan, body mass and phylogeny was also  
425 detected in the extant species subset (post-extinction datasets). In addition, we found that body  
426 plan convergence was more pronounced in the sample of extant species ( $SES = -3.415$ ;  $P =$   
427  $0.001$ ) than in the dataset containing extant and extinct species sampled together ( $SES = -2.364$ ;  
428  $P = 0.006$ ). This was also true for extant and extinct species:  $SES = -3.277$ ;  $P = 0.001$ ) but was  
429 less pronounced for Passeriformes ( $SES = -3.337$ ;  $P = 0.001$  and  $SES = -3.291$ ;  $P = 0.001$ ).  
430 These findings suggest that community convergence existed prior to human influences on island  
431 faunas, and that convergence has been further strengthened by anthropogenic extinctions.

## 432 **DISCUSSION**

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

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



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

466 Results from analyses based on endemic and non-endemic species separately confirm the  
467 general pattern of convergence, with both subsets structurally more similar than expected by  
468 chance. Assuming that non-endemic species are generally more recently derived from mainland  
469 populations and that endemic species reflect insular speciation events, these findings suggest that  
470 non-random patterns of colonization and *in situ* adaptation both contribute to community  
471 convergence. Overall, while our analyses show consistent evidence for convergent patterns in  
472 body plan and phylogenetic structure, evidence for body mass convergence, although significant  
473 for all species, was not detected for passerines, or archipelagic endemics. There are two potential  
474 explanations for these findings. First, larger-bodied species may not be able to overcome the  
475 dispersal barrier (Fig. 1) and colonize islands. Species belonging to Struthionidae (e.g. *Struthio*  
476 *camelus*), Rheidae (e.g. *Rhea americana*), and Casuariidae (e.g. *Casuaris casuaris*) are  
477 missing from island systems, and this may at least partly explain the pattern of body mass  
478 convergence when focusing on all species (body mass of archipelago species ranges from 5.17 to  
479 22,500 g, and for mainland species from 1.9 to 111,000 g). For passerines the ranges of body  
480 mass are very similar between archipelagos and mainland areas (Fig. S6), and so it follows that  
481 there is also less community convergence between archipelagos with regard to their respective  
482 species pools. Moreover, *in situ* speciation events within these groups (Figs 2, 3) resulted in the  
483 presence of several relatively large species, such as the pigeons *Raphus cucullatus* (12,450 g)  
484 and *Pezophaps solitaria* (22,500 g) in the Mascarenes, further diluting community convergence.

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

504 Historical contingencies arising from regional factors and chance events have resulted in  
505 the assembly of unique biotas on archipelagos worldwide, often featuring multiple narrowly  
506 endemic species (Whittaker & Fernández-Palacios, 2007; Gillespie & Clague, 2009). Hence,  
507 traditional comparisons of species or clade composition among oceanic archipelagos are not  
508 suitable for assessing convergence at the community level. By focusing on phylogenetic  
509 relationships and morphological traits in relation to distinct regional species pools, we have  
510 shown that avian community assembly on oceanic archipelagos is shaped by non-random,  
511 deterministic and therefore predictable process regimes over large temporal scales. Crucially, we  
512 show that non-random anthropogenic extinctions contribute to this pattern, yet are insufficient to  
513 explain its pervasiveness. These findings clarify that historical contingencies are overridden by a  
514 combination of biogeographical assembly, *in situ* evolutionary adaptation, and non-random  
515 anthropogenic impacts to generate convergent archipelagic bird communities worldwide. Similar

516 approaches should be extended to other vertebrate groups, as well as plants and invertebrates, to  
517 assess the generality of our findings across a wider sample of biodiversity.

518

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## 701 **ACKNOWLEDGMENTS**

702 We thank the numerous field biologists who collected specimens used in this study; the Natural  
703 History Museum, the American Museum of Natural History and 63 other research collections for  
704 providing access to specimens; Juan Carlos Illera for providing a list of Macaronesian birds; and  
705 Kostas Sagonas for drawing Fig. 1. We are also grateful to Robert Freckleton for statistical  
706 advice and Bob Ricklefs, Rosemary Gillespie and Jon Chase for feedback on previous versions  
707 of the manuscript. Luis Valente and an anonymous reviewer provided insightful comments that  
708 helped us improve the manuscript. The image of Hawaiian honeycreepers is courtesy of D.  
709 Pratt (North Carolina Museum of Natural Sciences, Raleigh).

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## 711 **AUTHOR CONTRIBUTIONS**

712 K.A.T, J.A.T., C.T., T.J.M., R.J.W., and F.R. developed the conceptual framework and  
713 coordinated the study; J.A.T., C.S. and J.P.H. compiled morphological data; K.A.T., D.P. and  
714 C.T. compiled species inventories and distributional data; F.R. designed and conducted all  
715 analyses. All the authors contributed to the interpretation of the results. K.A.T., R.J.W, F.R., C.T,  
716 T.J.M., J.A.T. wrote the final draft, with all authors contributing to reviewing and editing.

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## 718 **BIOSKETCH**

719 The author team consists of biogeographers, ecologists, ornithologists and paleontologists with  
720 diverse backgrounds including island biogeography, community ecology, taxonomy,  
721 macroecology and evolutionary biology. This work is a collaborative effort to enhance our  
722 understanding of the biodiversity patterns across macro-scales of space and time.

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## 724 **DATA AVAILABILITY STATEMENT:**

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

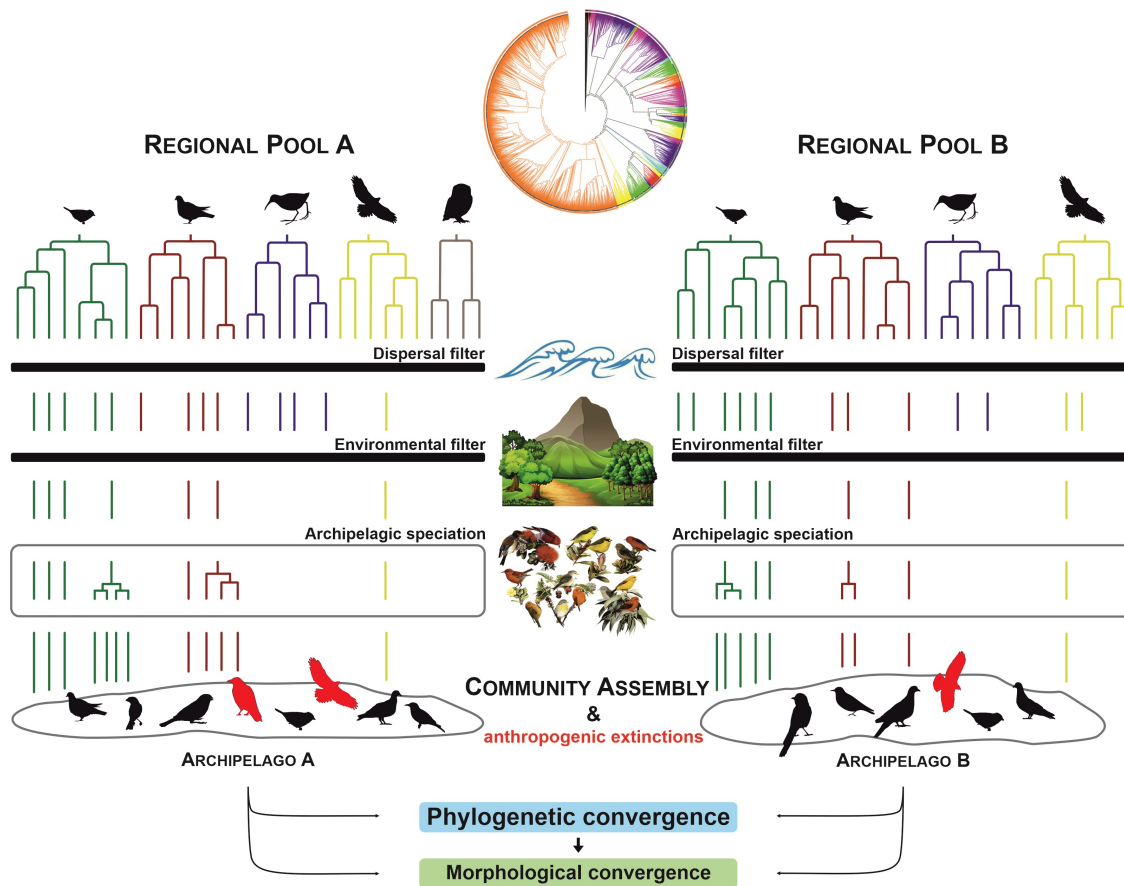
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## 728 **SUPPORTING INFORMATION**

729 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



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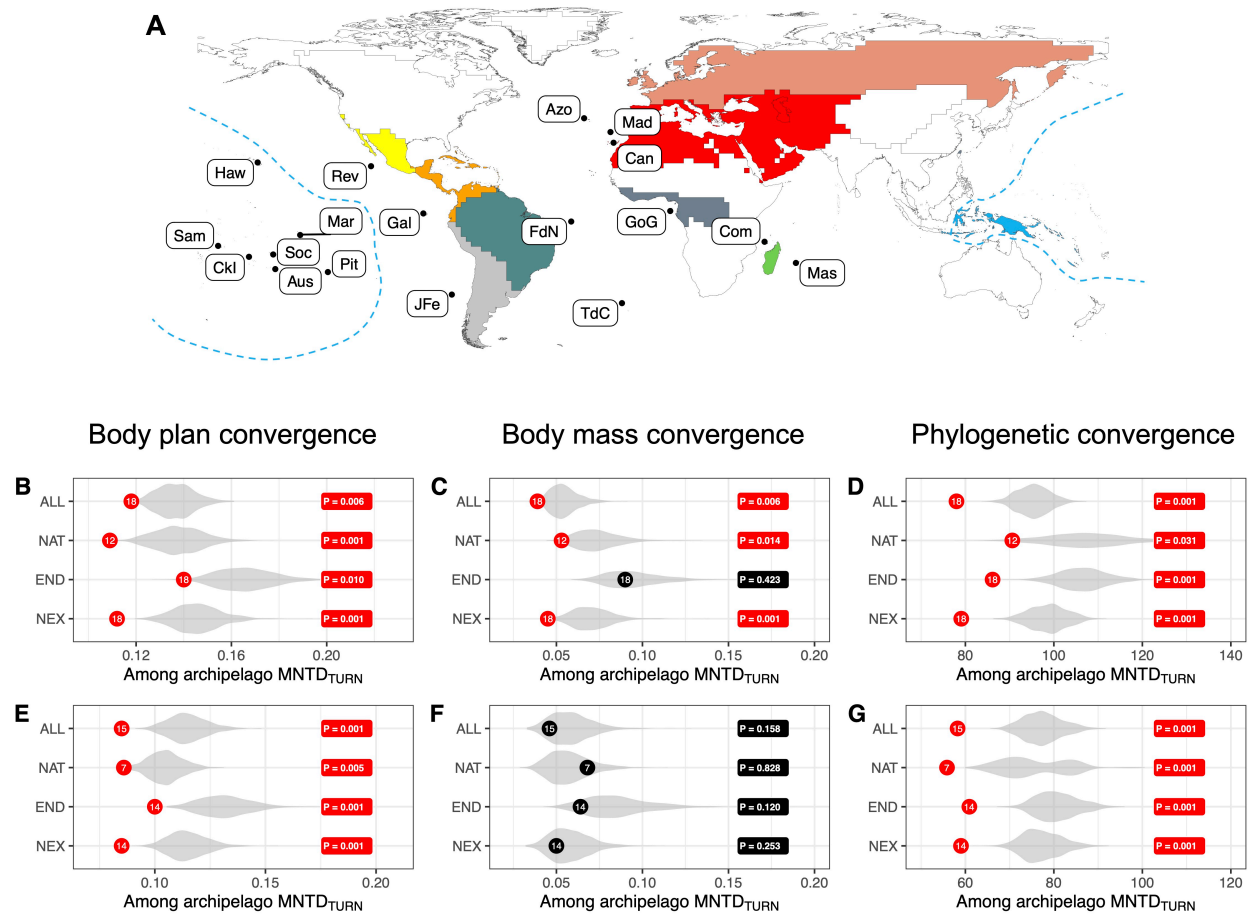
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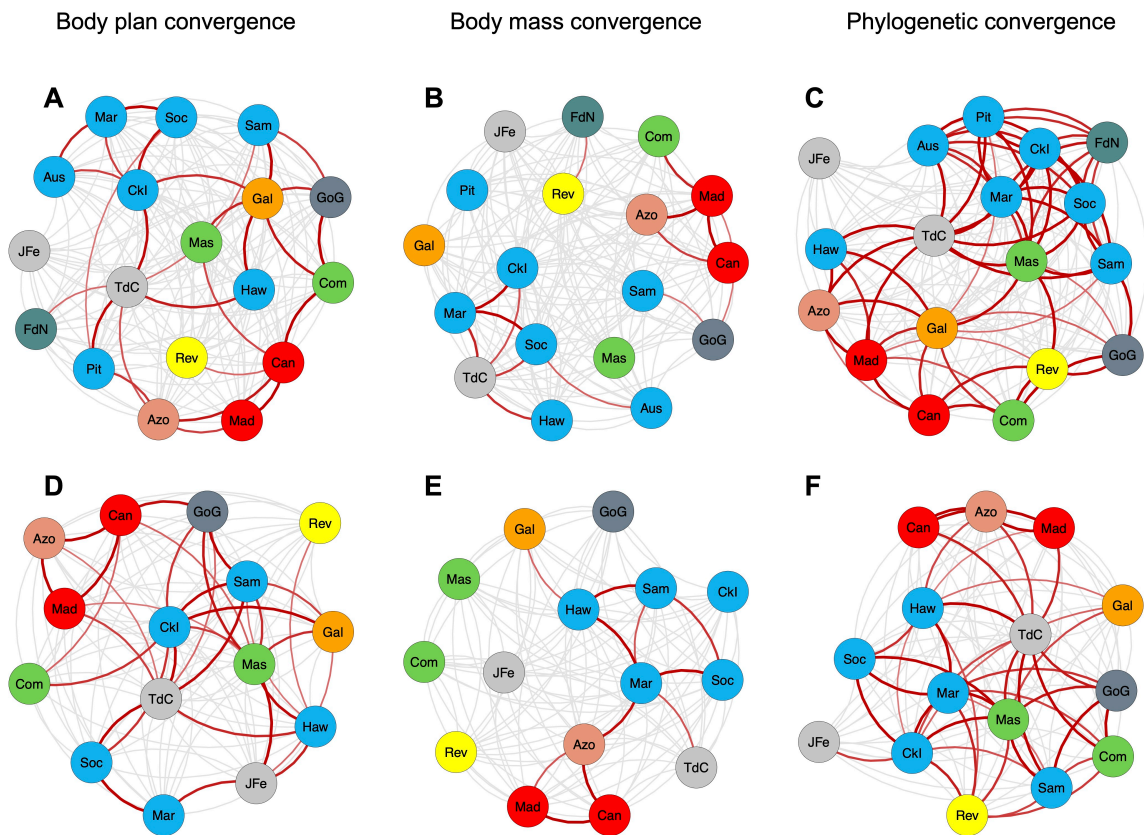
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**FIGURE 1** Quantifying convergent properties of archipelagic communities. If subsets of bird species from distinctive regional pools reach archipelagos A and B, the constraints of dispersal and environmental filters potentially select species with 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](http://www.phylopic.org)) and the image of Hawaiian honeycreepers is reproduced, with permission, from Pratt (2005).



**FIGURE 2** Island avifaunas converge on repeated patterns of morphological and phylogenetic structure. (A) 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 Islands; FdN = Fernando de Noronha; Gal = Galápagos; GoG = Gulf of Guinea; Haw = Hawaii; JFe = Juan Fernández; Mad = Madeira; Mar = Marquesas; Mas = Mascarenes; Pit = Pitcairn; Rev = Revillagigedo; Sam = 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 for all (ALL), native-non-endemic (NAT) and endemic (END) species, including extinct species, as well as a comparison with extant species (NEX), i.e. with all extinct species removed. Dots indicate average turnover between pairs of archipelagos (among archipelago turnover); numbers on dots are sample sizes (number of archipelagos).  $MNTD_{TURN}$  for body plan (unitless) and body mass ( $\log_{10}[g]$ ) were calculated using Euclidean distances between species and  $MNTD_{TURN}$  for phylogeny was calculated using cophenetic distances (million years) between species. Violin plots show the distribution of average  $MNTD_{TURN}$  calculated from 1,000 simulations using a null model with random morphological and phylogenetic structure. Boxes show  $P$ -values of one-tailed tests (red = significant; black = non-significant).



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

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