

# Avian Island Radiations Shed Light on the Dynamics of Adaptive and Nonadaptive Radiation

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Understanding the mechanisms underlying species formation and differentiation is a central goal of evolutionary biology and a formidable challenge. This understanding can provide valuable insights into the origins of the astonishing diversity of organisms living on our planet. Avian evolutionary radiations on islands have long fascinated biologists as they provide the ideal variation to study the ecological and evolutionary forces operating on the continuum between incipient lineages to complete speciation. In this review, we summarize the key insights gained from decades of research on adaptive and nonadaptive radiations of both extant and extinct insular bird species. We present a new comprehensive global list of potential avian radiations on oceanic islands, based on published island species checklists, taxonomic studies, and phylogenetic analyses. We demonstrate that our understanding of evolutionary processes is being greatly enhanced through the use of genomic tools. However, to advance the field, it is critical to complement this information with a solid understanding of the ecological and behavioral traits of both extinct and extant avian island species.

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Editors: Catherine L. Peichel, Daniel I. Bolnick, Åke Brännström, Ulf Dieckmann, and Rebecca J. Safran  
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## ISLAND AVIAN RADIATIONS IN THE LIGHT OF ADAPTIVE AND NONADAPTIVE PROCESSES

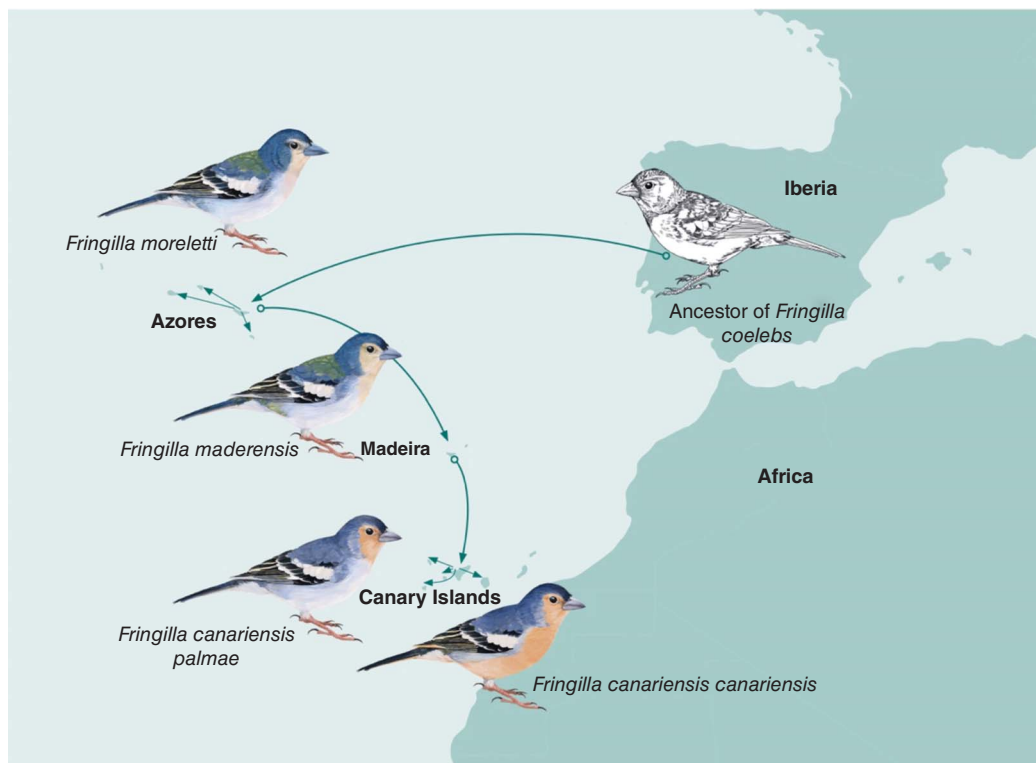
Radiation is a fascinating evolutionary process characterized by a rapid burst of lineage-splitting events, making it a prime subject for exploring the mechanisms driving speciation. However, the term radiation is frequently mainly associated with adaptive radiations, overlooking the important role of nonadaptive radiations in generating diversity. Herein we review the knowledge acquired over a century of studies on island bird species, both living and extinct, to provide an overview of what we have learned about speciation and identify areas for further study. In addition, we present a new comprehensive global list of potential avian radiations on oceanic islands, based on published island species checklists, taxonomic studies, and phylogenetic analyses.

### How Adaptive Radiation in Island Birds Has Shaped Evolutionary Thinking

Understanding how and why species change over time has captivated biologists, physicist, chemists, and philosophers (e.g., Nagai 1998; Grant and Grant 2008; Harms and Thornton 2013; Arnold et al. 2015; Denis 2017; Lässig et al. 2017; Seoane and Solé 2018) since Charles Darwin and Alfred Wallace Russell established their theory of evolution mediated by natural selection (Darwin and Wallace 1858). By virtue of their simplified environments and shared characteristics, oceanic islands provide ideal replicates for the study of ecological and evolutionary processes. As they have never had land connections to the mainland, they constitute discrete entities with distinct biotas (Whittaker and Fernández-Palacios 2007). Although they are home to fewer species and habitat types than the continents, with the subsequent fewer ecological antagonistic (e.g., predator–prey) and mutualistic (e.g., pollination) interactions, oceanic islands often feature a high diversity of habitats and high levels of endemism despite their limited area. The recurrent ecological disturbances and long-term geological changes experienced by oceanic islands

result in a constantly changing environment, providing a dynamic stage for evolution (Emerson 2002). Oceanic archipelagos have been the setting of considerable diversification events despite their small size, where groups of related endemic taxa share continental common ancestors, and the drivers of such diversity have captured the interest of evolutionary biologists and biogeographers (e.g., MacArthur and Wilson 1967; Warren et al. 2015; Whittaker et al. 2017; Valente et al. 2020).

The taxonomic diversification originating in a short time span from a common ancestor is named “evolutionary radiation.” The most well-known type of evolutionary radiation is “adaptive radiation,” in which a rapid increase in the number of species evolving from a common ancestor is characterized by ecological specialization (Schluter 2000; Gillespie 2009; Grant 2014; Gillespie et al. 2020). The proliferation of species within a clade does not necessarily have to be adaptive, and ecological differences among related taxa can be minimal. In this latter case, lineage diversification occurs with a limited role of ecological forces and is mostly driven by neutral processes (see the section Nearly Neutral Theory); it is thus referred to as “nonadaptive radiation” (Fig. 1; Rundell and Price 2009; Czekanski-Moir and Rundell 2019). Two other speciation processes can produce similar outcomes as those derived from nonadaptive radiations determined solely by neutral forces: mutation-order speciation and sexual selection. In mutation-order speciation, isolated populations experiencing advantageous mutations adapt via natural selection to similar environments following distinct genomic pathways. The resulting genetic differentiation sets the basis for genetic incompatibilities in case of secondary contact (Mani and Clarke 1990; Schluter 2009). Speciation by sexual selection occurs when reproductive isolation at the population level arises from changes in mate preference (Panhuis et al. 2001). These changes can be based on natural selection—with mating signals changing in different environments to optimize their transmission (e.g., “sensory drive”; Boughman 2002)—or on random factors, including genetic drift as well as cultural drift in the case of song, a very important



**Figure 1.** Example of a nonadaptive radiation involving three oceanic archipelagos with similar habitats. This case depicts a sequential colonization process within the common chaffinch complex (*Fringilla* spp.) that occurred during the last 800,000 yr in Macaronesia (Marshall and Baker 1999; Recuerda et al. 2021). An integrative approach including genomic and phenotypic information revealed that the speciation process in the Azores, Madeira, and the Canary Islands is complete, with genetic drift emerging as the main evolutionary force driving differentiation (Recuerda et al. 2021). Note that all species inhabit similar habitats, reflecting a lack of clear ecological specialization in the complex. In addition, Leroy et al. (2021a) found that the nearly neutral theory can explain the presence of slightly deleterious mutations, which are not systematically removed by natural selection in these island finches. (Illustrations by Ángel Morales.)



mating trait in birds (Slater 1986; Edwards et al. 2005; Laiolo and Tella 2007). The continuous coevolution between mating signals and preferences is expected to lead to cyclic changes in signal/preference trajectories (Pomiankowski and Iwasa 1998). As such, geographically isolated populations could easily fall out of phase with other populations (Iwasa and Pomiankowski 1995), becoming reproductively isolated (Mendelson and Safran 2021).

The mechanisms explaining the accumulation of species within lineages have been intensely studied in island birds. In his pioneering studies during the early twentieth century, Robert Cyril Layton Perkins introduced the general pro-

cesses operating during the differentiation of species, which he found to be associated with three main drivers (Perkins 1903): (1) natural selection through the ecological specialization and competition over food resources; (2) geographical isolation and subsequent accumulation of differences by chance (i.e., genetic drift); and (3) sexual selection (reviewed in Grant 2000, 2001). Later, the work of David Lack in the Galápagos (Lack 1947, 1971) and of Ernst Mayr together with Jared Diamond in the southwestern Pacific Ocean (Mayr and Diamond 2001) further expanded our understanding of the proximate and ultimate causes determining avian radiations on island ecosystems. Arguably, the

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most impressive and remarkable contributions on how natural selection drives adaptive radiations in island birds come from the detailed studies performed by Peter and Rosemary Grant on the Darwin's finches in the Galápagos. Their research showed that evolutionary outcomes can be monitored and studied on ecological time-scales (Grant and Grant 2008, 2019). In the course of more than 40 years, they have disentangled the mechanisms operating on population differentiation, and ultimately speciation, with fascinating results on the role of competition and introgression in shaping the phenotypic and genetic variability of island birds (Grant and Grant 2014, 2019).

Avian adaptive radiations are inevitably associated with the iconic Darwin's finches in the Galápagos and the “drepanidine finches” in the Hawaiian Islands, commonly known as the Hawaiian honeycreepers. The formidable range of beak and cranial sizes and shapes displayed by both avian groups (Reaney et al. 2020; Al-Mosleh et al. 2021)—particularly outstanding in the case of honeycreepers—exemplify how the acquisition of trophic innovations can foster speciation processes (Lovette et al. 2002; Tokita et al. 2017; Mosleh et al. 2023). While these two radiations have received the most attention in textbooks, both examples are extraordinary and represent exceptions among island birds (Ricklefs and Bermingham 2007; Valente et al. 2020; Miles et al. 2023). In fact, most evolutionary radiations on islands are less spectacular from a species-richness, morphological, and niche-differentiation perspective than those famous radiations. Insular radiations tend to be the result of geographic isolation with a strong effect of genetic drift, sexual selection, introgression, and mutation-order speciation (Losos and Ricklefs 2009; Nosil and Flaxman 2011; Warren et al. 2012; Irestedt et al. 2013; Gwee et al. 2020; Recuerda et al. 2021).

### Avian Radiations on Oceanic Islands

Evolutionary radiations are not discrete processes. Even classic “adaptive” radiations likely involve or have involved nonadaptive components, with different species arising primarily via ecological rather than mutation-order speci-

ation together with the contribution of neutral processes, sexual selection, and hybridization events (Gillespie 2004; Rundell and Price 2009; Lamichhane et al. 2018; Czekanski-Moir and Rundell 2019; Matsubayashi and Yamaguchi 2022; Cerca et al. 2023a,b). Selection and neutral processes are likely to be acting simultaneously, even if in different degrees, in shaping the genomic differentiation of diverging populations (Spurgin et al. 2011).

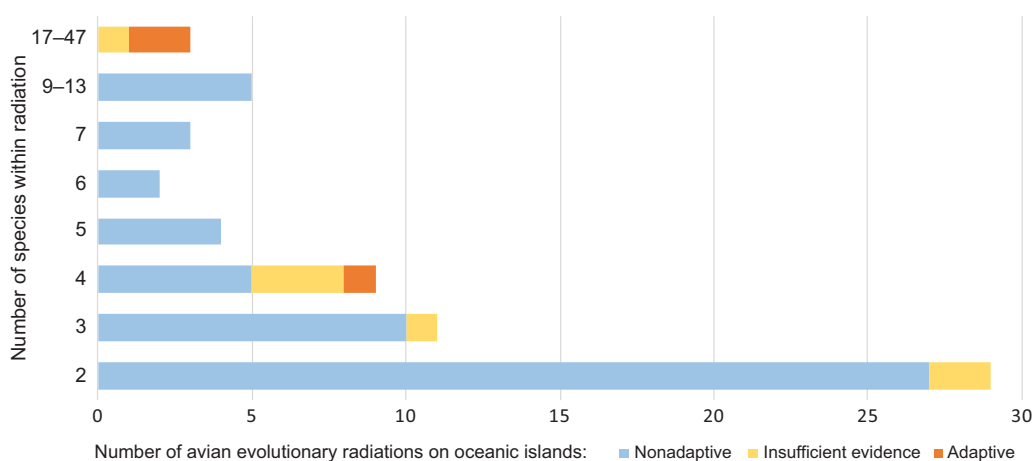
Acknowledging that distinct factors can contribute to any given evolutionary radiation, we distinguish two main types of avian radiations on oceanic islands: (1) adaptive, for those driven primarily by adaptation to ecological conditions, and (2) nonadaptive, where it is assumed that neutral forces were the determinant factor underlying species diversification (Leroy et al. 2021a). We are aware that our approach only allows outcomes from divergent adaptive responses to be assessed and potentially underestimates the roles of parallel adaptive responses (i.e., mutation-order speciation) and sexual selection. Whole-genome analyses scrutinizing the genomic structure of evolutionary radiations, combined with the identification of heritable traits associated with mating or fertilization success, are needed to understand the potential role of mutation-order speciation and sexual selection in avian radiations (Schluter 2009; Mendelson and Safran 2021; Miles et al. 2023). To determine the contributions of adaptive and nonadaptive radiations to island species richness, we have performed a global review of avian radiations on oceanic islands, with the intent of summarizing characteristics such as the number of species involved, whether they are extinct or extant, and their geographical distribution. Here we consider oceanic islands as a wide range of formations, including both “classic” volcanic islands and atolls/reef islands originating from underwater volcanos, with no minimum or maximum size criteria. This means that continental islands across, for example, the Greater Antilles and Wallacea, as well as large islands like Madagascar and New Zealand, are treated as “continental” and as putative sources for colonization of oceanic islands. Published lists including avian oceanic radiations were obtained from Valente



et al. (2020), Hume and Walters (2012), extensive searches of primary research literature, and a review of species accounts in Billerman et al. (2022). Two or more extant or extinct species that were part of a monophyletic clade were considered to constitute an insular evolutionary radiation. While considering two-species radiation can be considered both arbitrary in size and too general (e.g., Matsubayashi and Yamaguchi 2022), we follow previous work focusing on cladogenesis in avian island biogeography (e.g., Valente et al. 2017, 2020). We stress that the fossil and subfossil record is incomplete and, therefore, we do not know how many extinct species could have coexisted within a two-species radiation. In addition, while limiting the definition of evolutionary radiations to comprise at least three species considerably reduces the number of credible radiations (37 vs. 66), it does not change the patterns observed (Fig. 2; Supplemental Fig. S1; Supplemental Table S1). Importantly, our definition takes a radiation-centric rather than an archipelago-centric perspective, as in Valente et al. (2020). This means that if a monophyletic clade comprises two or more species distributed across multiple archipelagos, even if only one species occurs in any given archipelago, we define that as an insular evolutionary radiation. While

we use Gill et al. (2022) as backbone taxonomy, we have opted to include some taxa for which species status is debated, unclear, or differs between major taxonomic lists. We have done so particularly in cases where specialists who have authored studies on those specific systems support the recognition of those taxa as distinct species.

Due to their dispersal ability, many bird lineages are not exclusive to oceanic islands. As a result, we did not include these lineages as radiations in our list. For example, while there are some cases of putative radiations of flightless island rails (Gruiformes: Rallidae), fine-scale phylogenies are not yet resolved (Garcia-R and Matzke 2021; Kirchman et al. 2021), and the propensity for long-distance dispersal of mainland species combined with rapid loss of flight suggest that these are predominantly resulting from repeated colonizations rather than in situ diversification dynamics. Some penguin (Spheniciformes) species are exclusively breeding on islands, but no clade is solely oceanic and the order has continental origins; therefore, these were not considered in this work (Baker et al. 2005; Vianna et al. 2020). Many petrels, albatrosses, storm-petrels, and shearwaters (Procellariiformes) breed exclusively on oceanic islands,



**Figure 2.** Number of nonadaptive or adaptive evolutionary radiations recorded in avian systems on oceanic islands in relation to the estimated number of species per radiation. This is based on a set of 66 credible radiations, for which most in the category “Insufficient evidence” are likely nonadaptive (see Supplemental Table S1 for further details). Adaptive radiations appear to be very limited in number in comparison with nonadaptive radiations; however, they dominate the very speciose radiations ( $\geq 17$  species).

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but species belonging to this order are pelagic and very mobile, with extremely large distributions, leading us to exclude Procellariiformes from our review. To assess the support for in situ divergence, we have primarily scrutinized the topology and node support of phylogenetic trees. Furthermore, we have considered extinct genera or genus groups well supported if subfossils or fossils have only been found on islands.

We have further assessed whether speciation events within an evolutionary radiation have included adaptive responses based on two criteria: sympatric distribution and signs of functional phenotypic divergence caused by disruptive selection. While adaptive responses are easily observed in emblematic examples such as Darwin's finches and Hawaiian honeycreepers, they may be more subtle in other radiations. We generally follow characterizations in the primary literature (see supplemental information) but note that authors may vary in their evaluation of adaptiveness and that, sometimes, sufficient evidence is lacking (Fig. 2; Supplemental Table S1). Ultimately, ours is a qualitative assessment in which we have applied the above two criteria.

The results of our review are shown in detail in Supplemental Table S1 and are summarized in Table 1 and Supplemental Table S2. We identified a total of 76 putative insular avian radiations, of which 66 classified with strong or moderate support constitute a rather credible set of in situ divergence. Additionally, we list seven candidates where phylogenetic topology suggests in situ divergence but where node support is low or for which no molecular studies have yet been carried out. Finally, there are eight lineages that are commonly treated as insular radiations but for which the evidence supports origins following repeated colonizations (therefore, they may constitute radiations but are not exclusively insular according to our definition).

For the credible set of 66 insular evolutionary radiations, we find that at least 17 (26%) include species with sympatric distributions and that most radiations can be grouped in the nonadaptive category (Fig. 2). We found support for 92% of the 66 radiations having radiated in situ (on the islands), comprising 76% of species from a total of 314. The taxonomic distribution of oce-

anic island radiations overall largely echoes current global species diversity (Fig. 3; Table 1; Supplemental Table S2). At the level of order, the global number of species—excluding those in oceanic island radiations—largely predicts the number of radiations (linear regressions:  $b = 0.006$ ,  $P < 2.0 \times 10^{-16}$ ,  $r^2 = 0.96$ ; without Passeriformes  $b = 0.006$ ,  $P = 2.6 \times 10^{-4}$ ,  $r^2 = 0.28$ ) and the number of species within radiations ( $b = 0.034$ ,  $P < 2.0 \times 10^{-16}$ ,  $r^2 = 0.97$ ; without Passeriformes  $b = 0.023$ ,  $P = 7.2 \times 10^{-4}$ ,  $r^2 = 0.25$ ; Fig. 3). All statistical analyses were performed in R v. 4.3.0 (R Core Team 2023). The most notable deviations (i.e., with the largest residuals from predicted values) are pigeons (Columbiformes; eight radiations comprising 37 species, which constitutes six radiations and 27 species more than predicted) and woodpeckers (Piciformes; no radiations compared to a predicted three radiations of 14 species). Likewise, at the level of family for the most speciose order, Passeriformes, global species diversity is overall a good predictor (number of radiations:  $b = 0.005$ ,  $P = 2.3 \times 10^{-7}$ ,  $r^2 = 0.17$ ; number of species:  $b = 0.031$ ,  $P = 5.3 \times 10^{-6}$ ,  $r^2 = 0.14$ ), albeit with considerable positive deviations for monarch flycatchers (Monarchidae) and finches (Fringillidae), and negative deviations among the large suboscine families Furnariidae, Thamnophilidae, and Tyrannidae (Fig. 3). If narrowing our definition of evolutionary radiations to include at least three rather than two species, a credible set of 37 radiations comprising 258 species remains. The above associations to global species diversity remain, albeit with a somewhat weaker signal.

### Importance of Nonadaptive Radiations in Oceanic Island Ecosystems

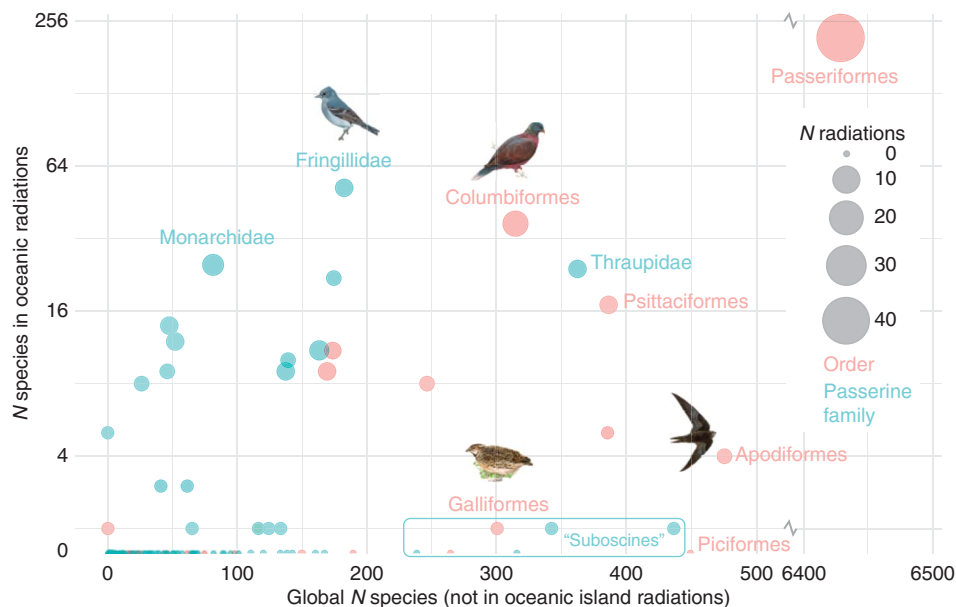
Recent genomic analyses have shed light on why some lineages experience high speciation rates, whereas others are species poor, by uncovering some of the underlying mechanisms. The combination of high standing genetic variation (or ancestral haplotype blocks) with hybridization events between different lineages seems to favor the formation of reproductively isolated populations that may produce new species over time (Lamichhaney et al. 2018; Marques et al. 2019;

**Table 1.** Summary of avian evolutionary radiations on oceanic islands and their distribution across avian orders and major oceans

Order	N species worldwide	Radiations (N radiations, N species)			
		Total	Atlantic Ocean	Indian Ocean	Pacific Ocean
Struthioniformes	2				
Rheiformes	2				
Apterygiformes	5				
Casuariiformes	4				
Tinamiformes	46				
Anseriformes	178	4	11	2 4	2 7
Galliformes	302	2	4	1 2	1 2
Caprimulgiformes	97				
Steatornithiformes	1				
Nyctibiiformes	7				
Podargiformes	16				
Aegotheliformes	9				
Apodiformes	479	2	4	1 2	1 2
Musophagiformes	23				
Otidiformes	26				
Cuculiformes	150				
Mesitornithiformes	3				
Pterocliiformes	16				
Columbiformes	351	8	37	1 2	7 35
Gruiformes	189				
Podicipediformes	23				
Phoenicopteriformes	6				
Charadriiformes	390	3	12		3 12
Eurypygiformes	2	1	2		1 2
Phaethontiformes	3				
Gaviiformes	5				
Sphenisciformes	18				
Procellariiformes	149				
Ciconiiformes	19				
Suliformes	61				
Pelecaniformes	118	2	4	1 2	1 2
Opisthocomiformes	1				
Accipitriformes	264				
Strigiformes	254	3	10	1 2	2 8
Coliiformes	6				
Leptosomiformes	1				
Trogoniformes	43				
Bucerotiformes	74				
Coraciiformes	184	3	11		3 11
Piciformes	449				
Cariamiformes	2				
Falconiformes	65				
Psittaciformes	403	3	17	1 2	2 15
Passeriformes	6647	45	230	12 33	4 15 29 182
<b>Total</b>	<b>11093</b>	<b>76</b>	<b>342</b>	<b>15 39</b>	<b>9 25 52 278</b>

The full list at the level of species is provided in Supplemental Table S1. Taxonomy and the number of extant and recently extinct bird species worldwide follow Gill et al. (2022); blue bars show the number of species. The list excludes cases for which repeated colonizations rather than in situ divergence is presumed; all details are available in Supplemental Table S1. The number of evolutionary radiations and species within them are shown by green bars. All evolutionary radiations are presumed nonadaptive, except three within the order Passeriformes and two possibly adaptive within the orders Eurypygiformes and Passeriformes (Fig. 2); details on this and on allopatric/sympatric distribution are provided in Supplemental Table S1. For a similar breakdown across families within the order Passeriformes, see Supplemental Table S2. For corresponding summaries, when requiring a minimum of three rather than two species to constitute a radiation, see Supplemental Tables S3 and S4.

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**Figure 3.** Relationship between global avian species diversity (number of species not in oceanic island radiations) and number of species within oceanic island radiations (the latter excluding cases with low or unresolved support or reflecting likely repeated colonization events; see Supplemental Table S1). The size of circles represents the number of evolutionary radiations. Pink circles signify avian orders, while turquoise circles represent families within the species-rich order Passeriformes. Note that the  $y$ -axis is drawn on a  $\log_2$ -scale and the  $x$ -axis is truncated. Some prominent clades are labeled. (Illustrations by Juan Varela.)



Gwee et al. 2020; Rubin et al. 2022). In addition to this dynamic genomic architecture, adaptive radiation (as opposed to nonadaptive radiation) requires the availability of a high diversity of ecological niches in which individuals may experience different selective pressures (Lamichhane et al. 2015; Lapiedra et al. 2021).

We identified a total of 76 putative insular radiations, and most of them can be grouped in the nonadaptive radiation category (see the section Avian Radiations on Oceanic Islands). The fact that many of these radiations are characterized by harboring a limited number of closely related species that are morphologically similar or undistinguishable supports the niche conservatism hypothesis (Wiens and Graham 2005). If allopatric species within a single clade and similar phenotypes occupy similar habitats, it is reasonable to assume they also share similar trophic resources. Consequently, it is plausible to conclude that the divergence observed may be driven by neutral evolutionary forces (Kimura 1968;

Ohta 1973; Leroy et al. 2021a) and/or sexual selection (Irestedt et al. 2009; Kearns et al. 2020; Stelbrink et al. 2022) rather than by natural selection, although mutation-order speciation and hybridization cannot be disregarded (Nosil and Flaxman 2011). Under this scenario, the emergence of new species in oceanic archipelagos would occur in a two-step process: first, after initial island colonization, individuals inhabiting one or several islands experience differentiation in allopatry or parapatry; second, after a variable time span, the new taxa would invade other islands or archipelagos, establishing new populations and accumulating neutral divergence in allopatry, with a limited role for natural selection. In the eventuality that divergent populations meet again, the accumulated molecular differences between populations have the potential to cause genetic incompatibilities (see Coyne and Orr 2004) and hence can constitute either a partial or complete reproductive barrier. At this stage, the new taxa may colonize nearby islands





harboring species with some degree of ecological similarity. In such a new setting, species from similar or different lineages could compete for resources, and natural divergent selection would favor ecological adaptations (e.g., morphological divergence) to avoid niche overlap (Grant and Grant 2008; see the section Character Displacement).

Importantly, extant avian distributions may confound our interpretations of relationships within island avian clades. Indeed, the occurrence of multiple closely related species within archipelagos is not necessarily the result of adaptive or nonadaptive radiation but may represent either independent waves of colonization (e.g., Valente et al. 2020; Melo et al. 2022a; Sangster et al. 2022; Stervander et al. 2022) and/or different levels of introgression if there is breakdown of lineage wholeness (Singhal et al. 2021). Distinguishing between independent arrivals and radiation resulting from a common ancestor can be particularly challenging when both extinct and extant taxa are involved (e.g., Rando et al. 2020). These examples demand the use of genomic approaches to unravel the nature of such colonizations (see the section Evolution of Molecular Techniques for Studying Diversification in Island Birds).

### Evolution of Molecular Techniques for Studying Diversification in Island Birds

Deciphering the processes operating in island avian diversification is key to allowing evolutionary biologists to understand how species multiply and vanish. Examining evolution at the population level offers a way of identifying and quantifying the role of each evolutionary and ecological pressure from the incipient differentiation phase until the speciation process is completed (Ryan et al. 2007; Grant and Grant 2008; Warren et al. 2012; Tobias et al. 2020). The use of Sanger sequencing technology since the late 1970s has facilitated remarkable advances in the reconstruction of evolutionary histories of island birds including pathways of colonization, periods of differentiation, demographic scenarios, founder effects, genetic drift, selection, allochronic speciation, immigration, and gene flow (Clegg et

al. 2002; Friesen et al. 2007; Milá et al. 2010; Melo et al. 2011; Spurgin et al. 2011, 2014a,b; Illera et al. 2014; Pepke et al. 2019; Morinha et al. 2020). However, the limited genetic coverage of Sanger sequencing has constrained our comprehension of the specific roles of different evolutionary forces operating during the speciation process. The development of massively parallel sequencing (or next-generation sequencing [NGS]) technologies in the early 2000s has enabled a detailed investigation of much larger parts of the target species genome, allowing for considerably increased understanding of the evolutionary processes. Technologies such as restriction site-associated DNA sequencing (RAD-seq), double digest RAD sequencing (ddRAD-seq), genotype-by-sequencing (GBS), and target capture of ultraconserved elements (UCEs) have produced data on thousands of anonymous regions in many avian genomes. These genomic data sets have informed us about complex evolutionary histories (Stervander et al. 2015; Oliveros et al. 2021; Brady et al. 2022; McCullough et al. 2022), introgressive hybridization (Andersen et al. 2021; Stervander et al. 2022), and dynamics of population structure and gene flow (Mapel et al. 2021). In addition, they have been used in genome-wide association studies (GWAS) to identify genes under selection (Chaves et al. 2016; Armstrong et al. 2018; Bourgeois et al. 2020; Gabrielli et al. 2020; Martin et al. 2021). The sequencing of whole avian genomes is further revolutionizing our understanding of evolutionary processes (Feng et al. 2020; Bravo et al. 2021) by providing unique opportunities to determine and quantify the role of each ecological and evolutionary mechanism driving population differentiation and the evolution of reproductive isolation. Remarkable advances have been achieved in identifying the genetic basis of the evolution of adaptive traits such as the color polymorphisms in island birds (Bourgeois et al. 2017), including the evolution of melanic morphs (Campagna et al. 2022); morphological traits under ecological character displacement in Darwin's finches (Lamichhaney et al. 2016); new species rapidly arising after hybridization events (Lamichhaney et al. 2018); adaptations to altitudinal gradients (Cumer et al. 2022); propensity

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for sedentarism versus migratory behavior (Delmore et al. 2020); and cryptic episodes of massive extinctions within songbird radiations (Wu et al. 2022). Future studies on avian radiations should enrich our understanding of the regulatory elements controlling gene expression, their functions and modes (*cis*- or *trans*-regulatory), and how interactions between them may drive differentiation processes.

### How Does the Loss of Genetic Diversity Affect Island Bird Species?

Following a colonization event, avian species are likely faced with the loss of genetic diversity. This is a consequence of the limited number of founders arriving on the islands in relation to the higher population sizes and genetic diversity harbored by their mainland ancestors (Clegg 2010). The magnitude of the decline in genetic diversity depends on the size of the founder flock, the number of consecutive colonization episodes, genetic drift, potential introgression, mutation rates, selection, and time of reproductive isolation of each population over evolutionary timescales (Estoup and Clegg 2003; Grant and Grant 2008; Spurgin et al. 2014a; Armstrong et al. 2018; Morinha et al. 2020; Sendell-Price et al. 2021). Severe bottlenecks and founder effects can result in a significant reduction in genetic diversity and high levels of inbreeding among some island species (Barrientos et al. 2014; Spurgin et al. 2014a; van Doren et al. 2017; Stervander et al. 2020; Sendell-Price et al. 2021; Martin et al. 2023), leading to reduced survival, fertility, and limited ability to respond to environmental changes (Charlesworth and Willis 2009; Agudo et al. 2012). However, it is intriguing that many native and endemic species are able to survive during thousands, hundreds of thousands, or millions of years on small islands (Richardson et al. 2004; Clegg 2010). It is possible that the small, bottlenecked populations have undergone stronger purging of harmful mutations than their mainland counterparts (Dusseux et al. 2021). After such episodes, subsequent rapid demographic expansions may then guarantee species persistence in island ecosystems over time (Spurgin et al. 2014b; van Doren et al. 2017; Martin et al. 2021). The

breakdown of reproductive isolation between related lineages has been identified to be a recurrent mechanism occurring in Darwin's finches (Enbody et al. 2023), and the genetic variation obtained during introgression events could explain their success on the Galápagos Islands.

Other than introgression, multiple genetic mechanisms could also explain the persistence of island birds. Innate and adaptive immune systems are key to protecting avian species against parasites and diseases. Recent results have provided insights on how birds can increase genetic diversity, including gene conversion. This micro-recombination process, combined with natural selection, has been identified as the main driver of genetic regeneration in the major histocompatibility complex (MHC) haplotypes of bottlenecked island populations (Spurgin et al. 2011). Gene duplications and cosegregation of linked genes within the MHC are also known to maintain genetic variation and maximize antigen recognition in island populations. These processes counteract the loss of genetic diversity experienced in other genomic regions and provide a mechanism for inbred island birds to cope with current and future parasites (Agudo et al. 2011; Stervander et al. 2020). Finally, the higher prevalence of weakly deleterious mutations found in island birds compared to their mainland counterparts is interpreted in terms of the limited scope for natural selection to erase these mutations in populations with lower effective population sizes (Kutschera et al. 2020; Leroy et al. 2021a).

### What Genomic and Ecological Data Are Needed to Understand Avian Island Radiations?

The increasingly common use of genomic technologies, particularly whole-genome techniques, has revolutionized our understanding of the genomic regions and genes involved in population and species divergence (see the section Evolution of Molecular Techniques for Studying Diversification in Island Birds). Yet, we still need to increase our understanding about genomic regions and specific genes associated with the ecological traits that are under selection, with the objective of establishing the much-sought link between the environment and the genotype via the phenotype.



Some genes may encode proteins and RNAs involved in the expression of a phenotype, and others may be regulatory, driving the expression of other genes. For the latter, technologies such as ChIP-Seq will help to identify the binding sites for specific proteins. These findings will illuminate how the transcription factor motifs work in the differentiation of populations and species (Delmore et al. 2020). However, it will be crucial to combine the genomic information with ecological data. Here, Darwin's finches can again provide an example of a perfect match between ecological and genomic data to unravel the evolutionary consequences of environmental changes. After an extreme drought caused by the "El Niño" climatic pattern in the Galápagos during 2004–2005, the seed size distribution changed and fueled competition between finches. Grant and Grant (2006) documented how the beak sizes of median ground finches (*Geospiza fortis*) living on Daphne Mayor diverged toward smaller beaks due to the competition with large ground finches (*Geospiza magnirostris*). This result is fascinating because it shows how natural selection works in real time, favoring the individuals best adapted to exploit available trophic resources while avoiding competition with ecologically related species (i.e., ecological character displacement; see the section Character Displacement). However, we have only recently learned about the genes involved in this process. Lamichhaney et al. (2016) sequenced the genome of individuals that survived and died after the El Niño episode. Their results showed that despite several genes being associated with beak size, a locus named HMGA2 was most strongly associated with beak size variation. After genotyping a key single-nucleotide polymorphism (SNP) at the HMGA2 locus in 71 birds (37 surviving and 34 deceased individuals), their results showed that most of the surviving individuals, those with smaller beaks, were homozygous for the "small beak allele," while the "large beak allele" homozygotes died. Importantly, this study echoes previous ecological findings supporting that variation in the beak morphology of Darwin's finches is the main trait driving the adaptive radiation within this group (Grant and Grant 2008). Overall, this case exemplifies the need for long-term ecological studies in combination with genomic information

gathered via massively parallel sequencing technologies to determine the role of different evolutionary forces underlying each avian radiation.

### What Are Extinct Species Telling Us about Avian Radiations on Islands?

Avian species have colonized the majority of archipelagos worldwide, including the most remote islands, giving rise to the most diverse group of tetrapods inhabiting these ecosystems. According to the fossil, archaeological, and molecular records, we know that during the Holocene no vertebrate group has suffered more extinctions than birds due to human arrival and subsequent actions (Hume and Walters 2012; Valente et al. 2019; Ceballos and Ehrlich 2023). Determining the number and the ecological role of extinct species can provide information on the magnitude of the diversity that has vanished (Illera et al. 2012, 2016; Cooke et al. 2023), the specific adaptations that have developed on islands, such as dwarfism, gigantism, and flightlessness (Covas 2016; Baeckens and Van Damme 2020; Sayol et al. 2020; Benítez-López et al. 2021), as well as the ecological interactions that may have been disrupted as a result of species loss (Rogers et al. 2017). Ultimately, this information can inform us on how island birds may respond to upcoming threats such as global climatic change (Akresh et al. 2021; Olsen and Cunningham 2022).

Some of these episodes of extinction on islands have been recorded in detail. For instance, since aboriginal settlement the Pacific islands alone have seen the extinction of at least 983 (95% CI: 731–1332) nonpasserine land birds (Duncan et al. 2013), including at least 442 rail species (Steadman 2006). In addition, multiple extinction events of seabird and passerine groups have been documented in the Pacific. Most of the Holocene species extinctions documented in oceanic archipelagos worldwide appear not to be by happenstance, and in most cases involved some direct or indirect human participation (van Riper et al. 1986; Hume 2011, 2014; Illera et al. 2012; Louchart et al. 2018). A recent estimation of lost species richness suggests that recently extinct insular birds make up 10%–20% of the global original avian diversity known (Fromm and

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Meiri 2021). This is remarkable given that islands represent <7% of the emerged land area on Earth.

The magnitude of avian extinctions has been so dramatic in some archipelagos that they entirely mask evolutionary radiations of endemic taxa (Table 1). Such is the case of the four extinct species of stilt owls belonging to the genus *Grallistrix*, endemic to the Hawaiian archipelago (Olson and James 1991), or the Macaronesian quails (*Coturnix* spp.), where a minimum of four extinct endemic species have been recognized (Rando et al. 2020). The extinction of these radiations is concordant with the human arrival to each archipelago. Extinction of some insular clades is sometimes incomplete but still dramatic. For instance, the diversity of the Hawaiian honeycreepers is now severely pauperized due to the many species extinctions that took place since human arrival. Thirty out of 50 recognized Hawaiian honeycreeper species are classified as extinct (26 during the aboriginal period, Boyer 2008), and 18 of the remaining extant species are classified as Critically Endangered, Endangered, or Vulnerable by the IUCN Red List (James and Olson 1991; Pratt 2005; Boyer 2008; Ricklefs 2017). One of the direct consequences of these extinctions is the loss of ecological functions, such as seed dispersal and pollination, with subsequent cascading effects. Avian extinctions have led to the loss of up to 80% of original ecological functional diversity on some Pacific Islands (Boyer and Jetz 2014). In Hawaii, for instance, the extinction of avian pollinators has likely triggered the extinction of more than 30 plant species (Cox and Elmqvist 2000). Thus, identifying avian extinctions is also key to understanding the loss of functional diversity, which constitutes a baseline for recovering depauperate ecosystems through the restoration of disrupted ecological interactions (Svenning et al. 2016; Barnosky et al. 2017; Wood et al. 2017).

The lack of knowledge about insular extinct birds may also limit our understanding of the convergent evolution of traits (referred to as the “island syndrome”), such as flightlessness. The number of insular extinct flightless bird species is four times higher than the number of extant flightless species, due to the intrinsic vulnerability to human activities that this trait confers. Recent insights

provided by paleontological studies suggest that flightlessness is a widespread phenomenon that has evolved independently at least 150 times in more than half of the avian orders (Sayol et al. 2020). The study of extinct species can also inform about past species interactions and help us uncover the mechanisms promoting island avian differentiation. The beak morphology (shape and size) of sympatric extant chaffinches and extinct greenfinches in Macaronesian forests suggests ancient lost interactions among these species, providing evidence for a process of ecological character displacement driving diversification within this group of birds (see the section Character Displacement). The effects of such past biotic interactions are still present in the beak morphology of extant finches, thus highlighting that a correct inference of phenotypic evolution in this group was dependent on including recently extinct relatives (Rando et al. 2010; Illera et al. 2018).

Future analyses of extinct birds would greatly benefit from an integrative approach. In addition to classical morphological, chronological, and palaeoecological perspectives (e.g., Cooper et al. 1996; Tokita et al. 2017; Oswald et al. 2021), they should include genomic, epigenomic, and/or proteomic analyses of fossil and subfossil remains. Such approaches may in the future allow (1) reconstructing phylogenetic relationships and origins of extinct lineages, (2) distinguishing between true island-restricted radiations and independent waves of colonization, (3) estimating times of colonization and informing us of diversification processes, (4) determining the genetic diversity lost over time, and (5) uncovering genomic regions involved in the evolution of conspicuous and hidden “island syndrome” traits, such as flightlessness and sedentarism, which could explain the effects of lowering or erasing gene flow among nearby populations favoring avian radiations (Burga et al. 2017; Horn et al. 2019).

#### HOW ECOLOGICAL AND EVOLUTIONARY THEORY HAS PROVIDED A FRAMEWORK FOR UNDERSTANDING ADAPTIVE AND NONADAPTIVE RADIATIONS

In this section, we review key recent theoretical advances that have shaped the way we view insu-



lar radiations and how new theory is being applied to empirical data across a broad spectrum of bird taxa and insular systems. Research in the last decades allows us to get closer to addressing questions such as why some islands and archipelagos host more avian radiations than others and whether we can predict global patterns of in situ radiation on islands.

### Theory of Island Biogeography

The isolation and well-defined borders of islands provide the setting for evolutionary radiation to occur in a discrete environment, away from the mainland. But this is just one of the ways in which geographical context is crucial for understanding the process of evolutionary radiation (Borregaard et al. 2017). Area, geographical distance from the continent or other landmasses, island and archipelago age, island configuration within an archipelago, elevation, topographical heterogeneity, geological dynamics, and sea-level fluctuations can all play a role in driving, triggering, or modulating radiations (Gillespie and Roderick 2014; Fernández-Palacios et al. 2016; Ávila et al. 2019; Barajas-Barbosa et al. 2020; Neves et al. 2022). Modern island biogeography theory increasingly incorporates all these factors, but this has been a decades-long process (Whittaker et al. 2017).

The original theory of island biogeography (MacArthur and Wilson 1963, 1967) focused on island area and isolation in a static context and only briefly touched upon the subject of in situ speciation and adaptive radiation. However, MacArthur and Wilson (1963, 1967) were visionary in proposing the existence of a “radiation zone,” that is, islands that are sufficiently isolated and large to be able to host species radiations. Several decades later, their idea was proved to be correct following studies using molecular phylogenies (Rosindell and Phillimore 2011; Valente et al. 2020), which confirmed that cladogenetic speciation in birds is more common on large, isolated islands, such as the Galápagos and Hawaii. A temporal aspect was also added to the theory of island biogeography following the publication of the general dynamic model of island biogeography (Whittaker et al. 2008), which pro-

### Adaptive and Nonadaptive Avian Island Radiations

posed that radiation should be more common on islands at the middle of their geological life span because it is at this stage that volcanic islands are larger and host a higher diversity of habitats and niches, and thus have a higher carrying capacity facilitating evolution of new species via in situ speciation. However, evolutionary radiations may persist for long periods after an island begins to lose key vegetation types and niches via erosion and subsidence. On very old islands, the “relicts” of past diversification may survive in the form of just a few species or even just a single endemic species (e.g., Stuessy et al. 2022), which can often be incorrectly interpreted as anagenetic species, even though they arose via cladogenesis (Fig. 4) in a past geological period in which the island or archipelago was larger and hosted higher habitat diversity. Other recent extensions of the theory of island biogeography have recognized the role of paleogeographic changes and sea level fluctuations in determining the number of islands and the levels of connectivity between islands within an archipelago, providing a dynamic ever-changing geographical setting for allopatric speciation (Fernández-Palacios et al. 2016; Weigelt et al. 2016; Aguilée et al. 2021).



**Figure 4.** The *Nesospiza* finches of Tristan da Cunha in the South Atlantic Ocean are an example of cladogenesis (i.e., of an ancestral species giving rise to two or more descendant species). This photo features the large- and small-billed finches that occur sympatrically on Inaccessible Island, currently classified as subspecies (*N. acunhae dunnei*, left; *N. a. acunhae*, right). The cladogenetic speciation has, in this evolutionary radiation, also resulted in a large-billed (*N. wilkinsi*) and a small-billed (*N. questi*) species on the neighboring Nightingale Island (Ryan et al. 2007). The *Nesospiza* finches also constitute one of the few cases of adaptive radiation in birds (Supplemental Table S1). (Photo: M. Melo.)

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A key proposal of MacArthur and Wilson's theory of island biogeography is that islands should tend toward a dynamic equilibrium in which the number of species remains constant even though the identity of the species can vary (turnover) (MacArthur and Wilson 1963, 1967). Therefore, whether avian radiations on islands tend toward a diversity equilibrium has been a subject of particular interest. For example, phylogenetic studies of the adaptive radiation of Malagasy vangas (Jønsson et al. 2012; Reddy et al. 2012) identified a pattern of an initial burst of speciation followed by slowdowns in diversification rate, consistent with the idea of an equilibrium diversity being reached. Indeed, phylogenetic analyses are providing new insights into the role of ecological limits and diversity dependence in regulating avian radiations on islands and are allowing the identification of exceptional evolutionary radiations such as Darwin's finches (Valente et al. 2015). Finally, the combination of dynamic stochastic models with the increasing availability of phylogenetic data are allowing tests of the equilibrium diversity dynamics over evolutionary timescales (Valente et al. 2017) including both radiating and nonradiating bird lineages.

### Nearly Neutral Theory

The neutral theory of molecular evolution has changed the paradigm of our understanding of molecular evolution by highlighting an important role of the fixation of neutral mutations in explaining genetic differentiation among species. While the neutral theory was originally viewed in opposition to the theory of natural selection, we now know that both are compatible when explaining the origin of genetic polymorphisms within and among species. In addition, the neutral theory predicted that random genetic drift should lead genes to evolve uniformly, that is, at constant rates (Kimura 1968, 1983). Because much of the genetic variation observed in island birds cannot be associated with the exploitation of new ecological niches (i.e., ecological speciation) or be the result of ecological interaction among species (i.e., competition and predation), neutral processes shaping genetic divergence are likely to be important, although parallel natural

selection (i.e., mutation-order speciation) and sexual selection could lead to similar outcomes. The potential role of parallel natural selection and sexual selection in promoting genetic differentiation is very promising, but we are far from fully understanding both processes, which can be difficult to identify and tell apart from neutral processes. Sexual selection could be the mechanism fixing the advantageous mutations arising from parallel natural selection through changes in mate preference or sexual conflict (Schluter 2009; Mendelson and Safran 2021). However, evidence supporting these processes remains scarce. The nearly neutral theory enriched the neutral theory by designating a significant role for slightly deleterious and scarcely advantageous mutations (Ohta 1973, 2013). This theory is particularly relevant for island organisms because their effective population sizes are much lower compared to those of their mainland counterparts. It could explain the presence of rare alleles and higher evolutionary rates in island taxa and, eventually, their persistence over time. In a recent study, Leroy and colleagues (2021a) analyzed the whole genomes of 14 island and 11 mainland passerine taxa, and demonstrated that slightly deleterious mutations found in island birds are not systematically removed by natural selection. Interestingly, most of these mutations are located in genomic chunks that rarely recombine, supporting the importance of recombination for purging harmful mutations (Leroy et al. 2021a). Overall, these findings unambiguously support the nearly neutral theory and suggest a pathway to understanding the persistence of island birds over time in the face of new environmental challenges (Burri 2021).

### Bird-Parasite Interactions Shaping Genomic Variation

Parasites play a central role in ecological communities, regulating species interactions, population sizes, and shaping genomic variation in their hosts (McCallum and Dobson 1995; Spurgin and Richardson 2010; O'Hanlon et al. 2018). One possible outcome of a host-parasite relationship is the extinction of the host species, which can have direct implications for biological

processes and the functioning of ecosystems, particularly on islands. Island bird species are prone to experience higher disease susceptibility than their mainland counterparts due to their higher inbreeding levels, lower effective population sizes, and reduction of immune function because of a lower pathogen pressure (Whiteman et al. 2006; Lobato et al. 2017; Barthe et al. 2022). In fact, the Hawaiian honeycreepers are, again, sadly symbolic of the devastating effects of emergent diseases on island birds. At least nine of these endemic species experienced rapid extinction episodes following the introduction of avian malaria parasites along with their vector species, the southern house mosquito (*Culex quinquefasciatus*; van Riper et al. 1986).

Ricklefs and Bermingham (1999, 2002), looking at the Lesser Antillean avifauna, speculated that taxon cycles on islands, that is, sequential episodes of expansion and contraction of species ranges, might be a result of coevolutionary dynamics between hosts and their parasites. Under this scenario, specific alleles of genes involved in the immune system of island birds could be selected to resist pathogen virulence. If so, bird-parasite interactions could be shaping genomic variation, which could spread by geographical expansion phases determined by taxon cycles (Ricklefs and Bermingham 1999, 2002). Patterns of host and parasite richness and endemism in the bird communities of the Gulf of Guinea islands has provided further empirical support for this hypothesis (Loiseau et al. 2017). Genetic drift and demographic dynamics play an important role in the evolution of immune functions in island birds (Agudo et al. 2011; Grueber et al. 2013; Gonzalez-Quevedo et al. 2015). However, the role of pathogens in shaping genomic variation and promoting population differentiation over time remains disputed. While some studies have shown a limited effect of parasite pressure driving variation of immune genes (Barthe et al. 2022), others have found evidence for significant associations between the presence and prevalence of pathogens and the levels of genetic variation of genes involved in the immune responses (Gonzalez-Quevedo et al. 2016; Armstrong et al. 2018, 2019; Sheppard et al. 2022). Nevertheless, most information available so far points to a sce-

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nario in which novel parasites are more likely to lead to a decreased species richness by killing their hosts (van Riper et al. 1986) than to stimulate evolutionary radiation by increasing genomic differentiation and reproductive isolation among host populations over time.

### Species Interactions and Speciation in Island Birds

#### Ecological Release

Oceanic island communities have fewer species than their mainland counterparts (MacArthur and Wilson 1967). Thus, species on islands are exposed to lower levels of antagonistic and mutualistic interactions than on the mainland. This, in turn, allows island taxa to occur at higher densities—resulting in increased levels of intraspecific competition (MacArthur et al. 1972). This interplay between low levels of interspecific interactions and high intraspecific competition is one of the key drivers of the evolution of island species. It is at the base of most hypotheses put forward to explain the convergent evolution of many of the traits referred to together under the “island syndrome” umbrella (Blondel 2000; Covas 2012, 2016; Baeckens and Van Damme 2020; Melo et al. 2022b). The “island syndrome” affects all island organisms, independently of whether they arose from independent colonizations from the mainland or from island radiations. Additionally, the species-poor island environment has other direct implications for radiations:

1. In nonadaptive radiations, dependent on multiple instances of isolation, interspecific interactions condition the size of the radiation. This is because in nonadaptive radiation communities are assembled via ecological assortment (Case and Sidell 1983; Dayan and Simberloff 2005)—where the success of a new colonizer is dependent on encountering its ecological niche free from competitors.
2. Reduced levels of interspecific interactions, and of interspecific competition in particular, mean that there is available ecological space on islands, the first condition for adaptive radiations to take place (Schluter 2000; Myers

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and Burbink 2012; Stroud and Losos 2016). In adaptive radiations, reduced levels of species interactions in species-poor oceanic islands facilitate the rapid expansion of a newly arrived colonizer. Such fast population growth, together with the appearance and accumulation of new mutations and/or gene flow from subsequent colonizations or closely related species, provides a rapid escape from the colonization bottleneck, leading to the build-up of genetic variation on which selection can act (Herrmann et al. 2021). The availability of standing genetic variation combined with the reduction of the constraints imposed by species interactions allow for the new arrival to expand and/or shift its niche (Herrmann et al. 2021). This eco-evolutionary response was described first in Darwin's finches (Lack 1944) and named "ecological release" by Wilson (1961). It has been extensively described in oceanic island birds, regarding not only the dietary niche (Van Valen 1965; Diamond 1970; Cox and Ricklefs 1977; Clegg and Owens 2002) but also the acoustic niche (Robert et al. 2021). The expansion of the niche breadth together with niche shifts creates the conditions for one species to branch into different species occupying different niches (Schluter 2000; Gillespie 2009; Grant 2014).

### *Character Displacement*

Although low interspecific competition is essential for the initiation of adaptive radiation, later events of interspecific competition play a crucial role in moving the radiation forward and, in particular, in driving the evolution of phenotypic differentiation and, often, reproductive isolation. This occurs when populations that started to diverge in neighboring islands meet on the same island (Grant 2001; Grant and Grant 2008, 2009). When closely related taxa occur in sympatry, their coexistence is only possible if neither outcompetes the other. If we exclude cases of non-adaptive spatial or temporal segregation, this can only be achieved if the two taxa are able to evolve adaptations to exploit different niches in the same place and time (Lack 1971; Diamond 1973). This is the case in 26% out of the 66 doc-

umented avian evolutionary radiations (Table 1). That ecological differentiation is necessary for coexistence has long been well established by evidence that congeneric species occurring in the same habitat are more distinct in relation to each other than they are in relation to congeners in different habitats (Mayr 1942; Lack 1947; Grant 1966, 1968; Williamson 1981). Upon secondary contact, competition can drive the evolution of phenotypic divergence between species so that each specializes on different resources, escaping the competition zone, in what is designated "character displacement" (Brown and Wilson 1956). Character displacement is one of the central tenets of the ecological theory of adaptive radiation (Schluter and McPhail 1993; Schluter 2000) but can be difficult to demonstrate directly (Grant 1972; Pfennig and Pfennig 2010; Stuart and Losos 2013). In fact, Darwin considered this process, which he called the "principle of divergence of characters" (Darwin 1859), as the main path to speciation and as a discovery as important as the principle of natural selection (Charles Darwin in Barlow 1958).

In island birds, besides the compelling indirect evidence provided by the comparison of sympatric and allopatric species pairs mentioned earlier, there are studies strongly supporting competition in sympatry as a driver of phenotypic evolution (Moulton 1985; Schluter et al. 1985, 1988; Diamond et al. 1989; Grant and Grant 2006; Rando et al. 2010; Melo et al. 2011). Theoretical work suggested that when two closely related taxa meet, it is the newcomer that changes the most (Doebeli and Dieckmann 2000). This asymmetrical character displacement has been confirmed in the evolutionary radiations of Darwin's finches (Petren et al. 2005) and the Gulf of Guinea white-eyes (Melo et al. 2011, 2022a).

## CONCLUSIONS

### *Deciphering Island Radiations: Contingency and Determinism in Evolution*

Avian island radiations have played a central role in our understanding of evolution, and particularly speciation (e.g., Darwin 1859; Wallace 1880). With their overall less complex abiotic and biotic





environment, in comparison to continental ecosystems, oceanic islands may be rather different from each other, yet display many similar qualities when compared to the mainland. Already Darwin and Wallace noted that these similar conditions seemed to lead to similar island-style phenotypes among animals and plants. This cuts across many morphological, ecological, and life-history traits, and has later become known as the “island syndrome” (Carlquist 1965).

Many taxa exhibiting classic island syndrome traits have not radiated (e.g., the dodo of Mauritius or the kakapo of New Zealand). Therefore, the island syndrome is not necessarily linked with evolutionary radiation per se. However, some island syndrome traits may fuel population differentiation and subsequent speciation over time, particularly those related with a reduction in dispersal, of which flightlessness is an extreme case. For instance, Wright et al. (2016) investigating ca. 900 volant land bird species found that island bird populations have a tendency to evolve flightless forms. A direct consequence of this result would be the reduction or elimination of gene flow among nearby populations, which would drive genetic differentiation and, ultimately, could favor evolutionary radiations (Delmore et al. 2020; Estandía et al. 2023a). Flight is energetically very costly (Schmidt-Nielsen 1972); hence, when the selection for flight is relaxed due to the lack of predators in a low-diversity insular fauna, energy allocation is shifted from fore- to hindlimbs and flight ability is often not sustained. Interestingly, the evolution of flight loss can be evolutionarily rapid (Slikas et al. 2002) and could be linked with other morphological changes such as the increase of brain size (Isler and Schaik 2006). Sayol and colleagues (2020) have shown that flightlessness has been far more common historically, especially in island ecosystems, but this trait makes birds extremely vulnerable to extinction once humans or other predators colonize the islands they inhabit (Wright et al. 2016; Sayol et al. 2020).

Evolution is often regarded as a predominantly stochastic process with unpredictable outcomes, contingent on the random nature of DNA mutations and environmental perturbations. Gould (1989) argued that the strong histor-

ical contingency means that if the tape of life was replayed from the same starting point, we would not see our world re-evolve as we know it but instead arrive at different outcomes every time. On the other hand, the “island syndrome” shows how phenotypes frequently evolve convergently as though following an island recipe, which begs the question whether evolution really is random or whether a set of similar ecological circumstances will deterministically generate very similar outcomes through natural selection (Grant 1998; Grant and Grant 2002; Losos and Ricklefs 2009). Yet, we have shown that most avian radiations may be identified as nonadaptive (Fig. 2; Supplemental Table S1), that is, genetic drift could shape most of the genetic differentiation observed, without rejecting that other selective forces such as mutation-order speciation, sexual selection, and hybridization could be involved as well (Enbody et al. 2023; Estandía et al. 2023b; Recuerda et al. 2023). Thus, the question of whether historical contingency or determinism are creating insular avian diversity and, ultimately, promoting evolutionary radiations, remains.

High-throughput sequencing now allows us to address whether, and to what degree, convergent phenotypes at different degrees of similarity evolve along the same genomic pathways (Sackton and Clark 2019), with varying results from insular avian systems (Lamichhaney et al. 2015; Campagna et al. 2022; Estandía et al. 2023b) as well as other animals (Foote et al. 2015; Hu et al. 2017; Kratochwil et al. 2018; Sackton et al. 2019; Winchell et al. 2023). This will also allow us to better understand complex differentiation and speciation scenarios, where in situ evolutionary radiation can be hard to distinguish from intricate scenarios of repeated island colonization (Warren et al. 2003; Sangster et al. 2022; Stervander et al. 2022) or where introgressive hybridization can lead to the incorrect inference of evolutionary history (Andersen et al. 2021; Stervander et al. 2022).

### What Kind of Abiotic and Biotic Information from Extant and Extinct Taxa Do We Need for Moving Forward?

Climatic and environmental changes together with human impact have shaped island biodiver-

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sity over time (Paxton et al. 2016; Wood et al. 2017; Steadman and Franklin 2020). Anthropogenic impacts such as hunting, habitat destruction, and the introduction of invasive species (mostly predators and parasites) have induced massive extinctions of island organisms, including birds (see the section What Are Extinct Species Telling Us about Avian Radiations on Islands?). Besides the need to increase our efforts in documenting more extinction episodes, we need to add new abiotic and biotic information such as on how island birds exploit their trophic niches and on the networks of ecological interactions with other species, including other vertebrates, plants, and microorganisms (e.g., Fleischer et al. 2020; González-Castro et al. 2022). In the case of extinct taxa, we should use morphological data in combination with isotopic analyses to understand the degree of trophic specialization among recently extinct and extant species. In addition, the increasing availability of palaeoecological data should provide a comprehensive ecological framework regarding when and where extinct and extant species coexisted, helping to uncover the effects of ancient human settlement (Wilmshurst et al. 2011; Nogué et al. 2021). Ancient, historical, and recent DNA should provide key information on the genomic architecture of traits underlying the “island syndrome” in birds, such as flightlessness, melanism, and the island rule (Wright et al. 2016; Sayol et al. 2020; Benítez-López et al. 2021; Campagna et al. 2022; Melo et al. 2022b). Information about the ecology and genomics of extant species should shed light on (1) the trophic differences among ecologically similar species (Reaney et al. 2020) or within trophic ecological networks, for instance, using fine-grained diet approaches such as metabarcoding (e.g., Lopes et al. 2019); (2) the role of competition mechanisms shaping the ecological niche specialization (see the section Species Interactions and Speciation in Island Birds); (3) hybridization; (4) the genomic architecture of morphological variation; and (5) microbiome composition (Lamichaney et al. 2018; Michel et al. 2018; Campagna and Toews 2022). Overall, to establish the links between the environment, the phenotype, and the genotype, we need to integrate archaeological and palaeoecological data with long-term field studies including trophic ecology, vocalization,

other behaviors, ecological interactions, and environmental variations (e.g., Grant and Grant 2008). This, combined with genomic approaches, appears as the optimal strategy to go further not only in our comprehension of island avian radiations but of the speciation process itself and, importantly, to predict the response of extant taxa to environmental changes (Grant and Grant 2017).

### Looking for Global Answers of How and Why Species Multiply

Since Charles Darwin and Alfred Russel Wallace introduced natural selection as the mechanism governing how species change over time (Darwin and Wallace 1858), we have greatly improved our understanding of the ecological and molecular processes involved. Despite substantial advances, we are still far from completely uncovering the ultimate mechanisms of every avian island radiation, even for the most well-known cases. Reproductive isolation after in situ divergence seems to be the mechanism explaining differentiation over time in most of avian island radiations (Supplemental Table S1). Neutral or nearly neutral processes have been identified as the dominant processes operating on island taxa (Leroy et al. 2021a). Nevertheless, the important role of selection (natural and sexual) cannot be neglected in island ecosystems (Grant and Grant 2008). In fact, selection is detectable even in bottlenecked or inbred populations (Spurgin et al. 2011; Uy et al. 2016; Armstrong et al. 2018; Barthe et al. 2022).

Most evolutionary radiations documented to date display conspicuous variation in phenotypic traits such as feather coloration and morphological variation. However, long-term reproductive isolation may produce similar phenotypes due to niche conservatism (see the section Importance of Nonadaptive Radiations in Oceanic Island Ecosystems), which can hamper our understanding of the number and magnitude of avian radiations (McCullough et al. 2022; Wu et al. 2022). This limitation can be reduced by increasing our knowledge of the genetic structure of extant and extinct taxa. Ecological, paleontological, and archaeological expeditions, and the subsequent analyses of tissues collected through phenomic,



genomic, or proteomic approaches (see the sections What Genomic and Ecological Data Are Needed to Understand Avian Island Radiations? and What Kind of Abiotic and Biotic Information from Extant and Extinct Taxa Do We Need for Moving Forward?) will provide insights into the genetic structure of the contemporary and vanished avifauna. Alternatively, we can employ “museumomics,” that is, the use of historical DNA from museum specimens. Natural history museums store millions of avian specimens around the world, which were collected over many temporal and spatial windows. These individuals not only inform us about past distributions, but they may be used in genomic studies thanks to the routine use of high-throughput sequencing (Card et al. 2021; Raxworthy and Smith 2021; Irestedt et al. 2022; Lalueza-Fox 2022), which is likely to uncover cryptic avian radiations (Ernst et al. 2022; Wu et al. 2022).

What do we need to know to be able to unravel the drivers of island avian radiations? Some lineages have produced a significant number of species, while others show limited diversification, although at the taxonomic level of orders the distribution of radiations largely mirrors the spe-

cies diversity across avian orders (Table 1). This pattern is evident also at the family level within the most speciose order Passeriformes (Supplemental Table S2), with the large suborder Tyranni (“suboscines”, comprising 1385 species) giving rise to only two small evolutionary radiations being an exception. In one of the “great speciators,” the white-eyes, Vinciguerra et al. (2023) demonstrated that island white-eyes have similar extinction rates as their mainland counterparts but a significantly elevated speciation rate. Nevertheless, the ultimate determinants of diversification are poorly understood. Brain size has been pointed out to be an important factor explaining speciation rates in birds (Sayol et al. 2019), and island birds show relatively larger brains than their continental counterparts (Sayol et al. 2018). However, brain size seems to evolve in situ as an island adaptation (Sayol et al. 2018), and this finding would limit a direct association with the number of species involved in island radiations. High-standing genetic variation and hybridization could promote some evolutionary radiations (see the section Importance of Nonadaptive Radiations in Oceanic Island Ecosystems). We also need to better understand how genomic organization in island birds,

#### BOX 1. OPEN QUESTIONS FOR FUTURE RESEARCH

Speciation is a continuous and complex process likely involving more than one evolutionary force operating at the same time. Unraveling the **role and strength of the specific mechanisms** driving each avian evolutionary radiation is a formidable challenge. However, this information is important to get a full understanding of how and why species multiply and vanish.

Detailed **genomic information** regarding how standing genetic variation, natural and sexual selection, genetic drift, and hybridization promote and shape evolutionary radiations is needed. In addition, an important step will be to understand how **genomic organization**—including large-scale inversions, neosex chromosomes, gene conversion, and transposable elements—may explain adaptation to island ecosystems and enhance reproductive isolation and differentiation over time.

Further advances about the **identity of genes under selection**, in combination with information about how they are activated, deactivated, and regulated will be decisive to understand the mechanisms operating in the genetic differentiation at the population and species levels.

New advances in the reconstruction of **phylogenetic relationships of extant and extinct species**, obtained from massively parallel sequencing, will provide the best way to distinguish true island-restricted radiations from independent waves of colonization, and to assess the genetic diversity lost over time.

**Multidisciplinary approaches** are likely the best way to explain island radiations worldwide. Comprehensive global analyses of genera with multiple species occurring in island ecosystems, where we can simultaneously incorporate genomic, morphological, behavioral, and environmental data, are a promising pathway to decipher the ultimate causes explaining avian radiations.

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including large-scale inversions (Sanchez-Donoso et al. 2022), neosex chromosomes (Dierickx et al. 2020; Leroy et al. 2021b), and transposable elements (Kapusta and Suh 2017), may explain adaptation to island ecosystems and enhance reproductive isolation and differentiation over time. Undoubtedly, multidisciplinary approaches are needed to explain island radiations worldwide. Comprehensive global analyses of genera with multiple species occurring in island ecosystems, where we can incorporate genomic, morphological, behavioral, and environmental data (e.g., Garcia-Porta et al. 2022), are a promising pathway to answer the question of how and why species multiply (for additional information see Box 1; Supplemental Tables S3 and S4).

#### AUTHOR CONTRIBUTIONS

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#### ACKNOWLEDGMENTS

J.C.I. was funded by research grants from the Spanish Ministry of Science, Innovation and Universities, Spanish Research Agency, and the Euro-

pean Regional Development Fund (PGC2018-097575-B-I00; PID2022-140091NB-I00) and by a regional GRUPIN grant from the Regional Government of Asturias (AYUD/2021/51261). M.S. was supported by a Marie Skłodowska Curie Grant from the European Commission (893225). M.M. was supported via the European Union's Horizon 2020 research and innovation programme under grant agreement 854248. Fundação para a Ciência e a Tecnologia (FCT, Portugal) provided structural funding to CIBIO (UIDB/50027/2021: to M.M.). L.V. was supported by a NWO Vidi Grant. We thank Ángel Morales for providing Figure 1. Juan Varela provided the drawings for Figure 3. José Cerca and Jaime A. Chaves made useful suggestions on a draft of this manuscript. Ulf Dieckmann, Sonya Clegg, and one anonymous reviewer provided valuable comments during the review process.

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## Adaptive and Nonadaptive Avian Island Radiations



# Cold Spring Harbor Perspectives in Biology

## Avian Island Radiations Shed Light on the Dynamics of Adaptive and Nonadaptive Radiation

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*Cold Spring Harb Perspect Biol* published online April 15, 2024

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