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Genomic patterns in the dwarf kingfishers of northern Melanesia reveal a mechanistic framework explaining the paradox of the great speciators

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Abstract

The paradox of the great speciators describes a contradictory biogeographic pattern exhibited by numerous avian lineages in Oceania. Specifically, these lineages display broad geographic distributions across the region, implying strong over-water dispersal capabilities; yet, they also display repeated genetic and phenotypic divergence—even between geographically proximate islands—implying poor inter-island dispersal capabilities. One group originally cited as evidence for this paradox is the dwarf kingfishers of the genus *Ceyx*. Here, using genomic sequencing and comprehensive geographic sampling of the monophyletic *Ceyx* radiation from northern Melanesia, we find repeated, deep genetic divergence and no evidence for gene flow between lineages found on geographically proximate islands, providing an exceptionally clear example of the paradox of the great speciators. A dated phylogenetic reconstruction suggests a significant burst of diversification occurred rapidly after reaching northern Melanesia, between 3.9 and 2.9 MYA. This pattern supports a shift in net diversification rate, concordant with the expectations of the "colonization cycle" hypothesis, which implies a historical shift in dispersiveness among great speciator lineages during the evolutionary past. Here, we present a formalized framework that explains how repeated founder effects and shifting selection pressures on highly dispersive genotypes are the only ultimate causes needed to generate the paradox of the great speciators. Within this framework, we emphasize that lineage-specific traits and island-specific abiotic factors will result in varying levels of selection pressure against dispersiveness, caused by varying proximate eco-evolutionary mechanisms. Overall, we highlight how understanding patterns of diversification in the *Ceyx* dwarf kingfishers helped us generate a cohesive framework that provides a rigorous mechanistic explanation for patterns concordant with the paradox of the great speciators and the repeated emergence of geographic radiations in island archipelagoes across the globe.

Keywords: speciation, reproductive isolation, biogeography, evolutionary genomics

Lay Summary

Understanding how and why global biodiversity has evolved is a key goal of evolutionary biology. Today, thanks to exciting advances in DNA sequencing technology, we can sequence thousands of pieces of DNA in a rapid and cost-effective manner. This sequencing revolution allows us to efficiently compare the genomes of organisms across space and time. We can now reconstruct the evolutionary history of entire radiations of organisms from which we can learn more about how evolution has shaped the patterns of biodiversity that we see today. Here, we sequenced DNA from dwarf kingfishers of the genus *Ceyx*, small colorful birds that are found from tropical Southeast Asia to the islands of the Pacific Ocean. We sequenced over 100 individual birds from "northern Melanesia," which includes Papua New Guinea and the Solomon Island archipelago off the northeastern coast of Australia. We were able to identify approximately 20,000 single-base pairs of DNA throughout the genome that varied among these 100 individuals. This variation in DNA allowed us to infer how these birds were related to one another, both within and between island populations. We found that all of the species we sequenced were distantly related genetically and diversified rapidly after a common ancestor first colonized the region, roughly 4 million years ago. Based on this evidence, we can reject the notion that these birds achieved their broad distribution by gradually colonizing one island after another and instead support a rapid period of repeated island colonization deep in the evolutionary past, followed by a sharp reduction in the frequency of colonizing new islands. Other researchers have typically explained this type of pattern by suggesting that there was a historical change in the birds' willingness or ability to fly across oceans sometime in the past. We agree with that interpretation and propose a detailed framework that explains the exact evolutionary forces that could create this pattern. Although we think this framework is broadly applicable across many different organisms and island chains

throughout the world, we highlight that the specific properties of each type of organism, like the flight ability of birds, will strongly influence how different evolutionary forces act. In sum, our results indicate that the evolution of new biodiversity is often not a continuous linear process and help us construct a new framework for understanding exactly how evolution shapes the diverse groups of organisms found in island archipelagoes across the world.

Introduction

The thousands of islands throughout the Pacific Ocean (i.e., Oceania), varying in size and degree of isolation, have long been recognized as a powerful arena for studying the process of biodiversity generation (i.e., speciation and diversification; MacArthur & Wilson, 1967; Wallace, 1880). For many terrestrial organisms, open ocean between these islands serves as a physical barrier, creating isolation between populations. This geographic isolation is expected to catalyze genetic divergence and eventually reproductive isolating barriers between disjunct populations (i.e., allopatric speciation; Mayr, 1942, 1963; Wilson, 1961). This canonical understanding of allopatric speciation as the dominant driver of ecosystem-level biodiversity accumulation in Oceania has been largely unquestioned. However, this process can also produce seemingly paradoxical patterns of diversity, dubbed "the paradox of the great speciators" by Diamond et al. (1976). The paradox is that for a broadly distributed, polytypic lineage to evolve, the lineage must be dispersive enough to reach and colonize a broad swath of islands, yet dispersal between these newly colonized island populations must be rare or absent for divergence (phenotypic and/or genetic) to subsequently occur (Diamond & Mayr, 1976; Diamond et al., 1976). The avifauna of Oceania is especially known for its preponderance of broadly distributed and highly polytypic avian lineages, which throw this paradox into sharp relief (e.g., *Zosterops*, Moyle et al., 2009; Manthey et al., 2020; Vinciguerra et al., 2023; *Pachycephala*, Andersen et al., 2014; *Todiramphus*, Andersen et al., 2013, 2015; DeRaad et al., 2023; *Myzomela*, Marki et al., 2017; *Horornis*, Gyllenhaal et al., 2020; *Rhipidura*, Klicka et al., 2023; *Monarcha*, Filardi & Smith, 2005; *Edolisoma*, Pedersen et al., 2018; *Turdus*, Reeve et al., 2023; *Erythropitta*, Irestedt et al., 2013; and *Ceyx*).

Yet, despite copious examples of the paradox of the great speciators, relatively few comprehensively sampled genomic datasets exist for these great speciator taxa. This makes it difficult to know whether the underlying assumptions of the paradox, such as rapid diversification, genetic divergence, and cessation of gene flow between islands (Diamond et al., 1976), hold true across many of these putative great speciator taxa. Therefore, documenting the patterns of diversification within these groups is a key first step toward understanding whether a consistent set of eco-evolutionary mechanisms can explain the repeated emergence of this widespread, paradoxical pattern. Furthermore, it is an open question whether the patterns and putative underlying mechanisms involved in the paradox of the great speciators are consistent with those involved more broadly in geographic radiations (Simões et al., 2016) occurring in island archipelagoes across the globe.

Historically, there have been two main competing hypotheses proposed to explain the paradox of the great speciators, each of which predicts a unique set of diversification patterns. The first, the intermediate dispersal hypothesis (Agnarsson et al., 2014; Venail et al., 2008), predicts that historical diversification happened at a moderate and consistent rate, with great speciator taxa possessing just enough dispersiveness to rarely reach new islands but not enough dispersiveness to prevent subsequent genetic and phenotypic divergence between isolated island populations. A group following this hypothesis would be expected to display

a stable net diversification rate throughout its evolutionary history as it gradually reached new islands via rare and stochastic dispersal events (Yamaguchi, 2022). In contrast, the colonization cycle hypothesis (Diamond, 1977; Diamond et al., 1976; Moyle et al., 2009) predicts that a single lineage will rapidly reach new, previously unoccupied islands across a broad area during the "colonization phase" when intrinsic dispersal is high. Subsequently, as the accessible, long-term habitable islands in an archipelago fill up, the cost of risky over-water dispersal events will begin to outweigh the benefit of potentially reaching a habitable island with unclaimed resources, creating selection pressure against dispersiveness that will reduce the rate of island colonization and eventually the intrinsic dispersiveness of the group. Therefore, we expect groups following the colonization cycle hypothesis to display a significant early burst of diversification upon arriving in an island archipelago, followed by a drop in net diversification rate upon the filling of accessible, long-term habitable islands.

While these two competing hypotheses can be differentiated based on observed diversification patterns alone, the underlying mechanistic bases of these hypotheses can be much more difficult to discern (Harrison, 1998). For instance, while the genetic loss of dispersiveness assumed by the colonization cycle hypothesis (Diamond et al., 1976) provides a compelling explanation for a shift in diversification rate that could explain the paradox of the great speciators (e.g., Estandía et al., 2023), the exact details of how intra (i.e., single island population) versus inter (i.e., lineage or archipelago wide) island selection pressures would interact to influence this complex phenotype (dispersiveness) remain poorly understood (Saastamoinen et al., 2018). Furthermore, the overall patterns of genomic relatedness within most great speciator taxa remain unclear. For these reasons, genomic investigations into great speciator taxa are greatly needed to resolve patterns of diversification and shine light on the exact mechanistic basis of the paradox of the great speciators.

Here, we sequence thousands of genomic loci from comprehensive geographic sampling of the northern Melanesian *Ceyx* kingfishers, which form a monophyletic geographic radiation in the region (Andersen et al., 2013, 2018; McCullough et al., 2019). *Ceyx* kingfishers have long been recognized as an exemplar of the paradox of the great speciators because of their broad geographic distribution spanning from mainland Asia through the Solomon Islands, with fine-scale phenotypic divergence among island populations (Diamond et al., 1976). We search for the expected genetic patterns of the paradox of the great speciators, specifically whether geographically proximate island taxa are genetically divergent and appear to have ceased interbreeding. We also generate a dated phylogenetic reconstruction to assess the tempo of evolution during the radiation of extant *Ceyx* lineages across northern Melanesia. We then use these modern genomic results to test classic biogeographic hypotheses and develop a mechanistic framework that predicts the paradoxical patterns of diversification observed in many great speciator taxa.

Methods
Geography
Here we focused on 10 *Ceyx* species, outgroup *Ceyx margarethae* from the Philippines, plus a monophyletic geographic radiation

of nine species from northern Melanesia (Table 1). Of note, four Wallacean species found on islands to the west of Papua New Guinea have been recovered as closely related outgroups to this northern Melanesian radiation, suggesting rapid colonization from west to east across northern Melanesia (see Figure 3 in Andersen et al., 2013; and Supplementary Figure S1 in McCullough et al., 2019). We constructed a map detailing the distribution and genetic sampling localities for each of the 10 sampled *Ceyx* species using the R package *ggplot2* v3.4.4 (Wickham et al., 2020) and a diverging color palette (Tol, 2021) that is maintained throughout the manuscript. We also present a detailed bathymetry map for the Solomon Islands generated from the 15 arc-second resolution ETOPO 2022 global relief model (NOAA National Centers for Environmental Information, 2022) which was retrieved via the "grid extract" web portal (https://www.ncei.noaa.gov/maps/grid-extract/). On this bathymetric map, we designed a color-coding scheme to display elevational data for present-day islands and color-code ocean depths of 0–130 m (putative minimum sea level during the Pleistocene, 2.6 Ma–11.7 Ka; Ludt & Rocha, 2015; Voris, 2000) in gray to display historical land bridges.

DNA sequencing, read mapping, and SNP calling

We followed the reduced-representation sequencing (i.e., RADseq) approach recounted in detail in recent publications (DeRaad et al., 2022b, 2023) with minimal alterations. We began by extracting genomic DNA from 127 specimen-vouchered tissue samples (Supplementary Table S1) from the 10 focal *Ceyx* species (Table 1) using a magnetic bead-based protocol (Rohland & Reich, 2012). Individual restriction-enzyme associated DNA sequencing (RADseq) libraries were constructed for each sample, including eight technical replicates, at the University of Kansas Genomic Sequencing Core, using the enzyme NdeI for shearing and a BluePippen Prep 2% cassette for size selecting fragments 495–605 base-pairs (bp) in length. These barcoded genomic libraries were pooled with libraries from other projects and sequenced on a flow cell of an Illumina NextSeq2000 machine, using P2 reagents to generate single-end 100 bp reads.

We demultiplexed the resulting reads using the *Stacks* v2.41 (Rochette et al., 2019) function "process.radtags," and mapped the reads from each sample against a publicly available reference genome for *Ceyx cyanopectus* (available at: https://www.ncbi.nlm.nih.gov/datasets/genome/GCA_013401355.1/; Feng et al., 2020), using BWA v0.7.17 (Li & Durbin 2009). We used *SAMtools* v1.3.1 (Li et al., 2009) and the *Stacks* module "gstacks" to identify and collate RAD loci throughout the genome and called single nucleotide polymorphisms (SNPs) via the *Stacks* "populations" module. Our unfiltered SNP dataset contained 135 samples (127 individuals plus eight technical replicates) and 179,940 SNPs, with 61.66% overall missing data.

Quality control

We used the R packages *vcfR* v1.14.0 (Knaus & Grünwald, 2017) and *SNPfiltR* v1.0.1 (DeRaad, 2022) to implement optimized SNP filtering thresholds. The entire filtering process can be viewed in detail with corresponding data visualizations at: (https://devonderaad.github.io/nmel.ceyx/ceyx.filtering.html). In brief, we removed genotypes covered by < 3 sequencing reads, with genotype quality < 30 Phred quality score, and with an allele balance outside of the range 0.1–0.9 for called heterozygous genotypes. We also removed SNPs from the dataset if their coverage was > 250 reads (likely paralogs) and dropped 21 samples (including one technical replicate) with > 80% missing genotypes. We then assessed the seven remaining technical replicates and found no detectable evidence for batch effects or contamination. We used these samples to estimate a genotyping error rate of 0.038%–0.149%, suggesting high repeatability and low amounts of technical error resulting from the DNA sequencing process and our genotyping pipeline. All technical replicates were then removed from the dataset and all SNPs that were not shared by > 90% of the remaining samples were also pruned from the dataset. This left us with a filtered SNP dataset containing 107 samples (each from a unique *Ceyx* individual), 20,831 SNPs, and 2.83% overall missing data, with no individual missing genotype calls at > 20% of SNPs. We thinned this filtered SNP dataset to a minimum distance of 10 kilobases (Kb) between SNPs for a final filtered, putatively unlinked SNP dataset containing 107 individuals, 2,580 SNPs, and 3.19% overall missing data.

Inferring genetic relatedness among samples

We constructed an unrooted phylogenetic network to visualize sample relatedness without the bifurcating assumptions of a rooted phylogenetic tree. To generate this network, we used the filtered SNP dataset as input for the R package *StAMPP* v1.6.3 (Pembleton et al., 2013) to generate a pairwise divergence (Nei's D; Nei, 1972) matrix among all samples and then constructed the network using the "neighbor net" algorithm in *SplitsTree* v4.19.2 (Huson & Bryant, 2006). After observing no evidence for intermediate sample placement in the unrooted phylogenetic network,

Table 1. A list of the nine northern Melanesian *Ceyx* species studied here, plus outgroup *C. margarethae*, and their general distributions.

Species	Countries	Islands
margarethae	Philippines	Banton, Tablas, Romblon, Sibuyan, Semirara, Negros, Cebu, Olango, Siquijor, Camiguin Sur, Mindanao, Basilan, Malamaui, Jolo, Tawitawi, and Bongao
solitarius	Papua New Guinea	Batanta, Misool, Salawati, Waigeo, Biak, Yapen, Aru, New Guinea, Kairiru, Karkar, D'Entrecasteaux, Fergusson, and Normanby
dispar	Papua New Guinea	Manus
mulcatus	Papua New Guinea	New Hanover, New Ireland, Tabar, and Lihir
sacerdotis	Papua New Guinea	New Britain, Umboi, Lolobau, and Watom
meeki	Papua New Guinea and Solomon Islands	Bougainville, Buka, Choiseul, and Isabel
gentianus	Solomon Islands	Makira
malaitae	Solomon Islands	Malaita
nigromaxilla	Solomon Islands	Guadalcanal
collectoris	Solomon Islands	(New Georgia group) New Georgia, Tetepare, Rendova, Kolombangara, Gizo, Vella Lavella, Ranongga, Vangunu, Nggatokae

Note. Detailed locality information retrieved from *Handbook of Birds of the World* (del Hoyo et al., 2020).

we constructed a maximum-likelihood-based phylogenetic tree including all samples as tips. To do so, we exported all 2,580 filtered loci (including invariant sites) for the 107 samples included in all downstream analyses as a single concatenated phylip file using the *Stacks* "populations" module. We used this phylip file as input for *IQ-TREE 2* v2.2.0 (Minh et al., 2020), allowing automatic model selection, implementing the best model based on Akaike information criterion (here, TVM + F + I + I + R3), and performing 1,000 ultra-fast bootstrap replicates. We used *FigTree* v1.4.4 (Rambaut, 2014) to root this tree on the branch leading to the Philippine endemic *C. margarethae*, which has been consistently recovered as an outgroup to this monophyletic northern Melanesian radiation in previous investigations using both mitochondrial (Andersen et al., 2013) and genome-wide nuclear loci (McCullough et al., 2019).

We then removed the seven outgroup *C. margarethae* samples and all SNPs with a minor allele count < 2 which are known to bias sample ancestry assignments (Linck & Battey, 2019) from our unlinked SNP dataset. We used this 100-sample, 1,666 SNP dataset as input for the program *ADMIXTURE* v1.3.0 (Alexander et al., 2009) to search for signatures of mixed genomic ancestry within individuals, which would suggest ongoing hybridization and gene flow between species. We allowed the number of ancestry bins (K) to vary from 1 to 15, presenting the iteration with the lowest cross-validation error ($K = 9$). For species that displayed strongly supported intra-species clades in the aforementioned phylogenetic reconstruction (indications of potential geographic substructuring in *Ceyx solitarius*, *Ceyx meeki*, and *Ceyx collectoris*), we repeated this procedure, generating single-species subset SNP datasets with minor allele count ≥ 2. Each of these subsets was run independently in *ADMIXTURE* with K varied from 1 to 5, with the optimal K value and $K + 1$ presented to the reader.

Reconstructing species trees and assessing patterns of diversification

We then followed the pipeline outlined by Stange et al. (2018) to simultaneously perform Bayesian divergence time estimation and infer a species tree topology using the multispecies coalescent model and population-level genomic SNP data. We first assigned samples to tips, following the sample assignments from *ADMIXTURE* at the optimal K of 9. The only deviation from this scheme was assigning the single *Ceyx dispar* sample to a unique species tip because the mixed ancestry recovered in this sample is likely an artifact of small sample size, and this sample was recovered as a distinct species-level lineage in the phylogenetic network and concatenated tree. We also assigned all outgroup *C. margarethae* samples (not included in the *ADMIXTURE* analysis) to a unique tip. We then constrained all ingroup species (all species except *C. margarethae*) as a monophyletic clade and placed a prior distribution (lognormal distribution with a mean of 3.9 MYA and standard deviation of 0.15) on the crown age of this clade, to approximate the results from the ultraconserved elements-based dated phylogeny of McCullough et al. (2019), which recovered a crown divergence age of ~3.9 MYA (95% HPD ~3–5 MYA) for this clade. We specified the starting topology for the tree search as the topology recovered in our maximum-likelihood reconstruction and specified an MCMC length of 5M, sampling from the posterior distribution every 2.5K iterations. For each of the three chains, we randomly downsampled our filtered, unlinked SNP dataset to a maximum of two individuals per species tip to ensure computational tractability. We then ran each of these three chains three times, with different starting seeds (3 downsampling schemes × 3

unique starting seeds each = 9 total replicate MCMC chains) using *SNAPP* v1.5.2 (Bryant et al., 2012) implemented in *BEAST2* v2.7.1. We confirmed convergence and appropriate effective sample sizes (> 200) for all key parameter estimates across all nine chains using *Tracer* v1.7.2 (Rambaut et al., 2018). We also confirmed Gelman–Rubin diagnostic values < 1.01 for all estimated parameters across these nine replicates using the R package *stableGR* (Vats & Knudson, 2021). After confirming that all three unique downsampling schemes converged on an identical topology, we chose to present the replicate with the greatest posterior probability. Discarding the first 25% of trees sampled from the posterior distribution as burn-in, we visualized the remaining 1,500 trees as a cloudogram and calculated posterior probabilities for the internal branches in the maximum clade credibility tree using *DensiTree* and *TreeAnnotator* (both distributed with *BEAST2* v2.7.1).

We then used the R package *phytools* v2.0-3 (Revell, 2012) to assess patterns of diversification within the northern Melanesian *Ceyx* clade. To do so, we read the maximum clade credibility tree with dated node ages into R and removed the root node, leaving only the 10 ingroup northern Melanesian lineages. We then simulated 1,000 trees following a pure-birth diversification model (i.e., continuous log-linear accumulation of species; Harmon et al., 2003) with an identical number of tips (10) and identical maximum node height to our empirical tree (~3.8 MYA). We used these 1,000 simulated trees to generate a 95% confidence interval around this null expectation of log-linear species accumulation through time and then plotted our empirical log-lineage through time accumulation curve on top of this confidence interval to visualize significant deviations from a pure-birth model through time. We repeated this procedure for all nine replicate versions of our *SNAPP* species tree to confirm that this early burst pattern was consistently recovered regardless of downsampling scheme or starting seed. We also calculated Pybus and Harvey's gamma statistic (Pybus & Harvey, 2000), which has a null expectation ($\gamma = 0$) under a pure-birth model of continuous species accumulation, while negative values indicate an early burst of diversification and positive values indicate a recent burst of diversification (Burbrink et al., 2012).

Quantifying divergence, diversity, and gene flow

To quantify divergence between the tips included in our species tree reconstruction, we used our filtered SNP dataset as input for *StAMPP* and estimated relative divergence (i.e., pairwise F_{ST}; Weir & Cockerham, 1984). We used identical sample assignments as in the species tree reconstruction, removed the seven outgroup *C. margarethae* samples and visualized these pairwise F_{ST} results as a heatmap using the R package *ggplot2* v3.4.4 (Wickham et al., 2020). We also calculated genetic diversity among these groups using *Stacks*. For each of the 100 ingroup samples passing filtering protocols, we used all sites that mapped to the reference genome in the ".bam" file, including invariant sites, before any filtering protocols were applied, to allow for the most comprehensive possible quantification of genome-wide levels of genetic diversity and prevent the introduction of biases via specific filtering thresholds (Shafer et al., 2017). We used these data to calculate the proportion of sites called heterozygous (i.e., heterozygosity) in each sample and the overall nucleotide diversity (Pi) within each of these nine species using the *Stacks* "populations" module. Finally, we tested for statistical signatures of excess allele sharing between nonsister lineages (i.e., gene flow) using an ABBA–BABA framework (Durand et al., 2011). We assigned all samples to tips following the same scheme used for species tree reconstruction

and used our filtered SNP dataset as input for the program *Dsuite* v0.4 (Malinsky et al., 2021), designating *C. margarethae* as the outgroup. We used the "Dtrios" module to perform block Jackknifing to estimate standard error and generate a *Z* score for each pairwise *D* statistic. Each *Z* score was then converted into a *p*-value representing the probability of getting a *D* statistic value as extreme or more extreme than the observed given a null hypothesis that *D* = 0. We interpreted the *p*-values for the 120 individual pairwise *D* statistics using a false discovery rate adjusted (Benjamini & Hochberg, 1995) critical value of $α = 0.05/120 = 0.0004167$.

Results

The unrooted phylogenetic network constructed from our filtered SNP dataset (20,831 SNPs, 2.83% missing genotypes) showed that previously described *Ceyx* species (Andersen et al., 2013) cluster distinctively based on thousands of genome-wide loci (Figure 1B). Nearly all of the allelic variation in the SNP dataset was attributable to divergence between clades, as revealed by the long internal branches and short terminal tips in the phylogenetic network. The placement of all samples into discrete clades which tightly correspond to a priori species assignments, suggests no evidence for recent interspecies hybrid ancestry in our dataset.

A concatenated phylogenetic tree for all samples revealed strongly supported (bootstrap support > 95), reciprocally monophyletic relationships among the nine ingroup species, except for the poorly supported internal branch determining the placement of *C. gentianus* (bootstrap support = 74; Figure 2A). Furthermore, the phylogenetic reconstruction revealed intraspecies geographic substructuring supporting nearly every sampled island as a discrete clade. The pattern of tight sample clustering observed in both phylogenetic reconstructions (Figures 1B and 2A) is further validated by the lack of shared interspecies ancestry apparent from individual ancestry assignments derived from the program *ADMIXTURE* (Figure 2B). The one notable deviation from this trend (99 out of 100 ingroup samples assigned > 99% intraspecies ancestry) is the single *C. dispar* sample, which is assigned a combination of five different genetic backgrounds corresponding to other species in the dataset. This pattern was seen consistently across multiple SNP filtering and sample inclusion schemes and likely resulted from the difficulty of fitting a unique ancestry group to a single sample in *ADMIXTURE*'s underlying model rather than any biological evidence of shared interspecies ancestry (for a detailed discussion of this phenomenon, see Wang, 2017).

Targeted investigations of intraspecies sample relatedness revealed evidence for geographic substructuring within multiple species (Figure 2B). In particular, *C. solitarius*, which we sampled broadly across eastern New Guinea (Figure 1A), is geographically delimited north-to-south with a break at roughly 6° latitude (Figure 2B). In addition, *C. meeki* can be divided into two reciprocally monophyletic clades corresponding to the described subspecies: *C. meeki pallidus* on Bougainville and the nearshore Shortland Islands and *C. m. meeki* distributed throughout Choiseul and Isabel. Even though this entire island chain was likely connected as recently as 10 KYA (forming the Pleistocene island "Greater Bukida"; Figure 2C), we find no evidence for ancestry sharing between these two clades (Figure 2B). Perhaps most strikingly, *C. collectoris* displayed extensive intraspecies geographic structure within the islands of the New Georgia group, with a deep phylogenetic break evident between the eastern and western island groups that are separated by a deep ocean channel (Figure 2C). Within each of these clades, further substructuring

was apparent, including a distinct clade corresponding to individuals sampled from Tetepare Island, despite its recent (~10 KYA) connection with nearby Rendova Island (forming the Pleistocene island "Greater Rendipari"; Figure 2B and C).

To assess the overall patterns of diversification among these lineages, we constructed a species tree with 11 tips corresponding to the nine lineages identified by *ADMIXTURE* (Figure 2B) plus *C. dispar* and outgroup *C. margarethae* (Figure 3). This species tree, inferred under the multispecies coalescent model (Degnan & Rosenberg, 2009), reconstructs a summary of the overall evolutionary history of this group while avoiding the pitfalls of concatenation (Mendes & Hahn, 2018). This dated, ultrametric species tree suggests that after reaching northern Melanesia ~3.9 MYA (McCullough et al., 2019), *Ceyx* rapidly colonized nearly every large island in the archipelago while diversifying into nine separate lineages over the next ~1 MY (Figure 3A). This rapid, successive colonization is underscored by the low posterior support values for internal branches along the backbone of the tree, which suggest extremely short waiting periods between speciation events (Degnan & Rosenberg, 2006; DeRaad et al., 2023). A log-lineage through time accumulation plot reveals that *Ceyx* experienced a statistically significant ($γ = –3.13$, $p = 0.0018$) early burst of diversification following the colonization of northern Melanesia, compared to the null expectation of a pure-birth model, which predicts the continuous log-linear accumulation of new lineages through time (Figure 3B).

Maximum pairwise *D* statistics for all possible pairwise comparisons revealed only mild deviations from the null expectation of equal allele sharing frequencies between non-sister lineages (i.e., $D = 0$), with no comparisons reaching our adjusted significance threshold ($α = 0.0004167$; Figure 4A). Pairwise F_{ST} values calculated between all lineages revealed deep relative divergence between currently recognized species (range = 0.65–0.91), with a comparatively modest $F_{ST} = 0.39$ recovered between the recently diverged eastern and western lineages of *C. collectoris* (Figure 4B). These surprisingly high divergence values were likely driven in part by an overall lack of genetic variation within lineages (Pi range: 0.00029–0.00076; Figure 4C), compared to the amount of genetic variation between lineages. Notably, all single island endemic lineages display low genetic diversity (Pi range: 0.00029–0.00052).

Discussion

> "This degree of differentiation seemingly requires that such species disperse sufficiently well to reach many islands, yet disperse sufficiently poorly that each population can diverge in isolation. How is this paradox to be resolved?" Diamond et al. (1976)

Here we have documented patterns of phylogeographic relatedness among the dwarf kingfishers of northern Melanesia, providing an exceptionally clear example of the paradox of the great speciators (Diamond et al., 1976). Specifically, our sampling across more than a dozen islands (most of which were never interconnected via land bridges) has confirmed repeated historical dispersal events over tens to hundreds of kilometers of open ocean. Yet, we have also recovered genetic divergence in nearly every inter-island comparison, including between Tetepare and Rendova islands, which are currently separated by just a ~2 km water gap (Figure 3). The dispersiveness required to colonize such a broad geographic area contradicts the limited inter-island colonization events that
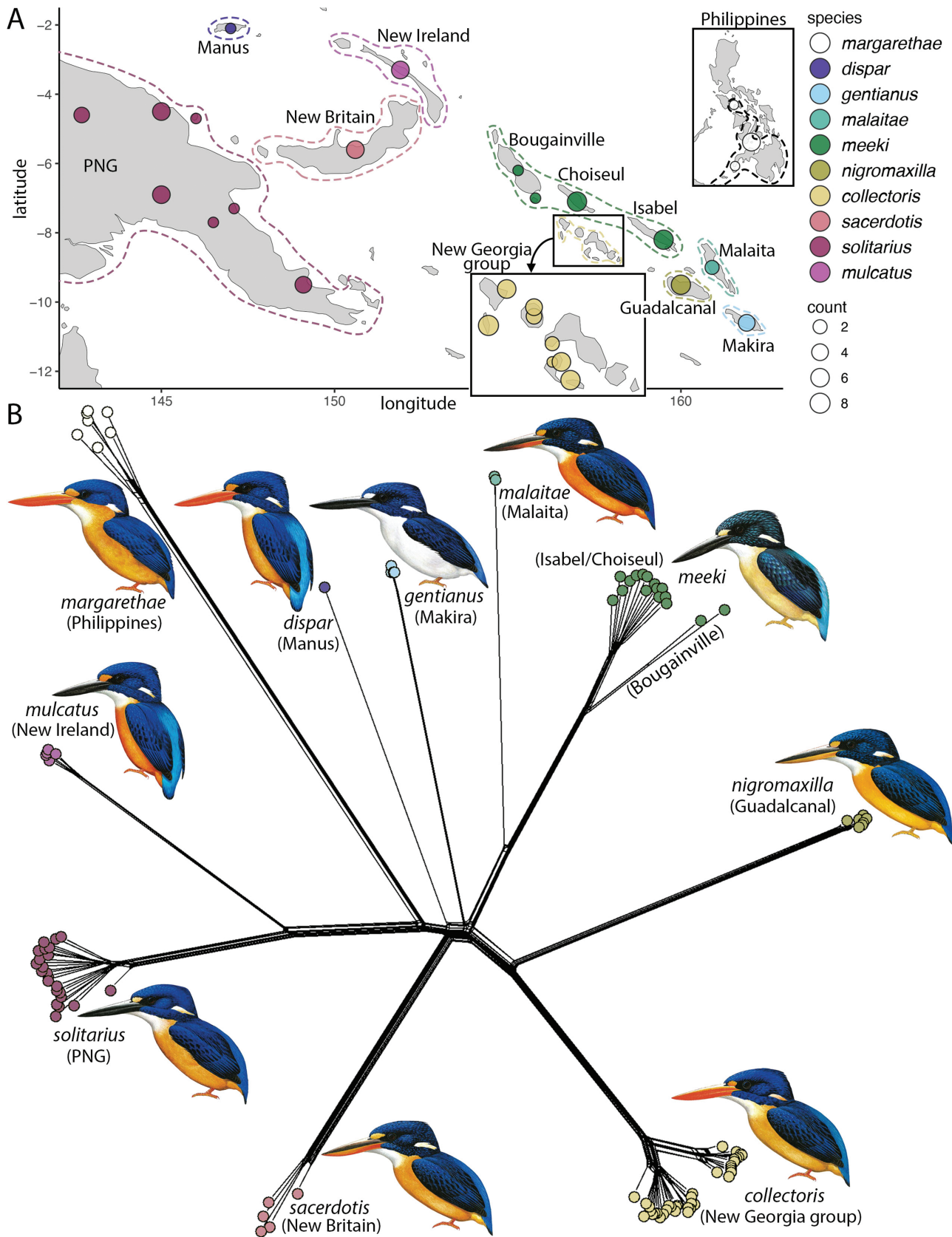
Figure 1. Sampling distributions and genetic relatedness among specimen-vouchered samples from across the range of the northern Melanesian *Ceyx* kingfishers. (A) Map showing northern Melanesia, with the range of each of the northern Melanesian *Ceyx* species outlined by a color-coded dashed line. The range of *C. solitarius* extends west across the island of New Guinea. Genomic sampling localities are shown with dots, color-coded by species and sized according to sample size in the filtered SNP dataset. (B) Unrooted phylogenetic network constructed from a pairwise genetic distance matrix using 20,831 genomic SNPs displays patterns of relatedness among all samples. Illustrations by Tim Worfolk, © Lynx Nature Books.
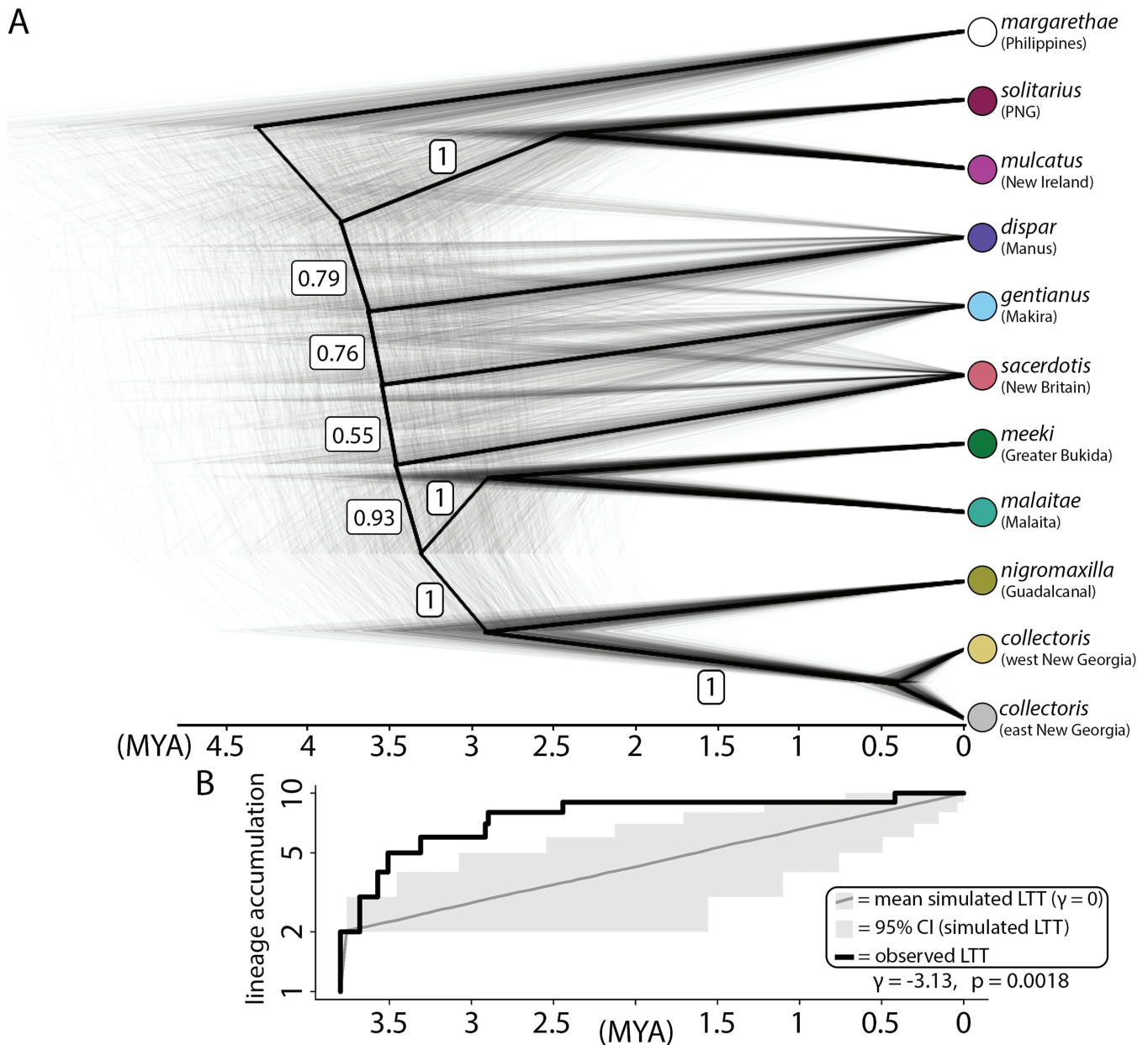
must be inferred from the deep genetic divergence and lack of gene flow we observe between island populations; hence the paradox of the great speciators. Here, we consider the implications of these results for understanding the specific evolutionary history of this group and the patterns that typify the paradox of the great speciators. We discuss the observed shift in diversification rate

Figure 2. Investigation of relatedness among all *Ceyx* samples. (A) A concatenated maximum-likelihood tree built from 2,580 loci, rooted on the outgroup *C. margarthae*, with bootstrap support values shown for key internal branches. Hash marks indicate arbitrarily shortened branches. (B) Sample ancestry assignments for all ingroup samples, plus subset runs for species displaying geographic substructure. Intraspecies clades are shown arbitrarily in gray, white, and black. For each run, an asterisk denotes the optimal K value. (C) Bathymetric map of the Solomon Islands, with putative Pleistocene land bridges (current sea levels 0–130 m) shown in dark gray.

Figure 3. Assessment of the speed and order of lineage branching among *Ceyx* species. (A) 1,500 dated species trees sampled from the posterior distribution are shown as a cloudogram. The maximum clade-credibility tree is shown on top in bold, with posterior probabilities labeled on each internal branch. Time is shown from past to present along the x-axis (MYA = millions of years ago). (B) A log-lineage through time (LTT) plot showing the accumulation of *Ceyx* lineages within northern Melanesia through time. The gray shaded area represents the 95% confidence interval for a pure-birth model ($\gamma = 0$), where lineage accumulation occurs at a log-linear rate. The negative γ value suggests an early burst of diversification, and the corresponding *p*-value represents the probability of seeing a γ value as extreme or more extreme than -3.13 given the null hypothesis of $\gamma = 0$.

(Figure 4), which supports the colonization cycle hypothesis as the most plausible explanation for the overall diversification patterns during the evolutionary history of the *Ceyx* dwarf kingfishers in northern Melanesia. We then incorporate various aspects of classic biogeographic theory with our genomic results to lay out a clear mechanistic framework predicting the paradoxical diversification patterns observed among great speciator taxa. We end with a detailed discussion of the various proximate mechanisms that may act within this framework in geographic radiations occurring in island archipelagoes across the globe.

Diversification patterns

Patterns of phylogenetic relatedness and sample ancestry assignments from this study reinforced known methodological

issues with commonly used genomic analyses. Specifically, *ADMIXTURE* failed to identify the single *C. dispar* sample as a unique population despite its unique ancestry, a known issue for allele frequency-based programs when the sample size is unbalanced between populations (Wang, 2017). In addition, our concatenated phylogenetic reconstruction recovered a different branching order than our coalescent species tree approach. This likely reflects known issues with the approach of concatenating genome-wide loci, which can generate misleading results in cases of high gene-tree discordance (Kubatko & Degnan, 2007) and anomaly zone cases (Mendes & Hahn, 2018), compared with more reliable approaches using a multispecies coalescent framework (Long & Kubatko, 2018). Ultimately, both phylogenetic reconstruction approaches used here resulted in short and poorly supported
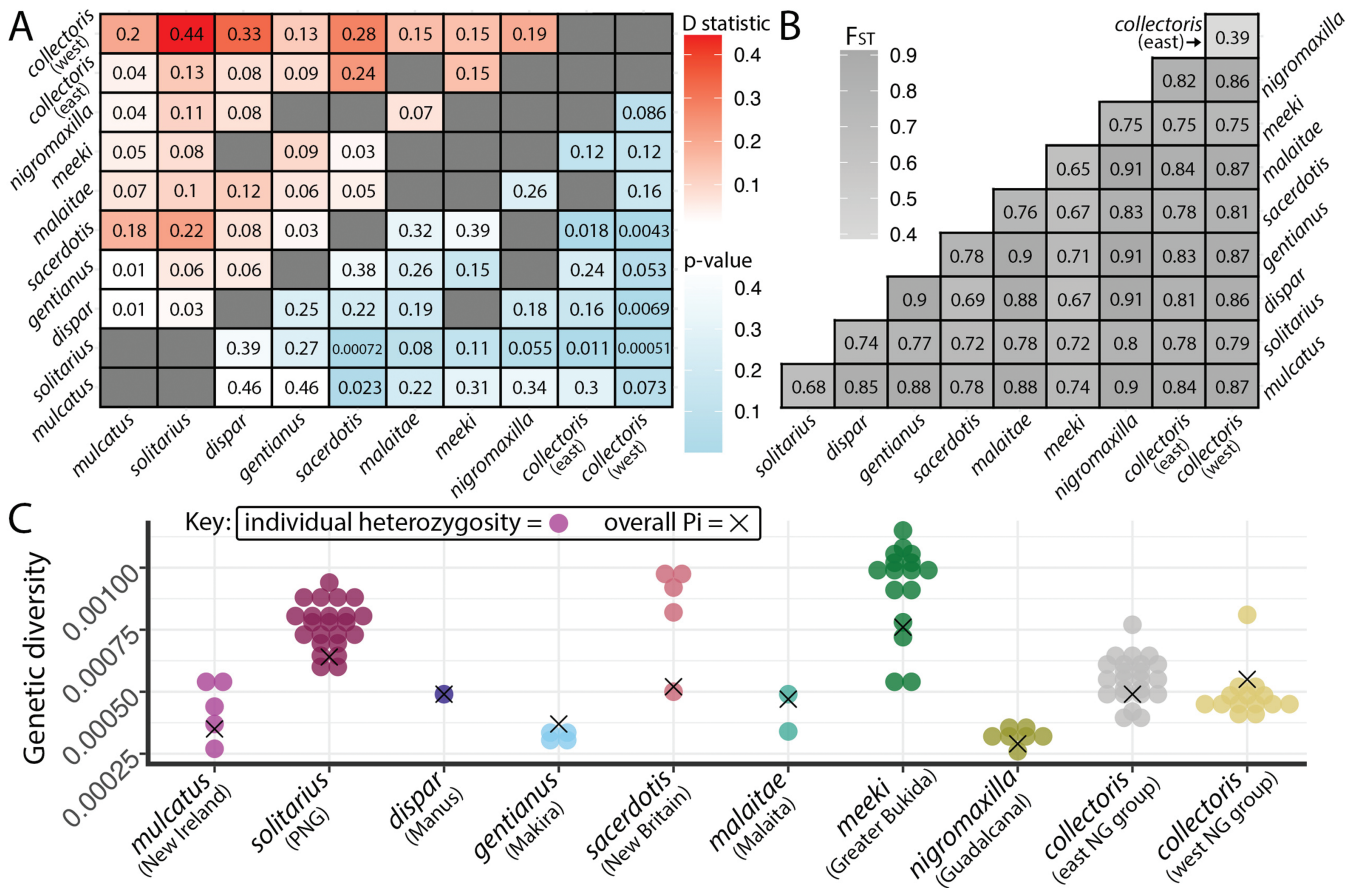
Figure 4. Assessment of gene flow, divergence, and genetic diversity. (A) *D* statistics and corresponding *p*-values are shown as a heatmap. Maximum *D* statistic values are shown for all possible comparisons above the diagonal, with the corresponding *p*-value for each cell shown below the diagonal. Gray cells indicate two lineages that cannot be compared as P2 and P3 under the requisite (((P1, P2), P3), OG) topology. No *p*-values reach the FDR adjusted significance threshold, $a = 0.0004167$. (B) Relative divergence is shown as a heatmap of pairwise F_{ST} values between all 10 ingroup lineages. (C) A dot plot comparing individual heterozygosity (colored dots) and overall genetic diversity (Pi; denoted for each lineage with a black "X"), calculated from all sites mapped to the reference genome, including invariant sites.

internal branches, similar to previously published *Ceyx* phylogenies derived from mitochondrial sequence data (Andersen et al., 2013) and thousands of ultraconserved element loci (McCullough et al., 2019).

The repeated inability to recover a single bifurcating topology that describes the branching history of the northern Melanesian *Ceyx* clade, regardless of data type or statistical approach, suggests that diversification in this clade was characterized by high levels of incomplete lineage sorting (ILS) and/or gene flow (e.g., DeRaad et al., 2023; Giarla & Esselstyn, 2015; Kutschera et al., 2014; Meyer et al., 2017). When waiting times (measured in coalescent units, i.e., generations/2N, where N = the number of individuals in a diploid population; Degnan & Rosenberg, 2006) between speciation events are short, confounding ILS topologies are expected to dominate genome-wide gene tree frequencies (Hibbins & Hahn, 2022). Our dated reconstruction lends support to a rapid burst of diversification following the arrival of *Ceyx* in northern Melanesia, creating an ideal scenario for extensive genome-wide ILS (Maddison & Knowles, 2006). Furthermore, we recovered a number of marginally significant pairwise *D* statistics, which could reflect short periods of historical gene flow following initial divergence, before reproductive isolation evolved between geographically proximate island populations, a scenario which would further muddy the signal of the true bifurcating history (Ferreira et al., 2021; Pavón-Vázquez et al., 2021). Ultimately,

future work utilizing as much genomic data as possible (e.g., Zhang et al., 2021) will be necessary to accurately resolve the single bifurcating topology that most accurately describes the evolutionary history of *Ceyx* in northern Melanesia.

A clear mechanistic framework to explain the paradox of the great speciators

By testing for a significant shift in net diversification rate through time, we constructed a framework to distinguish between two classic hypotheses purporting to explain the paradox of the great speciators. Based on the significant early burst in diversification (Burbrink et al., 2012) we observed, we can statistically reject the expectations of the intermediate dispersal hypothesis (Agnarsson et al., 2014; Venail et al., 2008), which predicts moderate, consistent diversification through time. Instead, the observed diversification patterns correspond closely to the expectations of the colonization cycle hypothesis (Diamond et al., 1976), which predicts rapid, archipelago-wide colonization during the "expanding" phase when intrinsic dispersiveness is high, followed by a low diversification rate and general stasis during the subsequent "local adaptation" and "retreating" phases, as intrinsic dispersiveness falls (Diamond, 1977). These patterns are reminiscent of the early stages of the well-studied but adjacent "taxon cycle hypothesis" (Ricklefs & Bermingham, 2002; Wilson, 1961), which seeks to explain the accumulation of diversity within islands via
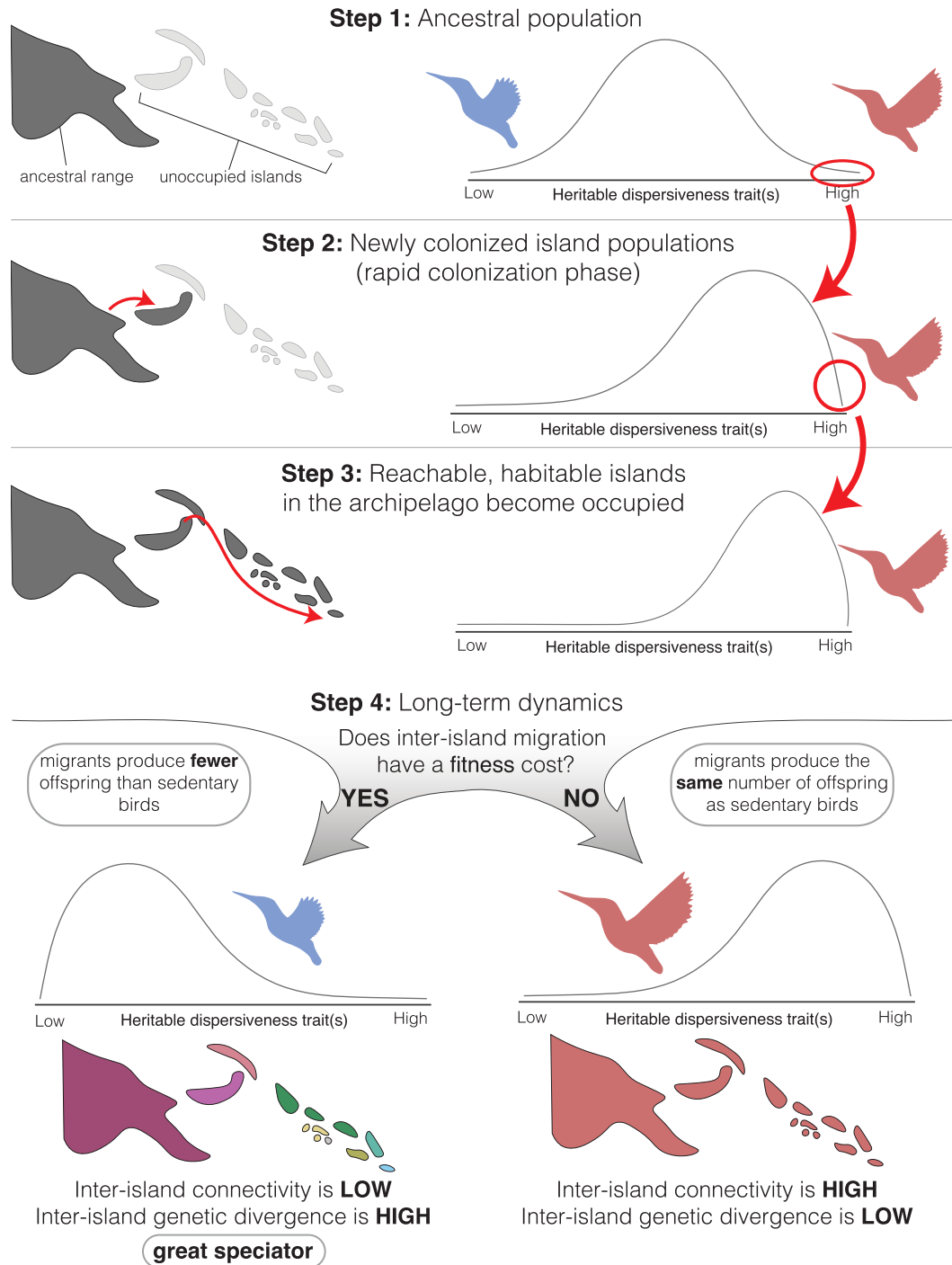
Figure 5. Graphical depiction of our proposed mechanistic framework predicting the paradox of the great speciators. The most dispersive individuals from a source population are most likely to attempt ocean dispersal, kicking off archipelago colonization with a strong founder effect where dispersive individuals are more likely to be sampled in the resulting archipelago population (step 1). This founder effect phenomenon is repeated with each subsequent stepping stone colonization event throughout the archipelago, resulting in highly dispersive island populations that could act as pumps to spur rapid, archipelago-wide colonization (step 2). Once habitable islands in the archipelago fill (step 3), the potential benefit of dispersal falls and natural selection will shift against dispersive behavior in proportion to its risk level (i.e., fitness cost; step 4). Overall, this framework outlines just two ultimate causes (repeated founder effects and a shift in natural selection pressure; the proximate mechanisms driving this shift will be idiosyncratic) required to predict the repeatedly observed diversification patterns associated with the paradox of the great speciators.

secondary contact. However, because we focus here on the process of archipelago colonization and primary diversification, we refer to this process exclusively as the colonization cycle hypothesis, as outlined most clearly by Diamond (1977).

While we find clear statistical support for diversification patterns concordant with the colonization cycle hypothesis, resolving the underlying eco-evolutionary mechanisms driving colonization cycles in great speciator lineages has presented an

enduring challenge (Engler et al., 2021; Pepke et al., 2019; Weeks & Claramunt, 2014), even as we have entered the era of big data in evolutionary genomics (Cornetti et al., 2015; Cowles & Uy, 2019; Eliason et al., 2022; Estandía et al., 2023; Manthey et al., 2020). This longstanding mechanistic unclarity dates back to the very origin of the idea, when Mayr (1942: p. 239) posited that a historical shift in the intrinsic willingness/ability to disperse over ocean barriers in great speciator lineages could explain the paradox of the great speciators, but offered no explanation for what evolutionary forces might generate this effect. Decades later, Diamond et al. (1976) formalized this notion as the "colonization cycle hypothesis." Diamond (1977) subsequently presented both an ultimate (natural selection for increased dispersiveness) and proximate (the availability of novel, accessible resources) mechanistic cause for increased dispersiveness during the broad colonization phase in great speciator lineages. Diamond (1977) also provided an ultimate (declining natural selection for dispersiveness) cause for the inferred reduction in dispersiveness at later stages in the colonization cycle, but provided no details regarding the proximate mechanisms that might cause this shift in selection pressure. Two decades later, Cody and Overton (1996) provided a compelling proximate mechanism for selection against dispersiveness, based on Darwin's "wind hypothesis" (1859), which posited that the wings of insects and birds, which initially allowed them to disperse from a continent to an island, would subsequently be lost via natural selection in isolated island populations. In specific, Cody and Overton (1996) suggested that increased mortality in dispersive individuals due to the risks of dispersal across ocean barriers would provide strong selection pressure against dispersive behavior in island populations. While all of these intellectual contributions steadily improved our understanding of the colonization cycle hypothesis, a single unified framework describing in detail how this process might work mechanistically in great speciator taxa was still lacking (although see Cody & Overton, 1996; Figure 1, which lays out details regarding the evolution of reduced dispersiveness but does not connect these concepts to the colonization cycle or the paradox of the great speciators).

Here, we integrate the decades of contributions outlined above into a single, clearly defined framework, which outlines a succinct set of ultimate causes that explain the colonization cycle hypothesis, therefore providing a mechanistic basis for the paradox of the great speciators (Figure 5). Although the ultimate causes (repeated founder effects and a shifting selection coefficient for highly dispersive genotypes) are consistent, we emphasize that the proximate mechanisms creating selection regimes will be highly system-dependent. By this, we mean that both organism-specific characteristics and geography will interact to determine the mechanisms that do (or do not) provide selection against dispersiveness once unoccupied islands become scarce. For instance, in expansive geographic regions dominated by open ocean habitat (e.g., Micronesia), the risk of mortality during oceanic dispersal events provides a plausible mechanism for selection against dispersive behavior in most taxa (Demeulenaere & Ickert-Bond, 2022). Meanwhile, in dense archipelagoes with many large islands (e.g., northern Melanesia) oceanic dispersal may be high risk for taxa that are passively dispersed via wind currents (e.g., many invertebrates and plants; Cody & Overton, 1996; Olesen & Valido, 2003) but low risk for highly vagile vertebrate taxa such as birds and bats (Gill et al., 2008; Lavery et al., 2024).

In the case of northern Melanesia's *Ceyx* dwarf kingfishers, the exact nature of the proximate mechanisms creating selection against dispersiveness cannot be revealed by genomic patterns alone. The *Ceyx* dwarf kingfishers are known as small, shy, understory specialists, which suggests that open-ocean dispersal may be uniquely challenging and risky for this lineage compared with other birds of northern Melanesia (Mayr & Diamond, 2001). Nonetheless, the modern dispersal capabilities of these birds may not accurately reflect their historical capabilities (Kennedy et al., 2016; Wright et al., 2016), especially considering that we inferred a decrease in dispersiveness during the evolutionary history of this lineage. During this group's broad colonization period, when the dispersal capabilities of *Ceyx* taxa were assumedly high (i.e., risk of mortality at sea would be low), alternate eco-evolutionary mechanisms may have played major roles in generating selection against dispersive genotypes. For instance, incumbency effects (Alroy, 1996; Rowsey et al., 2019; Schenk et al., 2013) predict that the first population arriving in an area will exclude subsequent colonizers. This exclusion can take the form of competition for resources, or the ability to behaviorally discriminate between intra-island individuals and inter-island migrants. Under our proposed framework incumbency effects could provide a key proximate mechanism beyond risk of mortality at sea, for generating selection against dispersiveness by reducing survival and fecundity after migrants successfully reach a new island (i.e., creating additional fitness costs for inter-island dispersers in steps 3 and 4; Figure 5). In cases where the inherent risk of oceanic dispersal is apparently low, as in the birds of northern Melanesia, this proximate mechanism may play a key role in shifting selection pressure against dispersive genotypes following the broad colonization of a given archipelago. Eventually, both prezygotic (e.g., mate discrimination based on plumage differences among *Ceyx* taxa; Fry et al., 1992; Woodall, 2001) and postzygotic (e.g., genetic incompatibilities; Orr & Turelli, 2001) reproductive isolating mechanisms are expected to emerge, creating obligate exclusion of inter-island migrants which will be unable to find suitable mates. At this stage, selection against inter-island migrants will be absolute unless these migrants are able to make a large niche shift to avoid competition and achieve secondary sympatry with congeners in the novel habitat (i.e., character displacement; Brown & Wilson, 1956). Based on the 3–4 million years of isolation we infer between most *Ceyx* lineages in northern Melanesia (Figure 4), we may be observing this late stage of the colonization cycle in our focal taxa.

Conclusions

Here we have presented a genomic case study in the *Ceyx* dwarf kingfishers of northern Melanesia, revealing an unusually clear example of the paradox of the great speciators. In line with recent genomic studies in other great speciator taxa (DeRaad et al., 2023; Manthey et al., 2020; Reeve et al., 2023), we find support for a rapid burst of diversification during the evolutionary history of this group that makes phylogenetic reconstruction challenging. These patterns are well explained by the colonization cycle hypothesis, which infers a shift in genetically inherited dispersiveness traits during the evolutionary history of a given group (Diamond, 1977; Diamond et al., 1976). While the mechanistic basis of this shift has remained largely inscrutable in modern empirical studies, we present a detailed framework outlining how only two expected forces—founder effects and shifting selection pressures—are required to construct a scenario that predicts the paradox of the great speciators (Figure 5). While we discuss this framework in the context of the paradox of the great speciators, we emphasize that it is broadly applicable and can explain the emergence of geographic radiations in island archipelagoes

across the globe. Importantly, we note that the proximate eco-evolutionary mechanisms that inform selection pressure on dispersiveness in each system will vary based on the life-history traits of the organism and the biogeography of the region. We also acknowledge that in some cases, inter-island migration will pose no apparent fitness cost and inter-island population connectivity will remain high indefinitely (e.g., *Chalcophaps indica*, DeRaad et al., 2022a; *Erythrura trichroa*, DeCicco et al., 2023). Ultimately, we have integrated results from the emerging bolus of empirical genomic datasets on great speciator taxa with the colonization cycle hypothesis, a classic explanation for the paradox of the great speciators. The resulting framework outlines how repeated founder effects during the rapid colonization phase will increase inherent dispersiveness until the archipelago fills, at which point the cost of dispersal may outweigh its benefit, causing natural selection to shift in the opposite direction against risky dispersive behavior. This straightforward scenario sheds new light on the mechanisms behind the paradox of the great speciators and on the emergence of geographic radiations in island archipelagoes across the globe.

Supplementary material

Supplementary material is available online at *Evolution Letters*.

Data and code availability

A detailed GitHub repository (github.com/DevonDeRaad/nmel.ceyx) holds all input files, code, and intermediate files used to create the figures presented in this manuscript. The main homepage contains detailed information and links directing the reader to all the necessary information to recreate the results presented here. This entire repository is also permanently archived via Zenodo at: (https://doi.org/10.5281/zenodo.12534731). Raw sequence data from all 135 samples sequenced for this project are available via NCBI's Sequence Read Archive, as part of the dedicated BioProject PRJNA1128088, which can be found at: (http://www.ncbi.nlm.nih.gov/bioproject/1128088).

Author contributions

L.H.D., J.M.M., T.H.L., P.H., D.P.J., I.G.T., M.J.A., R.G.M., and D.B. all contributed significant effort to securing the specimen-vouchered tissue samples that form the very basis of this study. D.A.D. and R.G.M. conceptualized and designed this study. D.A.D., L.H.D., and R.P.M. performed molecular lab work. D.A.D. and A.N.F. performed genomic data analyses. D.A.D. wrote the first draft of the manuscript. R.G.M. secured funding for genomic sequencing. All authors contributed feedback on the initial draft of this manuscript and approved the submitted version of the manuscript.

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