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RESEARCH ARTICLE

Niche filling predicts evolutionary trajectories in insular bird communities

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Abstract

1. Different theories have been proposed to explain the phenotypic changes observed in island lineages, but it remains unclear if predictable evolutionary trajectories can be identified within island communities.
2. Using a 3D functional space approach, we tested whether insular endemic species tend to evolve towards apparent holes in niche space (expecting niche filling) or tend to become generalists, that is, moving towards the centre of the functional space (expecting niche expansion).
3. We tested these two hypotheses in 378 insular endemic species from 24 islands of 8 archipelagos, including 177 prehistoric anthropogenically extinct species. Analyses were conducted with and without accounting for species size difference.
4. We found that 57% of island endemic species evolved towards more unoccupied regions of the global morphospace (i.e. more distinct body sizes compared to the ones of their ancestors), suggesting a tendency for niche filling. When adjusted traits for body size, we found that half of the endemic species (50%) showed more distinct trait values than their ancestors.
5. Results also revealed that certain dietary niches (terrestrial herbivores and nectarivores) evolved distinct body sizes more frequently. Differences noted between islands and archipelagos suggest that biogeographic factors may influence evolutionary trajectory and interactions between these two hypotheses.
6. Our study confirms that extinct species occupied specific niches that have been left vacant, suggesting that these evolutionary 'oddities' could be more sensitive to extinction. Overall, it calls for a global assessment of the avian functional diversity lost from recent extinctions.

KEYWORDS
avian communities, birds, evolutionary trajectory, extinct species, functional space, islands

1 | INTRODUCTION

Identifying predictable, directional patterns of evolutionary change has proven challenging (Clegg & Owens, 2002; Jezierski et al., 2023; Wright et al., 2016). For a long time, scientists have recognized that insular environments offer distinctive conditions that make species to evolve to different directions than on adjacent mainland areas (Wallace, 1880). Because of their isolation, island communities are often considered as reduced subset of their mainland species pools, which means that colonizing species encounter reduced competition and predation than in mainland areas (Grant, 1998; Lomolino et al., 2012). Consequently, two non-mutually exclusive theories have been proposed to explain the phenotypic changes observed in island lineages: the theory of adaptive radiation and the theory of ecological release. Both theories need a proper understanding of overall functional diversity on islands and can thus only be tested by including recently extinct species, to ensure that the diversity on islands is as unbiased as possible.

The theory of adaptive radiation proposes that single ancestral species lead to several descendants that evolve to use different resources (e.g. Darwin's finches; Schluter, 2000). In the debate over evolutionary contingency versus determinism on islands, Conway Morris (2003) supported the idea that island species should in principle evolve a variety of adaptations to perform similar, but distinct, ecological roles—expecting functional niche filling. The theory of adaptive radiation thus predicts that species should evolve to fill empty gaps in the functional space of the island community (Losos & Ricklefs, 2009). As an example, it has been suggested that endemic geese and ducks evolved to fill the niche of large herbivores usually occupied by mammals but left vacant on the Hawaiian archipelago (Paxinos et al., 2002; Sorenson et al., 1999). Hence, it is expected that species will shift their original niche to another niche in the functional space and we referred to this, hereafter, as the *niche shifting* hypothesis. Although the concept of niche filling has been explored in the context of diversification (e.g. Fritz et al., 2012; Ricklefs, 2010), its role in the evolutionary trajectory of island species and the formation of island communities has received much less attention.

The theory of ecological release, on the other hand, proposes that insular morphological changes are adaptations to facilitate ecological niche expansions, with selection favouring generalist behaviours in relatively depleted environments with low levels of interspecific competition (Grant, 1998; Wilson & MacArthur, 1967). It has been suggested that evolution may favour generality on isolated islands where species composition is characterized by little functional diversity (Olesen & Jordano, 2002). In some contexts, this flexibility can lead to the evolution of intermediate characters (i.e. a shift to an average or generalist morphology; Grant, 1998; Whittaker, 1998). For instance, there is evidence that the bodies and beaks of islands birds have shifted towards intermediate sizes (e.g. Maui Parrotbill *Pseudonestor xanthophrys*), reflecting evolution towards a more efficient generalist behaviour (Abbott, 1974; Boyer & Jetz, 2010; Clegg & Owens, 2002; Keast, 1970). We referred to this, hereafter, as the *niche expansion* hypothesis. Translated to the avian functional space, we would expect island endemic species to evolve towards the most general combination of traits (i.e. broad diet breadth, habitat generalist, intermediate body size) and hence to the centroid of the island community. We thus relied on the assumption that generalist species, in their behaviour, tend to be located in the centroid of the functional space, which has been corroborated in several studies for passerines (Ricklefs, 2012) and recently at global scale for birds (Pigot et al., 2020; Sayol et al., 2023).

Despite progress in the study of morphological evolution in insular communities (Losos & Ricklefs, 2009; Navalón et al., 2020; Pinto et al., 2008), it is not clear if one of these two hypotheses is favoured in island communities. Furthermore, the lack of clear evidence probably stems from the fact that these two hypotheses are not mutually exclusive. Indeed, one can imagine a gradual process with species first expanding their niche to establish on the newly colonized islands (i.e. niche expansion), before subsequently specializing to use unique resources and thus following the niche shifting hypothesis. It is then possible that morphological evolution also follows this gradual process. From the view of a functional space, an evolutionary trajectory can in theory follow both hypotheses at the same time. Island species may have more intermediate trait values (i.e. closer to the centroid and closer than those of its ancestor), which may also be more distinct (i.e. not near many other species in trait space) if all the species in the community are dispersed around the centroid but not directly adjacent to it.

Examination of hypotheses about evolutionary trajectories in functional space for insular communities requires communities to be studied as they were at the time of the colonization and evolution of endemic species. It is thus important to include recently extinct species to avoid biased sampling (i.e. to work with the most complete community possible), as we suspected that extinct species are not randomly placed in the functional space (see Matthews et al., 2022; Sayol et al., 2021) and that they may also have followed specific evolutionary trajectories. We used recently published databases of morphological traits for extant and extinct species (Sayol et al., 2021; Tobias et al., 2022) to test whether island lineages evolve towards filling a functional gap (i.e. the niche shifting hypothesis) or towards common morphological traits in the community (i.e. the niche expansion hypothesis; see Figure 1). From the position of the island endemic and its likely ancestor in a 3D functional space of the community summarizing nine body and beak traits, we tested whether birds have evolved towards more distinct or more intermediate trait values (i.e. like other lineages of the community). We first identified the proportion of endemic species that follow one of these two hypotheses using the first three PC axes and then repeated the analysis without the first PC axe (i.e. using the PC axes 2 to 4) to adjust the traits to body size and mostly capture variation in shape (Pigot et al., 2020). Finally, we tested whether support for these hypotheses of niche shifting,

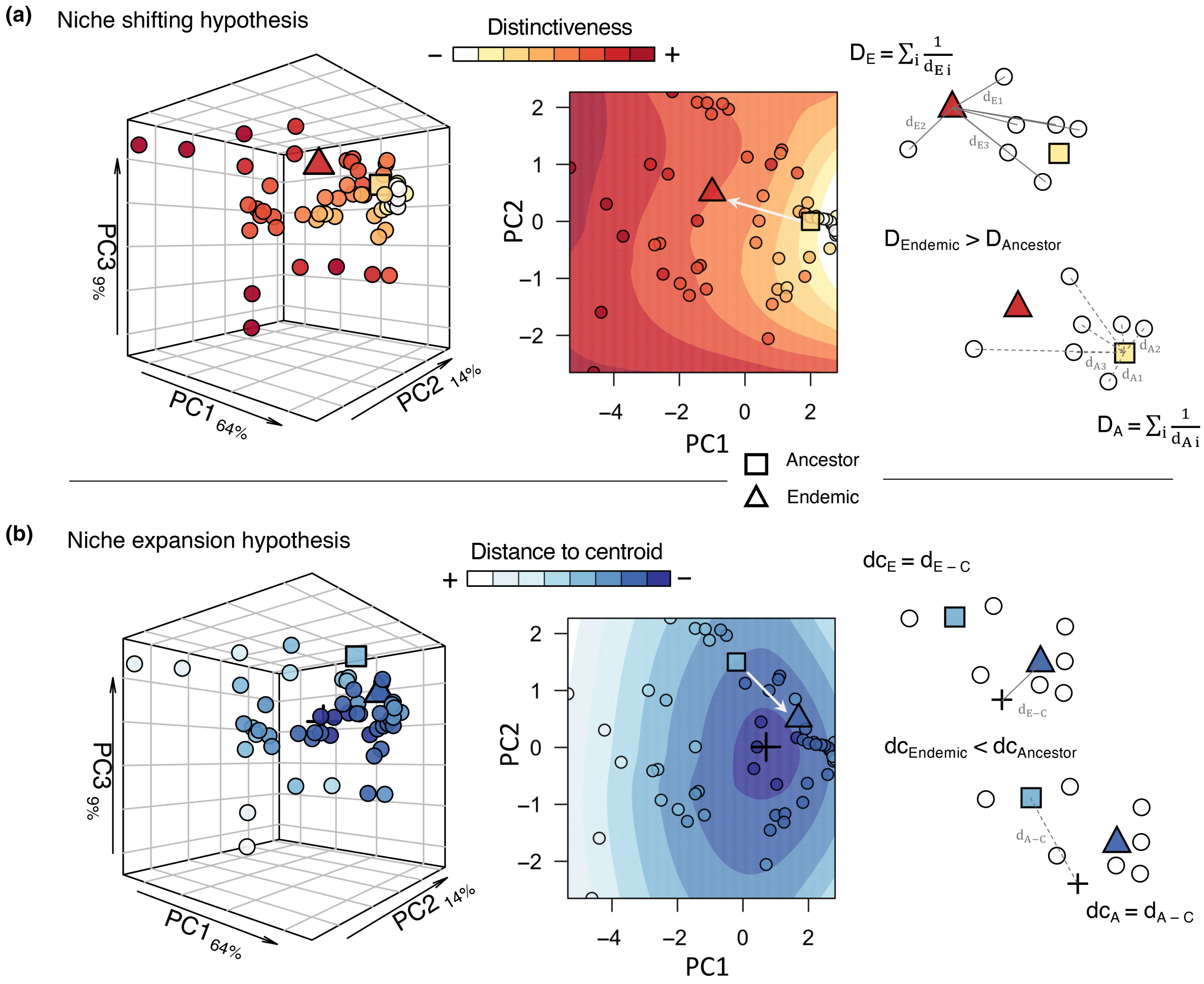

FIGURE 1 Examining evolutionary trajectories of endemic species within island communities. We tested if species tend to evolve towards filling a functional gap in the island community (i.e. the niche shifting hypothesis = a) and if species tend to evolve towards the most general combination of traits (i.e. broad diet breadth, habitat generalist, intermediate body size) and hence to the centroid of the island community (i.e. the niche expansion hypothesis = b). In the functional space (left, represented by the first three PCA axes) each dot represents a native species of the community, coloured according to its distinctiveness (a) or distance to centroid values (b). The 2D plots highlight variations in distinctiveness and distance to centroid values within the same functional space. An endemic species (large triangle) and its ancestor (large square) are identified. The centroid of the island community is represented by a cross in (b), and its position logically depends on the positions of other species in the community. The evolutionary trajectory between the ancestor and the endemic species is represented by the white arrow. As schematized in the right part of the panel (a) with few schematic species, the distinctiveness values of each endemic species (D_E) and its ancestor (D_A) were calculated as the sum of inverse distances with other species of the community, to identify species that evolved towards more distinct traits than their ancestor (when $D_E > D_A$). In other words, the more isolated the endemic or its ancestor, is from other species in the community, the more distinct it is. Similarly, as shown in the right part of the panel (b), the distance between each endemic species and the centroid of the island community (dc_E) was estimated and compared with the distance between the centroid and their ancestor (dc_A), to identify species that are closer to the centroid than their ancestor (when $dc_E < dc_A$).

and niche expansion varied with island geography and trophic groups for birds.

2 | MATERIALS AND METHODS

All analyses were performed in R version 4.3.0. (R Core Team, 2023).

2.1 | Geographic and taxonomic data

We investigated evolutionary trajectories of 378 insular endemic species, including 177 prehistoric anthropogenically extinct species, from 24 islands of 8 archipelagos (Figure 2). We followed the archipelago definition used in Cooke et al. (2023). We studied the evolutionary trajectories of endemic species that evolved on islands from continental ancestors (following a colonization event). We therefore excluded species that have no close continental relatives to compare their morphology, that is, families that are entirely endemic to an archipelago and have derived more than 15 million years from their continental relatives (e.g. we retained the Teretistridae from Cuba but excluded the Acanthisittidae and Dinornithidae from New Zealand).

We worked at the island scale, including islands with sufficiently large communities. Islands were selected based on the available phylogenetic knowledge of extinct and existing endemic species. We also selected islands where the fossil record is the best known according to Cooke et al. (2023) to avoid studying biased communities. Island communities were defined as all endemic and non-endemic species that regularly breed on an island. We collected the list of extant species from the Handbook of the Birds of the World checklist (Billerman et al., 2022) and the list of extinct species (extinct over the last 125,000 years) from an updated version of a previous publication (Sayol et al., 2020). To compare species that share the same niches and habitats, we excluded seabirds. We also excluded alien species (according to Dyer et al., 2017) and species that colonized the archipelago within the last few centuries (see Holdaway et al., 2001). Undescribed extinct species for which we did not have sufficient information to estimate their phylogenetic placement more finely than at family level (e.g. Fringillidae sp./Madeira in Illera et al., 2012) were also excluded.

The 24 island communities we studied represented an average of 55 species (minimum of 16 species for Rodrigues and maximum of 155 species for Cuba) and an average of 51% were endemic species (minimum of 13% for Gran Canaria and maximum of 86% in Reunion). The proportions of extinct species per island were highly variable with 23% of extinct species on average, from a minimum of 0% for Sao Tome, Principe and all Galapagos Islands included in this analysis to a maximum of 71% for Rodrigues. Note that endemic species that have been excluded from filtering (because they have no close continental relatives to infer their morphological trajectories) have still been included to estimate the morphospace of the island community. As an example, the Rifleman (*Acanthisitta chloris*) and other species of New Zealand wrens were included to estimate the morphospace of both North and South Islands, even though we did not estimate their evolutionary trajectory as they have no close continental relatives.

2.2 | Phylogenetic construction

As we were interested in reconstructing the evolution of morphological traits through time, we needed the most complete phylogeny available, including all the species from the island communities. Therefore, we grafted all the extinct species onto a composite phylogeny of BirdTree (Jetz et al., 2012). Our composite tree compiled the backbone of the phylogeny of Prum et al. (2015) and the maximum clade credibility tree of Jetz et al. (2012), following the method described in Cooney et al. (2017). In addition, we also grafted onto the same phylogeny extant species that have been described since the publication of BirdTree and changed the position of extant species, already present in BirdTree, for which the position has been reassessed in recent literature (e.g. Salter et al., 2020).

For each endemic extinct species, we used information in the published literature to identify either the closest mainland-relative or the continental lineage to which the species belongs and distinguished three cases for adding extinct or extant species that were missing or incorrectly positioned in the phylogeny. Details about

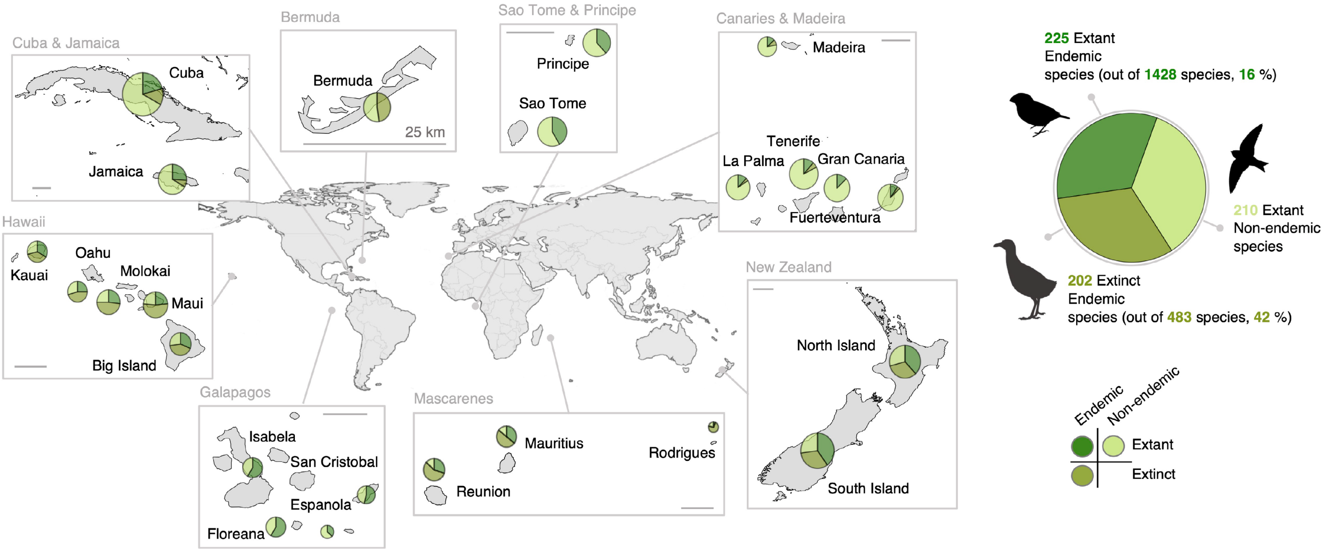

FIGURE 2 Proportions and total number endemic and non-endemic, extinct and extant species considered in the study. The evolutionary trajectories of 378 endemic species from 24 islands of 8 different archipelagos from diverse biogeographical regions were estimated. The total number of extinct endemic species was found in (Billerman et al., 2022) and the total number of extant endemic species in (IUCN, 2020). The size of the pie is proportional to the size of the avian insular community (i.e. the total number of species). In each archipelago panel, unless otherwise stated, the grey bar represents a scale of 100 km. Silhouettes were downloaded or deposited at Phylopic.org under a public domain licence.

the grafting procedure can be found in Supporting Information (see also Figure S1). In total, we grafted 174 extinct species and added or changed the position of 69 extant species onto the composite phylogeny of BirdTree. Given the uncertainty of the grafting procedure, we repeated the grafting procedure to construct 100 different tree topologies.

2.3 | Trait data

For morphological traits, we used nine trait measurements that provide accurate information on the functional role and trophic status of birds at the global scale (Pigot et al., 2020). For extant species, we sourced trait data for all the world species from the AVONET trait dataset (Tobias et al., 2022). For each species, we used average measurements based on intra-specific sampling ranging from five to nine individuals per species (Tobias et al., 2022). We sourced the same trait measurements for extinct species presented in Sayol et al. (2021). In this study, the authors measured the traits from preserved skins for recently extinct species, measured traits from the skeleton for older extinctions with subfossil data and employed a machine learning algorithm (the BHPMF) to infer missing data in the morphological matrix with 10 imputation runs (Sayol et al., 2021). The output of these imputations is an average value for each of the nine linear morphological measurements including four beak measurements (beak length measured from tip to skull along the culmen, beak length measured from the tip to the anterior edge of the nares, beak depth and beak width) and five body measurements (tarsus length, wing length from carpal joint to wingtip measured on the unflattened wing, Kipp's distance measured directly or calculated as wing length minus first-secondary length, tail length and body mass; see details in Tobias et al., 2022). This study used only previously collected morphometric data and did not involve any handling of animals.

2.4 | Evolutionary trajectories in the functional space

Our aim was to position the ancestor of each island endemic species in the functional space of the bird community. To do this, we estimated the trait values of that ancestor. For each endemic species and for each of the nine traits considered, we performed ancestral state reconstructions to obtain the trait values at the node corresponding to the common ancestor of the endemic species and its mainland-relative (or the closest affinity group). We used the *phylopars* function in Rphylopars R package with the Brownian Motion model (Goolsby et al., 2020). For each reconstruction, we omitted the focal endemic species to prevent biasing the trait evolutions towards the trait values of the endemic species. We used a maximum likelihood approach even though it does not allow for the integration of uncertainty in the analysis, as errors between species are not independent, which is a common issue with any maximum likelihood method. Since the grafting procedure can lead to significantly different positions for extinct species within the phylogeny, it can result in quite different estimates of trait values through ancestral state reconstructions. Therefore, we opted for functions that allow fast estimation across many trees to capture the major sources of uncertainty. Consequently, we repeated the analysis on all 100 tree topologies.

To model the evolutionary trajectory of each endemic species within the functional space of each island community, we summarized trait variation with a principal component analysis (PCA). For each endemic species, we performed a PCA with the nine morphological traits of all the species of the island community (i.e. we calculated PCA axes for each of the 24 island communities) and including the focal endemic species. We then placed, onto the same PCA, its theoretical ancestor based on the trait values estimated by ancestral state reconstructions. In both cases, we selected the first three PC axes, which allowed us to position each species and its ancestor in a 3D functional space.

From the PCA loadings of each species (i.e. values of the first three PC axes), we first calculated distinctiveness values for the endemic species and its ancestor to test the niche shifting hypothesis. We calculated distinctiveness as the sum of the inverse distances to other species in the community, with a low value indicating isolated species in the functional space. We used the function *dist* (stats package), with a measure of the Euclidean distance, to estimate the distance between the endemic species or its ancestor and all other species of the community. From the ratio, adaptive ratio hereafter, of the distinctiveness value of the ancestor (D_A) to that of the endemic species (D_E), we identified species (i.e. value greater than 1) that have evolved to a spot in the functional space that is emptier (more distinct) than the one in which their ancestor is found.

From the same PCA loadings of each species, we calculated the distance from the centroid of the community to the endemic and its ancestor to test the niche expansion hypothesis. Again, we used the function *dist* to compute the distances between the endemic species or its ancestor, and the centroid of the community (i.e. the coordinates: 0, 0, 0). A low value indicated species close to the centroid of the community. From the ratio, generalist ratio hereafter, of the distance to the centroid of the ancestor (dc_A) to that of the endemic species (dc_E), we identified species (i.e. value greater than 1) that are closer to the centroid than their ancestor and which evolved towards more central trait values. This second hypothesis assumes that morphospace within each archipelago represent a scaled-down representation of the global morphospace and that species close to the centroid on a global scale remain close to the centroid even if the size of the community decreases. We tested this assumption with different community sizes and presented the methods and results in the Supporting Information.

To test whether evolutionary changes are mostly affected by body size, we replicated the same analyses estimating the 3D functional space with PC axes 2 to 4, which mostly represent variation of shape (the first PC axe mainly concerns allometric changes with body size, here the body mass; see Pigot et al., 2020; Sayol et al., 2023 and Figure S2 with percentages of variance explained by each axis). To test whether PC scores could change because of small size communities and species sampling within islands, we repeated the same analyses (using PC axes 1 to 3 and PC axes 2 to 4) by calculating PC scores based on all the 637 species (extant and extinct endemic and non-endemic species) occurring on any of the islands we analyse. We then calculated the functional space for each of the 24 islands using these alternative broader PC scores.

Finally, to test whether the evolutionary trajectory of endemic species tend to follow the niche shifting or the niche expansion hypothesis, we performed both linear regression intercept-only models and intercept-only phylogenetic generalized least square (PGLS) models using mean values of the distance to centroid and the distinctiveness values estimated from the 100 different tree topologies. In separate models, we modelled the adaptive ratio (D_A/D_E) and the generalist ratio (dc_A/dc_E; both log-transformed) ratio values for all endemic species studied ($n=378$). The p-value associated with the intercept-only model assessed whether the intercept is significantly different from zero. For PGLS models, we used the package phylolm (Tung Ho & Ané, 2014) with evolution estimated to follow a Pagel's lambda model (Pagel, 1999). The analyses were run with a maximum clade credibility of the 100 tree topologies containing all the species added. Because of the presence of several evolutionary radiations, we suspected endemic species that derived from island speciation (i.e. cladogenetic species; Warren et al., 2015) to share similar traits and similar evolutionary trajectories. Hence, we replicated the analysis by using a median value for each lineage of cladogenetic species (for a total of 212 clades), calculated from the values for all cladogenetic species by lineage.

2.5 | Associations with evolutionary trajectories

We investigated whether dietary guild or island geography can influence the tendency of species in following either of these two hypotheses. We thus performed two different PGLS models, modelling the adaptive ratio (D_A/D_E) and the generalist ratio (dc_A/dc_E; both log-transformed) and the trophic position as explanatory variables, using the package phylolm (Tung Ho & Ané, 2014). We assigned dietary guild based on nine different categories (frugivore; granivore; nectarivore; terrestrial herbivore; aquatic herbivore; invertivore; vertivore; aquatic predator; scavenger) encompassing major resource types utilized by birds (Pigot et al., 2020). The data were collected from recently published datasets (Soares, de Lima, et al., 2022; Soares, Palmeirim, et al., 2022; Tobias et al., 2022) and were curated to match the categories of the AVONET trait dataset (Tobias et al., 2022). For a few species missing, we used the categories of closely related species as a surrogate. For island geography, we modelled the proportions of species following the two hypotheses per islands with age and area of the islands as explanatory variables. We collected the area data from Weigelt et al. (2013) and the estimated age of the islands from Shaw and Gillespie (2016) and Valente et al. (2020).

3 | RESULTS

When conducting the analysis on the overall phenotype (i.e. with PC axes 1 to 3), we found that 214 out of the 378 endemic species (56.6%) showed more distinct values of traits than their ancestors. This was greater than expected at random and thus provides support for the niche shifting hypothesis (significantly different from a 50% value; $p=0.012$, two tailed binomial test). In contrast, only 185 species (48.9%) were closer to the centroid than their ancestors (not significantly different from a 50% value; $p=0.719$, two tailed binomial test). We also found that 20 species have evolutionary trajectories that follow both hypotheses at the same time, suggesting that they may not be mutually exclusive. Both linear regression and PGLS intercept-only models showed significant support for the niche shifting hypothesis but, as suspected only without the phylogenetic correction (Table 1) or when considering a median value for each lineage of cladogenetic species (for both linear and PGLS models; Table 1). This result suggests that different species within evolutionary radiations may have followed the same evolutionary trajectories (e.g. the two Kioeas in Hawaii with *Chaetoptila angustipluma* on Big Island and *Chaetopitla* sp./Maui on Maui or in the Mascarenes with the Rodrigues Solitaire *Pezophas solitarius* on Rodrigues and the Dodo *Raphus cucullatus* on Reunion).

When adjusted traits for body size (i.e. using PC axes 2 to 4 rather than 1 to 3), we found that half of the endemic species (190 out of the 378; 50%) showed more distinct values than their ancestors and that 170 species (45%) were closer to the centroid than their ancestors (both not significantly different from a 50% value). While we only found significant support for the niche shifting hypothesis when considering a median value for each lineage of cladogenetic species (Table 1), we found that endemic species tend to be significantly further from the centre of the functional space with or without the phylogenetic correction (Table 1). Note that we found that species close to the centroid on a global scale remain close to the centroid even if the size of the community decreases (Figure S3). We replicated the analyses with PC scores calculated across all species included in the analysis (rather than island-level PC scores), yielding very similar results (Table S1), suggesting that small size communities and species sampling within islands had little influence on our results.

Regarding the overall phenotype, most of the species that have shown the greatest changes in morphology compared to their theoretical ancestors are extinct species (Figure 3a). For instance, the morphologies of the Dodo (*R. cucullatus*) from Mauritius or the Cuban Giant Owl (*Ornimegalonyx oteroi*) are substantially different from their ancestors. There were however also extinct species that instead have evolved closer to the centroid (i.e. towards intermediate values of traits), compared to the position of their ancestors, including the Oahu Kioea (*C. angustipluma*) the Maui Nui Kioae (*Chaetoptila* sp. From Maui) from Hawaii and the two Mascarene Scops Owls (*Otus murivorus* from Mauritius and Otus *gruchenti* from Reunion). More example species are highlighted in Figure 3a. Considering the shape, we found both extinct and extant species among the species with the greatest changes in morphology (e.g. the Huia *Heteralocha*

TABLE 1 Results of linear regression intercept-only and PGLS models applied to 378 endemic species from 24 islands of 8 archipelagos for PC axes 1 to 3 (overall phenotype) and PC axes 2 to 4 (adjusted for body size).

Functional space	Variable	Species	Model	Lambda	Est.	SE	*t*-value	*p*-value
PC axes 1 to 3	Distinctiveness	All			0.08	0.02	4.06	<0.001***
		All	PGLS	0.39	0.10	0.10	1.06	0.29
		Median			0.07	0.02	3.23	0.001**
		Median	PGLS	0.06	0.09	0.04	2.13	0.03*
	Distance to centroid	All			−0.03	0.02	−1.33	0.18
		All	PGLS	0.86	−0.11	0.23	−0.47	0.64
		Median			−0.04	0.03	−1.23	0.22
		Median	PGLS	0.02	−0.05	0.04	−1.20	0.23
PC axes 2 to 4	Distinctiveness	All			0.03	0.02	1.77	0.07
		All	PGLS	0.16	0.05	0.06	0.84	0.39
		Median			0.04	0.02	2.29	0.02*
		Median	PGLS	0.06	0.04	0.03	1.17	0.24
	Distance to centroid	All			−0.07	0.02	−3.02	0.002**
		All	PGLS	0.14	−0.08	0.07	−1.16	0.24*
		Median			−0.08	0.02	−3.22	0.001**
		Median	PGLS	0.01	−0.07	0.02	−3.22	0.001**

Note: By pooling all endemic species, we studied the general trend of endemic species to follow the niche shifting or the niche expansion hypotheses. *Median* refers to median value for each lineage of cladogenetic species (equivalent to a total of 212 taxonomic units; see Methods). SE is the standard-error and significant *p*-values are denoted with asterisks: $p < 0.05$ (*), $p < 0.01$ (**) and $p < 0.001$ (***).

acutirostris from New Zealand or the Galapagos Flycatcher *Myiarchus magnirostris* from Galapagos) as illustrated in Figure 3b.

We found that 16 (67%) out of the 24 islands studied have a higher proportion of species that evolved according to the niche shifting hypothesis than according to the niche expansion hypothesis when using PC axes 1 to 3 (Figure 3a). Interestingly, while all the island communities in the Hawaiian, Galapagos or New Zealand archipelagos consistently followed one of the two hypotheses, we found contrasting patterns between the islands of other archipelagos. For example, we found opposite patterns between the two Mascarene Islands with Mauritius showing majority niche shifting and Reunion showing majority niche expansion. When using PC axes 2 to 4, we found fairly similar results, with 16 (67%) out of the 24 islands studied with a higher proportion of species that evolved according to the niche shifting hypothesis (Figure 3b).

For both body size and shape, we found that terrestrial herbivores and nectarivores were more likely to evolve towards distinct trait values, compared to other dietary niches (Table S2). When considering shape only, we also found that terrestrial herbivores were more likely to evolve further to the centroid (Table S2). Finally, we found no clear influence from the age or surface area of the island in following either of these two hypotheses (Table S3).

4 | DISCUSSION

Our results suggest that endemic species from diverse islands over the world have predictable evolutionary trajectories. Indeed, considering the overall phenotype, we found that species tend to evolve towards distinct morphological trait values more often than towards intermediate values. Then, when adjusted the traits for body size, we found that species also tend, to a lesser extent, to evolve towards distinct morphological trait values, but they also evolved more often further from the centre of the functional space. For the overall phenotype, our findings support the niche shifting theory (Losos & Ricklefs, 2009) and suggest that insular species mostly evolve towards distinct body sizes to fill empty gaps in the functional space of the community, instead of evolving towards intermediate body sizes. This is in line with the idea of ecological niche partitioning discussed in several large island radiations, where these radiations evolved a wide variety of sizes and morphologies to occupy different regions of the available niche space (e.g. in Darwin's finches: Schluter, 2000; in Hawaiian honeycreepers: Lovette et al., 2002; in Madagascan vangas: Jønsson et al., 2012). Our results also corroborate the idea of body size shifts in island endemic species (Benítez-López et al., 2021), related to the 'so-called' island rule and the general pattern of both small-animal gigantism and large-animal dwarfism largely discussed in the literature (Lomolino, 2005), but they also provide a further insight into this phenomenon. Indeed, when adjusted the traits for body size, we found that species traits still shift to more distinct values but also further from the centre of the functional space, meaning that the species become less generalists. These results tend to contrast with studies highlighting evolution towards intermediate trait values in island environments in birds (Boyer & Jetz, 2010; Keast, 1970). Further research would be required

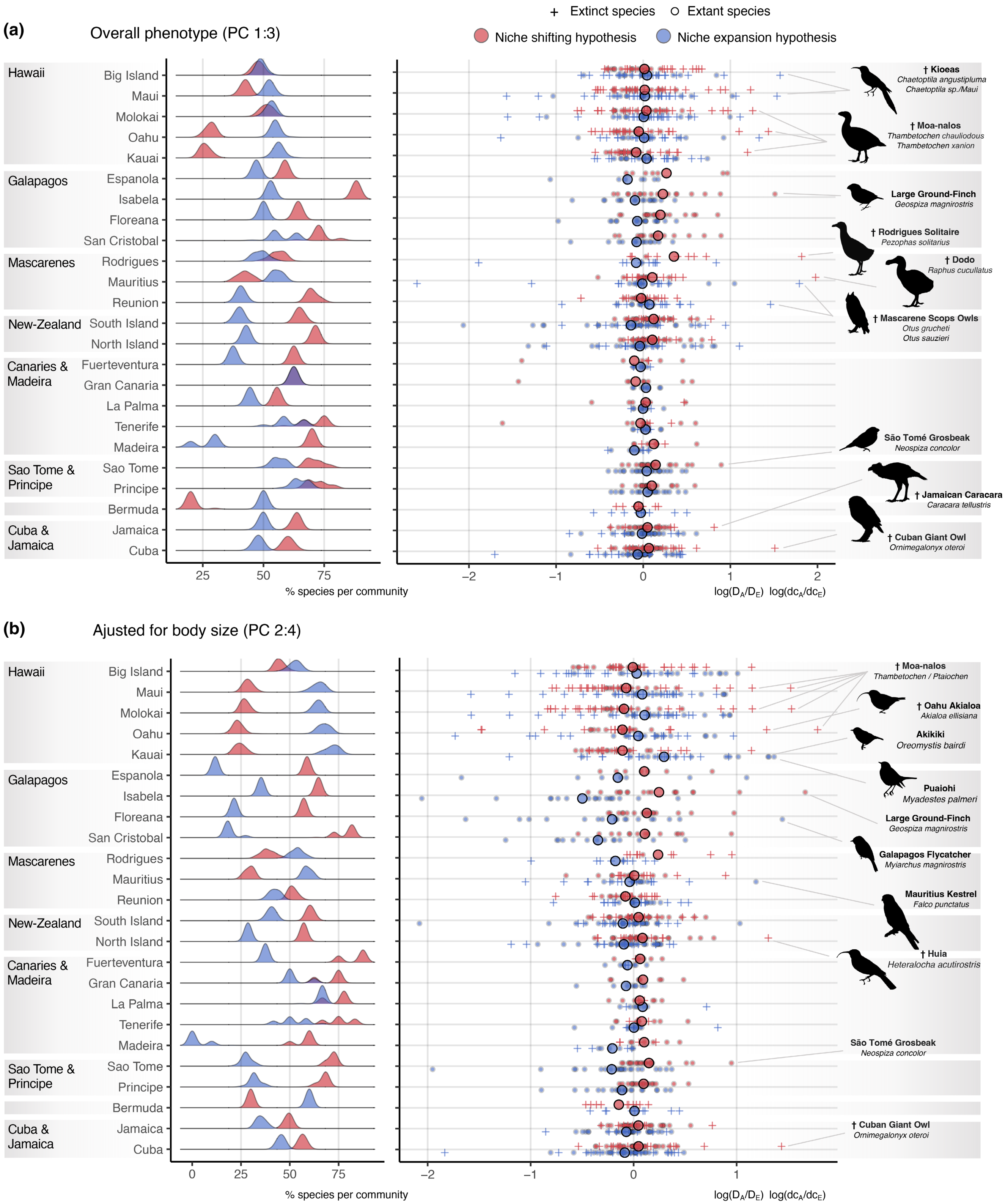

FIGURE 3 Distribution of species according to the niche shifting or the niche expansion hypotheses for the 24 islands. The panel (a) presents results for the overall phenotype with PC axes 1 to 3 and (b) for traits adjusted for body size with PC axes 2 to 4. Analyses were repeated for 100 different phylogenies to take into account the uncertainty of the placement of extinct species. The left panels indicate percentages of species per community that follow each of the two hypotheses (niche filling or niche expansion). On the right, the position of each endemic species according to its distinctiveness or distance to centroid values, compared to the values of their ancestor. The large dots indicating the mean value. Extant species are indicated with dots and extinct species with crosses. Species with the most remarkable evolutionary trajectories are illustrated with silhouettes. Silhouettes were downloaded or deposited at Phylopic.org under a public domain licence. '†' indicates extinct species.

to decompose the biological hypotheses between body size and shape, but previous studies argued that there is likely no single biological explanation, with different ecological factors affecting different morphological traits. Changes in body sizes are likely linked to the high population densities known to characterize island populations (MacArthur et al., 1972) while changes in beak shape are likely linked with foraging and diet ecology (Clegg & Owens, 2002; Grant, 1965). Going further will probably require large scale data with intra-specific measurements per species as our study does not consider possible morphometric differences between island and mainland populations (Andrade et al., 2021; Grant, 1971). Such data are not yet available on a global scale, and while we believe their inclusion should not have a major impact on our results, they will certainly be important to investigate in more details the biological explanations at play in island communities.

Our results show that certain dietary guilds such as terrestrial herbivores and nectarivores more often evolved towards distinct body sizes. For terrestrial herbivores, it has been suggested that extreme morphological changes correspond to the filling of the niche of large herbivores normally occupied by mammals and left vacant on several archipelagos (Wood et al., 2013) discussing the case of moas in New-Zealand. In our study, despite excluding several herbivore endemic families (e.g. Dinornithidae), we found extreme morphological changes in geese and ducks from the Hawaiian archipelago (*Branta*, *Thambetochen*, *Ptaiochen*) and the Vegetarian Finch (*Platyspiza crassirostris*) from the Galapagos. Hawaiian geese derived from terrestrial herbivore ancestors and their morphological changes are likely related to the absence of herbivorous mammals in the archipelago. Conversely, Moa-nalos were a group of ducks likely derived from ancestors of the genus *Anas* which are mainly composed of aquatic herbivores, suggesting that their changes can also be attributed to the evolution of their folivorous regime (as suggested by James & Burney, 1997). This is probably also the case for the Vegetarian Finch, whose ancestors switched from a mainly granivorous diet to an herbivorous one (Meiri, 2008). Regarding nectarivores, most extreme morphological changes correspond to lineages of Hawaiian honeycreepers who shifted towards a nectarivore diet, and which include several species of *Drepanis* or *Akialoa* with various sizes and completely unique beak forms (Cooney et al., 2017; Pigot et al., 2020). Interestingly, we found that the Hawaiian honeyeaters, which are also nectarivores, instead evolved towards intermediate values. It probably means that the ancestors of the Hawaiian honeyeaters (Mohoidae), close relative of the Ptiliogonatidae and Bombycillidae (Fleischer et al., 2008), were certainly more distinct from the other species of the island community than the Hawaiian honeyeaters themselves. Because of their isolation, certain groups such as insects that feed on nectar are less represented on certain islands, and groups such as herbivorous or nectarivores birds may have become more prominent in trophic networks on islands than they are on the mainland (Traveset et al., 2015; Wood et al., 2013). It would be interesting to investigate whether all the species that have evolved towards morphologically specialized traits are also ecological specialists. While this seems to be the case for several island species in our study (e.g. Hawaiian honeycreepers), there are also many examples of ecological generalists being morphologically specialized in the literature (i.e. the resources they specialized in exploiting only made up a small part of their diet; see the Liem's paradox, Liem, 1980). This phenomenon seems rather uncommon among extant species, but we cannot know if it was more common among the extinct species included in the analyses.

It is interesting to note that while all the island communities in the Hawaiian, Galapagos or New Zealand archipelagos consistently followed one of the two hypotheses, we also found contrasting patterns in some archipelagos like between Mauritius and Reunion (Mascarene Islands). A common pattern between islands of an archipelago can possibly be explained by common biogeographical factors (but likely not related to age and surface area of the islands) and by the fact that same species can occupy several islands within the archipelago (Triantis et al., 2022). The opposite pattern is more intriguing and could potentially reveal a lack of knowledge of the communities, with many extinct species likely undiscovered (Duncan et al., 2013; Hume, 2022). This is unlikely to be the case for the Mascarene Islands, which have some of the best-known fauna, but it is possible that the large distance between each of the islands and the fact that there were possibly distinct colonization events within the same families (e.g. in Sturnidae discussed in Hume, 2014), may have had an influence on the evolutionary trajectories in this archipelago (see Valente et al., 2020). In the same perspective, we found that species exhibiting the most extreme morphological changes, whether following the niche filling theory or the ecological release theory are extinct species. This result supports the idea recently published about island mammals that evolutionary 'oddities' are likely more sensitive to extinction (Rozzi et al., 2023, see also Duhamel et al., 2020; Faurby & Svenning, 2016). In addition, the fact that most of these species evolved towards distinct trait values corroborates the idea that extinct species occupied niches in the functional space that have been left vacant (Sayol et al., 2021; Wood et al., 2013) and calls for a global assessment of the avian function diversity lost from recent extinctions. This result also highlights that any analyses omitting recently extinct species (in the anthropogenic time) will be analysing biased subsets of the natural diversity potentially leading to incorrect conclusions about the patterns processes of diversity (see also Dufour et al., 2024; Sayol et al., 2020).

AUTHOR CONTRIBUTIONS

P. Dufour and S. Faurby conceived the study. P. Dufour analysed the data, generated the figures and led the writing of the manuscript with substantial guidance of S. Faurby, F. Sayol and R. Cooke. All authors read, made substantial comments and approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

Authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data and code supporting the results are available in Zenodo: https://doi.org/10.5281/zenodo.10894682 (Dufour, 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: Decision tree for adding new species in BirdTree.

Figure S2: Variable correlation plots.

Figure S3: Comparison of the distance to centroid values estimated within the functional space of all species (>11,000 species) with the values of estimated in hypothetical communities of different sizes (250, 150, 50 and 25 species, see methods in Supporting Information).

Table S1: Results of linear regression intercept-only and PGLS models applied to 378 endemic species from 24 island of 8 archipelagos for PC axes 1 to 3 (overall phenotype) and PC axes 2 to 4 (adjusted for body size).

Table S2: Results of the generalized least square phylogenetic models testing the effect of trophic position on the niche shifting or the niche expansion hypothesis for 378 endemic species from 24 island of 8 archipelagos.

Table S3: Results of linear regression models testing the effects of age and area of the islands on the proportions of species following the two hypotheses per islands.

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