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RESEARCH ARTICLE

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Deterministic assembly and anthropogenic extinctions drive convergence of island bird communities

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Abstract

Aim: Whether entire communities of organisms converge towards predictable structural properties in similar environmental conditions remains controversial. We tested for community convergence in birds by comparing the structure of oceanic archipelago assemblages with their respective regional species pools.

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

Major taxa studied: Terrestrial birds.

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

Kostas A. Triantis, Francois Rigal and Joseph A. Tobias contributed equally.

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

Main conclusions: Consistent convergence in phylogenetic and morphological structure among archipelagic communities arises through a combination of non-random colonization and *in situ* 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 show that convergence existed even before anthropogenic extinctions, owing to deterministic community assembly in similar environmental settings at the global scale.

KEYWORDS

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

1 | INTRODUCTION

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

A major challenge for the study of community convergence is posed by extinct taxa. In particular, if anthropogenic extinctions are non-random (e.g., Sayol et al., 2020; Steadman, 2006) and biased towards outliers, such as the largest and smallest species in an assemblage (e.g., Ripple et al., 2017), then apparent evidence of community convergence might be explained by non-random or clustered extinctions rather than by any deterministic process based on environmental filtering or evolutionary adaptation (Tobias et al., 2020). Robust tests of community convergence therefore need to account for extinct taxa, particularly in island systems where anthropogenic extinctions have often altered native communities (e.g., Boyer, 2008; Boyer & Jetz, 2014; Sayol et al., 2021; Sobral et al., 2016; Steadman, 2006). 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 detected, at the level of individual islands (e.g., Gillespie, 2004; Losos, 2011; Mahler et al., 2013), but has never been evaluated at the archipelago level. Nonetheless, several filtering processes operate at the scale of archipelagos (Figure 1), with convergence generated via two primary pathways:

(1) the non-random selection of colonists reaching the archipelago from the regional species pool, resulting in greater phylogenetic or morphological similarity than expected by chance; and (2) *in situ* evolutionary change, including lineage diversification, leading to greater trait similarity among archipelagos than expected by chance (Barnagaud et al., 2014; Emerson & Gillespie, 2008; Grant & Grant, 2008; Losos & Ricklefs, 2009; Weigelt et al., 2015; Wiens & Graham, 2005). The relative contribution of these alternative pathways to community convergence is unclear, although they should leave different signatures in the community structure of native non-endemic and endemic lineages, respectively.

To test for community convergence in the phylogenetic and morphological structure of oceanic archipelago bird assemblages, in relationship to their respective regional species pools, we compiled comprehensive data on species composition, phylogenetic history and morphological traits for birds occurring on volcanic archipelagos across the Pacific, Atlantic and Indian oceans. Given that faunal assembly is mostly sourced from larger, older and more complex continental pools, we also collected equivalent data for a far larger number of bird species occurring in the continental source pools for each archipelago (see

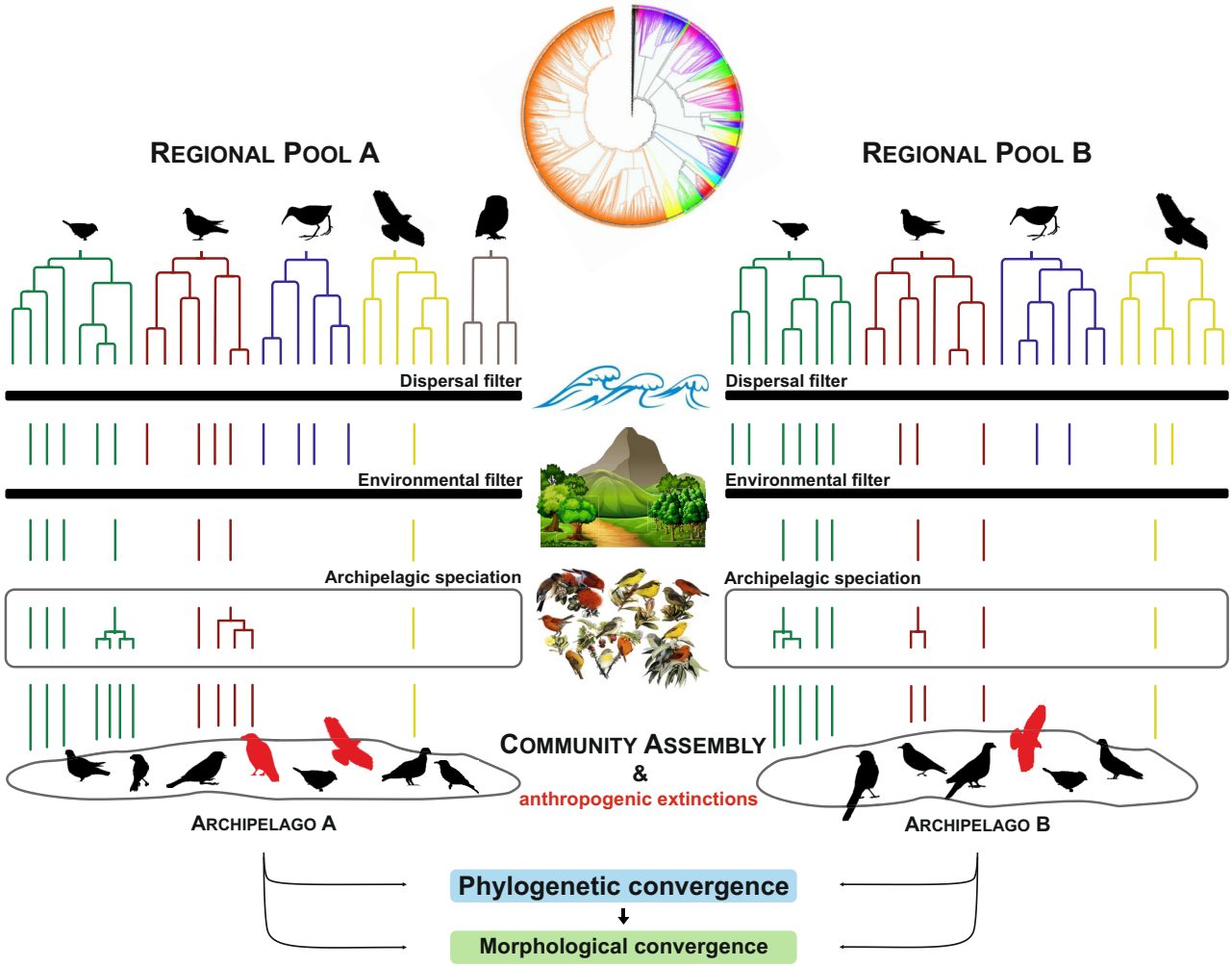

FIGURE 1 Quantifying convergent properties of archipelagic communities. If subsets of bird species from distinctive regional pools reach archipelagos A and B, the constraints of dispersal and environmental filters potentially select species with similar traits from the same regions of the evolutionary tree. *In situ* cladogenesis (archipelagic speciation) generates endemic lineages, further modifying the morphological and phylogenetic profiles of archipelagic communities, theoretically increasing the number of species with combinations of traits adapted to insular environments. Thus, morphological or functional similarity between archipelagos can 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)
[Correction added on 23 June 2022, after first online publication: Figure 1 has been updated.]

also Cardillo et al., 2008; Graves & Gotelli, 1983; Santos et al., 2016 for previous approaches). We focused on all extant land-bird species, in addition to lineages driven to extinction by anthropogenic causes. The focal archipelagos share five key features: limited land area, persistent geographical isolation, volcanic origin, tropical/subtropical latitude and oceanic climate (Gillespie & Clague, 2009; Triantis et al., 2015; Weigelt et al., 2013; Whittaker & Fernández-Palacios, 2007).

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., Grant & Grant, 2008; Losos & Ricklefs, 2009; Whittaker & Fernández-Palacios, 2007). At the archipelagic level, island communities respond to the insular geography on evolutionary time-scales, with species undergoing "taxon cycles" (i.e., sequential phases of expansion and contraction across an archipelago (Ricklefs & Bermingham, 2002; Wilson, 1961), and with the divergence of populations in allopatry being, arguably, the main driving force of diversification (Grant & Grant, 2008; Losos & Ricklefs, 2009). Thus, oceanic archipelagos can be seen as macroevolutionary metacommunities (i.e., sets of interacting island communities linked by dispersal). They therefore represent a higher level of hierarchical organization than individual islands and are amenable to framing analyses of large-scale patterns, such as community-level convergence (see also Triantis et al., 2015; Valente et al., 2020; Whittaker et al., 2017).

We developed a novel framework to test for community convergence in both morphological and phylogenetic structure of archipelagic land-bird faunas relative to their respective regional species pools (Figure 2a). To assess the influence of different assembly or disassembly mechanisms, we re-ran our analyses on five subsamples: (1) native non-endemic species; (2) endemic species (including extinct species); (3) a subsample with all extinct species removed; and (4) a monophyletic group (i.e., Passeriformes) that is also the largest order of birds. Our results show that multiple dimensions of archipelagic bird communities are more similar than expected by chance, even accounting for the influence of extinction, providing strong support that community convergence arises through deterministic community assembly.

2 | MATERIALS AND METHODS

2.1 | Species lists and regional pools

Contemporary biogeographical patterns on islands have been strongly influenced by historical and prehistoric anthropogenic extinctions (Hume, 2017; Steadman, 2006; Valente et al., 2020). Thus,

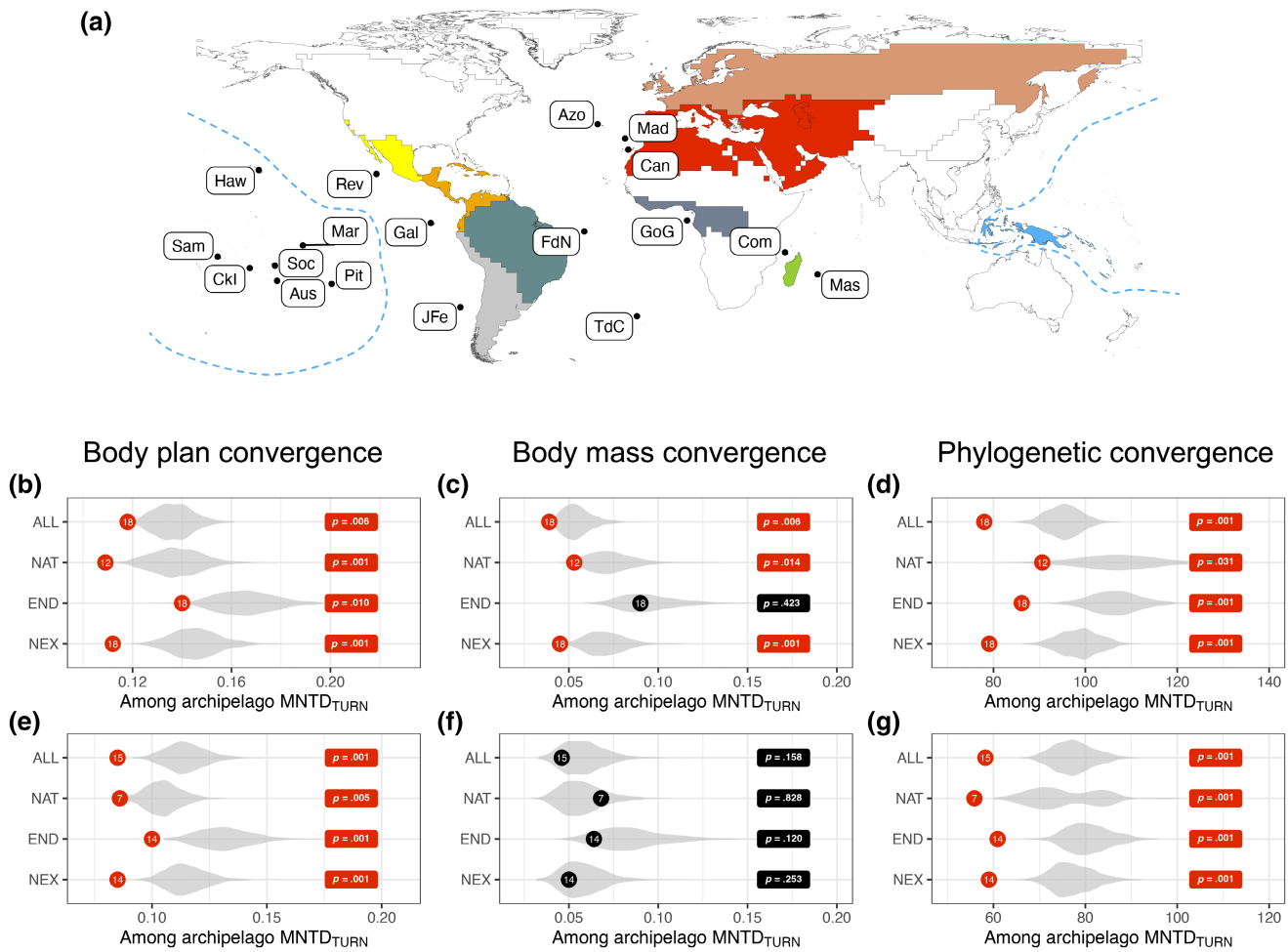

FIGURE 2 Island avifaunas converge on repeated patterns of morphological and phylogenetic structure. (a) Assignment of 18 archipelagos to nine biogeographical regions (Supporting Information Tables S1–S3). Regions are indicated by colour and archipelagos by the following abbreviations: Aus = Austral islands; Azo = Azores; Can = Canaries; Ckl = Cook Islands; Com = Comoros; 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 = 495 species) and for Passeriformes (e–g; n = 284 species). The panels provide results for all (ALL), native non-endemic (NAT) and endemic (END) species, including extinct species, in addition to 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). The values of $MNTD_{TURN}$ for body plan (unitless) and body mass (log_{10}[g]) were calculated using Euclidean distances between species, and the $MNTD_{TURN}$ for phylogeny was calculated using cophenetic distances (in millions of 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)

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

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

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

Archipelago	Species richness	Endemic species	Extinct species	Colonization events (minimum–maximum)
Austral	7	6	4	5–7
Azores	20	7	5	17–20
Canaries	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

Note: For the respective numbers of Passeriformes, see the Supporting Information.

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

2.2 | Morphological and phylogenetic data

We collated a range of morphometric data for our combined sample of 6,579 species (Supporting Information Data S1 and S2). For each extant study species (n = 6,423), we used a global dataset derived from linear measurements of wild birds and museum specimens (Pigot et al., 2020; Tobias et al., 2022) to compile estimates of wing length, tail length, tarsus length and beak length (in millimetres). These traits were selected because they reflect the overall body plan (Bauplan) and are correlated with important dimensions of the avian niche, such as habitat use, dispersal and foraging strategy (Pigot et al., 2020). We also compiled body mass (in grams) from the study by Wilman et al. (2014). For 36 (23%) of 175 extinct species, measurements were extracted from specialist literature. A list of the data sources is given in the Appendix (see also Supporting Information Data S1 for sources, including Amadon, 1950; Rothschild, 1907). 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 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 capabilities or flightlessness, and the ratio of femur/tibiotarsus/tarsometatarsus to highlight arboreal or terrestrial modifications (Steadman, 2006). Given that flightless species tend to be relatively heavy, we estimated the body mass of extinct flightless taxa known only from fossil remains with reference to similar-sized extant flightless species (e.g., flightless rails; J. P. Hume, unpublished data). Given that all trait data were calculated as species averages, we do not account for intraspecific variation, although previous analyses have shown this to be negligible in comparison to interspecific variation in the same avian traits at global scales (Tobias et al., 2022).

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

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

2.3 | Colonization events

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 examined whether congeneric endemic species from a particular archipelago formed a monophyletic group and assumed that such cases were the product of a single colonization event (Cornuault et al., 2013). Thus, for a particular archipelago, the number of colonization events 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.

Molecular data are lacking for most archipelagic extinct species, which can lead to phylogenetic uncertainty; therefore, we estimated the minimum and maximum number of colonization events for these species. The minimum number of events was calculated by assuming that congeneric 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-monophyletic, with each species representing a different colonization event (see sections B3 and C3 in the Supporting Information). Subsequent analyses were implemented in two ways, initially using the minimum number of colonization events, then by randomly selecting a number of colonization events between the minimum and the maximum.

2.4 | 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

Figure S1, Table S4) 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 $MNTD_{TURN}$ (Holt et al., 2018; Webb et al., 2008). 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 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, and min d_{jA} is the distance between each species j of archipelago B and the nearest species of archipelago A. 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 Section B1). Morphological distances (for both body mass and body plan) between species across archipelagos were measured using Euclidean distances, and pairwise phylogenetic distances between species were quantified using a cophenetic distance matrix (i.e., the phylogenetic branch length distance between species).

2.5 | 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 with 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 (Table 1; Supporting Information Tables 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 Species lists and regional pools). Once sampled, each colonizer was assigned randomly to a specific trajectory: either it stays unchanged (native non-endemic) or it speciates (becomes endemic) via anagenesis or cladogenesis (Supporting Information Figure S2), with the number of native non-endemic and endemic species being constrained to the current totals observed in the archipelago (see Supporting Information Figure S2). For instance, if two colonization events have generated current totals of one native non-endemic and five endemic species, respectively, in a particular archipelago, then in our simulation, one colonizer fails to speciate or evolve new traits, whereas the other gives birth to a monophyletic clade of five endemic species.

For each colonizer that undergoes speciation, morphological features of the resulting endemic species were simulated through a Brownian motion (BM) model of evolution (Freckleton et al., 2002). Under a BM model, a trait value changes as a function of time (t) and rate (σ^2), such that the simulated value is normally distributed, with the mean equal to its initial value (x_0) and the variance equal to the product of rate and time. For body mass, simulations were performed using a univariate BM model, and for body plan, a multivariate BM framework was used to fit the BM model simultaneously to the four size-corrected traits together, while assuming that traits are correlated (Clavel et al., 2015). The BM model was implemented on a birth–death (BD) tree (Supporting Information Figure S2), with the number of branches corresponding to the number of species in the endemic clade (see details in Supporting Information- Part B2. Null models). The time since the most recent common ancestor was fixed for the stem node at the geological age of the archipelago (using the oldest island currently present; Valente et al., 2020; Supporting Information Table S1).

To simulate the BD tree, we identified the family to which each speciating island-colonizer belongs, 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 in our study (the 349 endemic species of 18 archipelagos were excluded from these analyses). For families with <10 species, we sampled species more widely from the order to which the family belongs (see Supporting Information Section B2). We then applied a BM model to the branches of the BD tree using the estimated trait value of the speciating colonizer (i.e., the ancestral state x_0) as a starting point, and the σ^2 value was retrieved by fitting a BM model (univariate for body mass; multivariate for body plan) to the phylogeny and the traits of the family members as identified above. Therefore, for a given archipelago A, a species S belonging to the family F is randomly selected from the regional pool of potential colonizers and is allowed to generate an endemic clade containing N species. We used: (1) the geological age of archipelago A, with λ and μ values estimated for the tree of the family F, to create the tree of the endemic clade using the BD tree; and (2) the trait value of S as the ancestral state, with σ^2 estimated for the tree and traits of family F, to generate trait values for the N species along the BD tree previously generated. It 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.

We constructed a null phylogeny for each simulation by retaining the phylogenetic relationships between colonizers randomly selected from the pool as a backbone tree onto which we grafted the associated simulated BD tree(s) of the endemic clade. For each archipelago, the simulation protocol was independently implemented 1,000 times. Simulated data (body mass, body plan and phylogeny) were used to generate 1,000 random values for each pairwise $MNTD_{TURN}$ value and 1,000 average pairwise $MNTD_{TURN}$ values among all pairs of archipelagos. To test whether archipelagos overall were convergent in morphological and phylogenetic structure in relationship to their respective species pools, we tested whether

pairwise turnover and average turnover (measured by $MNTD_{TURN}$) were less than expected under the null model simulation (one-tailed test). To compare the relative roles of potential influences on community convergence, we also calculated how far the observed overall mean $MNTD_{TURN}$ among archipelagos deviated from null expectations using the standardized effect size (SES). The SES was calculated as $(MNTD_{TURN} - \mu_{sim})/\sigma_{sim}$, where μ_{sim} is the mean index of the simulated values, and σ_{sim} is the associated standard deviation. Negative SES values indicate lower morphological/phylogenetic $MNTD_{TURN}$ than expected by chance (i.e., negative numbers farther from zero indicate stronger convergence).

Null model approaches that involve sampling from a (larger) species pool can suffer high type I error rates owing to differences between the species richness of the focal assemblages and that of the pool (Kraft et al., 2007). To evaluate the type I error of our approach in detecting community convergence, we first designed a set of simulations to test the type I error associated with using the metric $MNTD_{TURN}$ to detect community convergence by using different combinations of community (i.e., archipelago) and pool size (i.e., regional pool). Second, we re-ran our convergence analyses by randomly selecting, for each archipelago, a subset of the species in the pool. Two subset sizes were used, corresponding to the number of species where the species richness of an archipelago represented 30 and 60% of the pool (Kraft et al., 2007; for further details of our approach, see Supporting Information Section C2).

2.6 | Assessing mechanisms of convergence

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

We tested further 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 Section C5) 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 1,000 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 Sections B and C. All statistical analyses were implemented within the R programming environment (R Core Team, 2019).

3 | RESULTS

Simulations showed that our framework for testing community convergence had very low type I error, and convergence detection was not sensitive to community size or pool size (see Supporting Information Figures S2 and S4).

When all extant and extinct land-bird species were analysed together, we found that 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 community structure (Figure 2b–d; Supporting Information Table S6). The strongest evidence for convergence was detected in phylogenetic structure. Results were similar when we restricted analyses to Passeriformes only, with the exception of body mass, which did not appear to show a pattern of community convergence (Figure 2e–g; Supporting Information Table S6). All archipelagos (except Juan Fernández) exhibited significant body plan and phylogenetic similarity (i.e., lower pairwise $MNTD_{TURN}$ than expected) with at least one other archipelago (Figure 3a–c). For body mass, several archipelagos showed no significant similarity with any other archipelago (Figure 3b,e). The lack of significant findings for Juan Fernández was attributable to the presence of two hummingbird species (*Sephanoides fernandensis* and *Sephanoides sephaniodes*, Trochilidae) on the archipelago, the only species in this morphologically distinct family present on any oceanic archipelago included in this study. A re-analysis of the convergence pattern without the two hummingbirds showed convergence of Juan Fernández with at least four archipelagos for body plan and phylogeny, but still no evidence of convergence for body mass (Supporting Information Figure S5).

Sensitivity analyses (Supporting Information) revealed these findings generally to be robust to: (1) assumptions regarding species pool definition; and (2) the estimated number of colonization events; with the analysis based on the number of colonization events randomly selected between the minimum and maximum numbers retrieved from the literature providing similar results to the main analysis (Table 1; Supporting Information Tables S7–S9). Our analyses testing for differences in taxonomic composition between archipelagos and their species pools for all land birds revealed that most of the avifauna in each of the 18 archipelagos was dominated by two main orders, passerines (Passeriformes) and pigeons (Columbiformes), with the latter being overrepresented on islands compared with the respective zoogeographical regions (Supporting Information Table S10). In addition, we found a significantly reduced number and different composition of families in most archipelagos compared with null expectations (Supporting Information Table S11), both for all land birds and for Passeriformes only.

Significant convergence in body plan, body mass and phylogenetic structure was also found for the native non-endemic species

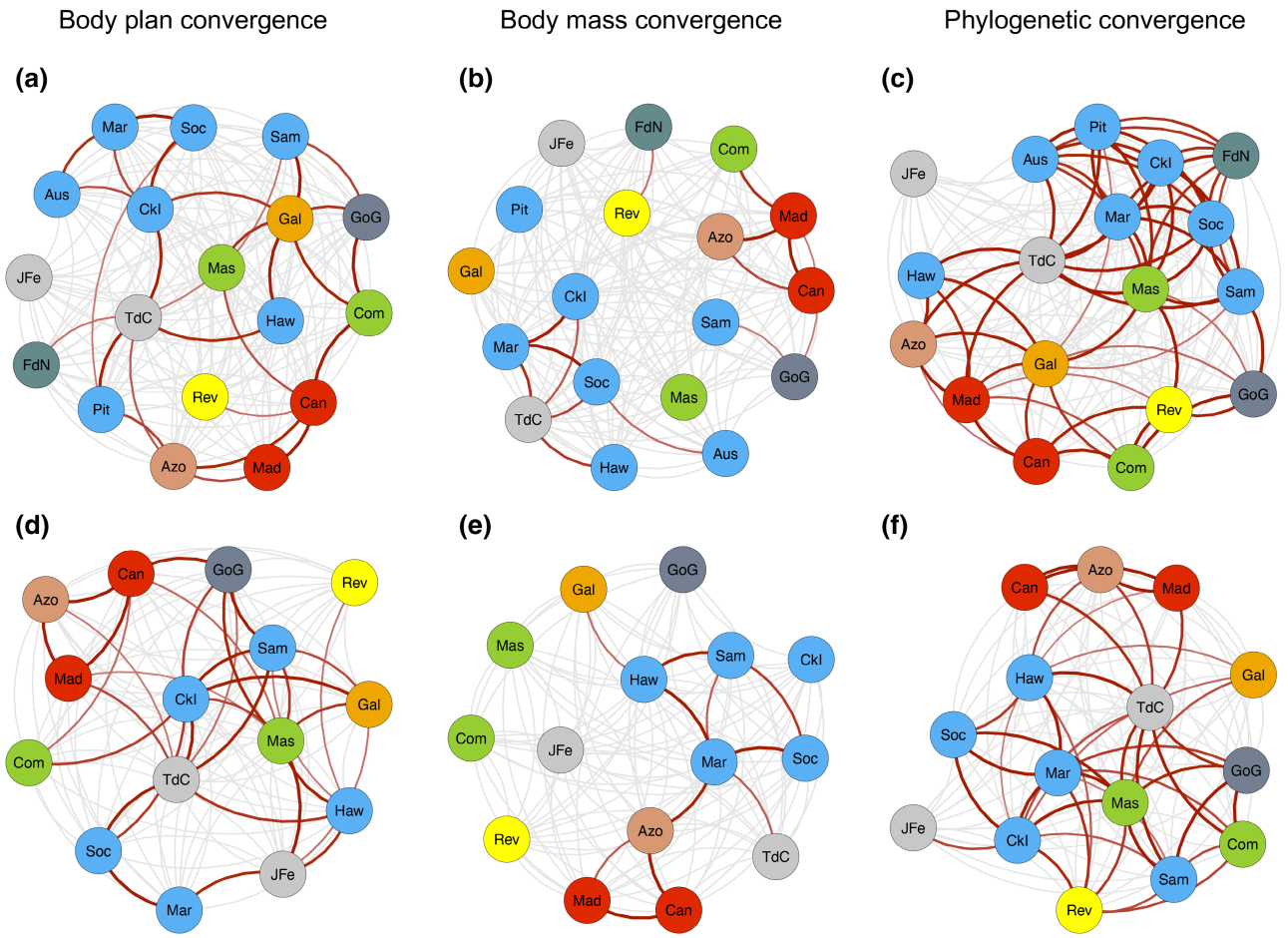

FIGURE 3 Convergent properties in morphological and phylogenetic structure of archipelagic avifaunas. The networks show convergence properties in body plan, body mass and phylogeny for: (a–c) all land birds; and (d–f) Passeriformes only. Nodes correspond to the 18 and 15 major oceanic archipelagos for all land birds and Passeriformes, respectively. Red and grey connectors depict convergence and non-convergence, respectively. Convergence was estimated by comparing pairwise morphological and phylogenetic turnover between pairs of 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 observed dissimilarity was below the lower bound of the 95% confidence limits of the null model distribution. Colours indicate the biogeographical region to which each archipelago belongs (for regions and archipelago names, see legend to Figure 2; Supporting Information Tables S1–S3)

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

Significant convergence in each of body plan, body mass and phylogeny was also detected in the extant species subset (post-extinction datasets). In addition, we found that body plan convergence was more pronounced in the sample of extant species (SES = −3.415; p = .001) than in the dataset containing extant and extinct species sampled together (SES = −2.364; p = .006). This was also true for extant and extinct species (SES = −3.277; p = .001) but was less pronounced for Passeriformes (extant species SES = −3.337; p = .001; and extant and extinct species, SES = −3.291; p = .001). These findings suggest that community convergence existed before human influences on island faunas and that convergence has been strengthened further by anthropogenic extinctions.

4 | DISCUSSION

Our results reveal clear evidence of convergence in both the phylogenetic structure and the morphology of archipelagic avifaunas, despite their assembly from distinct mainland source pools. The pattern of convergence was particularly strong for phylogenetic structure, suggesting that archipelagic assemblages are drawn from a non-random set of clades predisposed to over-sea dispersal and/or successful establishment in insular environments. The concordance

of evidence from phylogeny and key aspects of phenotype can be assigned to the fact that, in general, morphology is phylogenetically conserved in birds and also reflects dispersal propensity (e.g., Barnagaud et al., 2014; Jønsson et al., 2015; Ricklefs, 2012; Sheard et al., 2020; Tobias et al., 2020; Supporting Information Table S4).

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

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

Results from analyses based on endemic and non-endemic species separately confirm the general pattern of convergence, with both subsets being structurally more similar than expected by chance. Assuming that non-endemic species are generally more recently derived from mainland 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 convergence. Overall, our analyses show consistent evidence for convergent patterns in body plan and phylogenetic structure, whereas evidence for body mass convergence, albeit significant for all species, was not detected for passerines or for archipelagic endemics. There are two potential explanations for these findings. First, larger-bodied species might not be able to overcome the dispersal barrier (Figure 1) and colonize islands. Species belonging to Struthionidae (e.g., *Struthio camelus*), Rheidae (e.g., *Rhea americana*) and Casuariidae (e.g., *Casuarius casuarius*) are missing from island systems, and this might explain, at least in part, the pattern of body mass convergence when focusing on all species (body mass of archipelago species ranges from 5.17 to 22,500 g and for mainland species from 1.9 to 111,000 g). For passerines, the ranges of body mass are very similar between archipelagos and mainland areas (Supporting Information Figure S6), hence there is also less community convergence between archipelagos with regard to their respective species pools. Second, *in situ* speciation events within these groups (Figures 2 and 3) resulted in the presence of several relatively large species, such as the pigeons *Raphus cucullatus* (12,450 g) and *Pezophaps solitaria* (22,500 g) in the Mascarenes, further diluting community convergence.

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

Historical contingencies arising from regional factors and chance events have resulted in the assembly of unique biotas on archipelagos world-wide, often featuring multiple narrowly endemic species (Gillespie & Clague, 2009; Whittaker & Fernández-Palacios, 2007); hence, traditional comparisons of species or clade composition among oceanic archipelagos are not suitable for assessing convergence at the community level. By focusing on phylogenetic relationships and morphological traits in relationship to distinct regional species pools, we have shown that avian community assembly on oceanic archipelagos is shaped by non-random, deterministic and therefore predictable process regimes over large temporal scales. Crucially, we have shown that non-random anthropogenic extinctions contribute to this pattern, but are insufficient to explain its

pervasiveness. These findings clarify that historical contingencies are overridden by a combination of biogeographical assembly, *in situ* evolutionary adaptation and non-random anthropogenic impacts to generate convergent archipelagic bird communities world-wide. Similar approaches should be extended to other vertebrate groups, plants and invertebrates to assess the generality of our findings across a wider sample of biodiversity.

AUTHOR CONTRIBUTIONS

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

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data are available via the Dryad Digital Repository: https://doi.org/10.5061/dryad.k6djh9w8x The code for analyses in R can be download from https://github.com/frigal001/Functions-Birds-Convergence.

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BIOSKETCH

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

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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APPENDIX

DATA SOURCES

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