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**Phylogenomics of a genus of ‘Great Speciators’ reveals rampant incomplete lineage sorting,
gene flow, and mitochondrial discordance in island systems**

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14 ABSTRACT

15 The flora and fauna of island systems—especially those in the Indo-Pacific—are renowned for
16 their exceptional diversification and for shaping key evolutionary theories. Yet, phylogenetic
17 studies often undersample the full diversity of these geographic radiations. This gap stems both
18 from the challenges of collecting single-island endemics and from the poor performance of
19 degraded DNA when using museum specimens to infer evolutionary relationships. Advances in
20 generating genome-wide datasets with degraded DNA from museum samples are overcoming
21 these obstacles. Here, we leveraged whole genome resequencing (20X average coverage) and
22 extensive sampling of all taxonomic diversity within *Todiramphus* kingfishers, a rapid radiation
23 of largely island endemic ‘Great Speciators.’ We found that four types of molecular markers
24 (UCEs, BUSCOs, SNPs, and mtDNA) and tree building methods did not recover a single well-
25 supported and concordant species-level topology. Instead, we revealed pervasive incomplete
26 lineage sorting and both ancient and contemporary gene flow, processes contribute to conflicting
27 evolutionary histories. Complete taxonomic sampling uncovered a novel case of mitochondrial
28 discordance between two allopatric species, consistent with a historical (but since lost) hybrid
29 zone during successive island colonizations. Together, these results underscore how dense
30 genomic and taxonomic sampling can reveal complex evolutionary dynamics in rapid island
31 radiations.

32
33 KEYWORDS: Ancient DNA, Artefactual branch effect, incomplete lineage sorting, Indo-
34 Pacific, mitochondrial discordance, molecular phylogenetics, whole genome resequencing

Islands play an outsized role in the study of speciation of wild populations (Wallace 1881; MacArthur and Wilson 1967; Whittaker et al. 2017). Indeed, some of the most influential examples of species diversification stem from island systems. These include the adaptive radiations of Darwin’s finches in the Galapagos (Darwin 1859; Grant and Grant 2006; Lamichhaney et al. 2015), Hawaiian silverswords and honeycreepers (Baldwin and Sanderson 1998; Lerner et al. 2011; Landis et al. 2018), and Caribbean *Anolis* lizards (Mahler et al. 2010). These examples have provided substantial insights in evolutionary biology, they are unique cases in which results may not be generalizable to other groups of organisms. Conversely, many lineages have evolved equally rapidly on islands without morphological novelty or obvious adaptive consequences—hereafter referred to as geographic radiations (Rundell and Price 2009; Simões et al. 2016). As distinct from adaptive radiations, geographic radiations occur across spatially structured landscapes, such as island archipelagos, without the evolution of key innovations or obvious adaptive changes (Moyle et al. 2009; Lieberman 2012; Moen and Morlon 2014). By studying organisms that occur across island systems, researchers can more readily parse how these forces shape the evolutionary history of clades during bouts of rapid and successive speciation events.

However, the study of rapid geographic radiations across island systems is not without its challenges. For example, neutral processes like genetic drift and mutation are stronger evolutionary forces in small populations such as those found in island systems (Baum et al. 2017). Additionally, rapid and successive speciation events contribute to short internode distances that prove difficult for phylogenetic inferences (Whitfield and Lockhart 2007; Bagley et al. 2020; Roycroft et al. 2020). These events also contribute to incomplete lineage sorting (ILS), which is more frequent when successive speciation events occur at a faster rate than the

coalescence of alleles (Degnan and Salter 2005; Maddison and Knowles 2006; Scornavacca and Galtier 2017). These issues are magnified when historical samples, often sourced from clippings of museum study skins, are included in analyses (Smith et al. 2020; Ernst et al. 2022; Roycroft et al. 2022), a necessary, yet adverse, byproduct of the gaps in modern genetic sampling. As our ability to collect better genetic data from degraded source material increases, empirical studies are turning to museum specimens to include these range-restricted or rarely collected populations to broadly sample the entirety of geographic radiations.

The varied geographic radiations across the Indo-Pacific, spanning Southeast Asia to Polynesia, have shaped many core theories in ecology and evolution. These include the early foundations of biogeography (Müller 1846; Wallace 1863, 1881; Lydekker 1896), the Theory of Island Biogeography (MacArthur & Wilson, 1967), the ‘Great Speciator’ paradox (Diamond et al., 1976), taxon cycles (Wilson, 1959, 1961), and allopatric speciation (Mayr 1942, 1963). Allopatric speciation, considered to be the main mechanism of speciation, invokes geographic isolation as a prerequisite for reproductive isolation and subsequent lineage divergence. Before his work on speciation and the Biological Species concept (Dobzhansky 1937; Mayr 1940, 1942), Ernst Mayr wrote extensively on Indo-Pacific fauna during his tenure as curator of ornithology at the American Museum of Natural History. He was particularly interested in describing geographic variation based on specimens collected during the Whitney South Seas Expedition (Chapman 1935), including honeyeaters (Mayr 1932a), *Rhipidura* fantails (Mayr 1931a), *Pachycephala* whistlers (Mayr 1932b), and kingfishers (Mayr 1931b, 1935, 1941). These geographic radiations provided the empirical foundation for his influential evolutionary theories (Mayr 1940, 1942, 1963). In particular, Mayr’s studies of *Halcyon* kingfishers—now *Todiramphus* (Moyle 2006)—led him to propose the ‘superspecies’ concept (Mayr 1931b), or

what we now refer to as geographic radiations. This idea describes a taxonomic ‘grey zone’ in which insular populations diverged recently in isolation and evolved distinctive phenotypic characteristics, yet could not be recognized as separate species under the Biological Species concept, which requires evidence of reproductive isolation when in sympatry (Dobzhansky 1937; Mayr 1942, 1963; Mayr and Diamond 2001).

Shifts in species concepts and advances in molecular systematics have fundamentally reshaped the taxonomy of geographic radiations, altering how species limits and richness are estimated. Alternative views on species boundaries, such as the Generalized Lineage Species Concept (de Quieroz 1998; de Queiroz 1999), led to an increase in recognized species-level diversity within allopatric superspecies complexes. For example, there has been a sea change in the way species limits are applied to insular geographic radiations, due to the resolution of paraphyly or recognition of phylogenetically divergent lineages, including in whistlers (Andersen et al. 2014; Marki et al. 2018), thrushes (Reeve et al. 2023), pittas (Irestedt et al. 2013), Australasian robins (Kearns et al. 2016), monarch flycatchers (Andersen et al. 2015a, 2021; McCullough et al. 2021), white-eyes (Lim et al. 2019), sunbirds (Ó Marcaigh et al. 2022), and kingfishers (Andersen et al. 2013; Sin et al. 2022). Increasingly, our understanding of speciation with gene flow in these radiations has brought a more nuanced approach to species limits (Nosil 2008; Campbell et al. 2018; Gyllenhaal et al. 2020; Mapel et al. 2021).

Todiramphus kingfishers represent the most species-rich and widespread genus within its taxonomic order (Aves: Coraciiformes), distributed from the Red Sea to French Polynesia (Fig. 1). They are generalist predators, not obligate plunge-diving piscivores, as their common name suggests. The Collared Kingfisher (*Todiramphus chloris*) is among the most widespread and polytypic avian superspecies complexes in the Indo-Pacific. Andersen et al. (2015b) argued for a

revised classification based on a phylogeny that found no less than 10 species embedded within the *T. chloris* species complex, thus rendering *T. chloris* paraphyletic. Moreover, this study found that multiple instances of sympatry and obvious reproductive isolation within this group suggested that species limits within *Todiramphus*, and especially within the *T. chloris* species complex, were inadequately circumscribed.

Subsequent analyses highlighted the rapid diversification rate of *Todiramphus* kingfishers, rivaling the textbook geographic radiation of *Zosterops* white-eyes (Moyle et al. 2009; Andersen et al. 2018; McCullough et al. 2019; Lim et al. 2019). Unsurprisingly, the phylogenetic history of *Todiramphus* kingfishers has proven recalcitrant, likely owing to their high speciation rate and relative limitations of prior Sanger and reduced-representation sequencing datasets (Andersen et al. 2015b, 2018; McCullough et al. 2019). More focused work employing RADseq data, particularly assessing a major clade within the genus once considered a part of the *T. chloris* complex, has highlighted a case of mitochondrial discordance within one clade of *Todiramphus* comprising the migratory Sacred Kingfisher (*T. sanctus*), Islet Kingfisher (*T. colonus*), and Torresian Kingfisher (*T. sordidus*; DeRaad et al. 2023). However, this study found negligible levels of gene flow between these species and instead showed patterns consistent with high rates of incomplete lineage sorting.

Because of the relatively rapid timing and phylogenetic diversity in the group, *Todiramphus* kingfishers provide an opportunity to investigate how and when rapid radiations occur across the Indo-Pacific. *Todiramphus* kingfishers originated in Sahul (Australia and New Guinea; Andersen et al. 2018), having diverged from its sister taxon *Syma* approximately 10.3 Ma (McCullough et al. 2019). Since then, they dispersed eastward to French Polynesia and westward across Southeast Asia to western India and as far as the Arabian Peninsula (Fig. 1).

The genus exhibits a high degree of secondary sympatry in island systems. For example, five *Todiramphus* species can be found on Halmahera Island, Indonesia (17,780 km²; Woodall 2001), and three species can be found on the much smaller Tetepare Island, Solomon Islands (118 km²; McCullough et al. 2023). These kingfishers show marked geographic diversity, with noticeable differences in plumages and body size within the same archipelago (e.g., Cinnamon-banded Kingfisher *T. australasia* in the Lesser Sundas) or continental landmasses (Blue-black Kingfisher *T. nigrocyaneus* in New Guinea). Of the 29 currently recognized extant species of *Todiramphus* (Clements et al. 2023; Gill et al. 2024), 28 occur on islands and seven are single-island endemics (Fry et al. 1992; Woodall 2001). At the subspecific level, for which there are 93 named taxa (henceforth our use of taxa is inclusive of all subspecies and monotypic species), 70 occur only on islands and 28 are restricted to single islands (Fig. S1). Indeed, they occur on nearly every island from Southeast Asia, through Wallacea, Melanesia, Micronesia, and Polynesia—they truly are a quintessential geographic radiation.

Various studies have addressed species-level relationships at the family and ordinal levels (Moyle 2006; Andersen et al. 2018; McCullough et al. 2019) or have addressed specific clades (Andersen et al. 2015b; O’Connell et al. 2019; DeRaad et al. 2023). Yet to date, only half of the total taxonomic diversity within *Todiramphus* has been included in a phylogenetic analysis due to the lack of accessible modern tissue samples. Owing to these sampling gaps, the taxonomy and evolutionary history of *Todiramphus* kingfishers remains unresolved. In this study, we employed whole-genome resequencing of all 93 extant *Todiramphus* taxa to produce the first fully sampled phylogeny of one of Mayr’s classic examples of a geographic radiation. From whole genome resequencing data of 127 samples, we extracted four types of molecular data for phylogenetic inferences: ultraconserved elements (UCEs), single nucleotide polymorphisms

(SNPs), Benchmarking Universal Single-Copy Orthologs (BUSCOs), and mitochondrial genomes (mtDNA). In doing so, we provide the most detailed study to date on the evolution of one of the most widespread of the ‘Great Speciator’ genera. Our results reveal how incomplete lineage sorting and gene flow during a rapid radiation have contributed to phylogenetic uncertainty as well as another case of mitochondrial discordance within this complex. Together, our study highlights the complicated evolutionary history of one of the Indo-Pacific’s greatest avian radiations.

METHODS

Sampling and laboratory methods

We sampled at least one individual for all 92 extant and named *Todiramphus* taxa (Table S1). Because the number of taxa considered for each species varies widely, our species-level sampling ranged from a single sample representing the monotypic Sombre Kingfisher (*T. funebris*) to 22 samples representing all the taxa within the widespread Pacific Kingfisher (*T. sacer*). We also sampled two populations of *T. sacer* that Mayr considered as possible separate taxa but refrained from naming both as separate subspecies, from Tucopia Island, Solomon Islands and Aneityum Island, Vanuatu (Mayr 1931b). Moreover, we sampled multiple individuals for two range-restricted Beach Kingfisher taxa that exhibit various head-color morphotypes (*T. saurophagus admiralitis* and *T. s. anachoreta* which have green/blue or white color on their heads). The only *Todiramphus* species we did not sample was the extinct Mangareva Kingfisher (*T. gambieri*), whose species is represented by a single specimen collected from Mangareva Island in 1838 (Thibault and Cibois 2017). Many *Todiramphus* taxa are endemic to a few or single islands across the Indo-Pacific and are thus rarely collected, so we

relied heavily on clippings of toepads from museum study skins ($n = 76$, 59% of total sampling). All other samples were either sourced from blood ($n = 4$) or ethanol- or frozen-preserved tissue samples ($n = 47$) loaned to us from natural history collections. Our sampling scheme spans nearly one and a half centuries of collecting effort by countless collectors (1887–2019, toepads span 1887–1987). In total, we had 127 samples representing all 92 extant taxa within the genus; because of differing levels of sample quality, not all samples are present in each generated dataset (Table S1). We chose four representatives from each of the three kingfisher subfamilies as outgroups, sourced from higher-level work on genomic evolution across the family (Eliason et al. 2023). Because DNA sourced from museum study skins is known to have higher rates of degradation than high quality tissues, we treated toepad-sourced samples differently than tissue-sourced samples at all stages of wet lab work (see Appendix 2 for more details). We prepared libraries with Kapa Biosystems Hyper Prep Kit and the iTruStub dual-indexing system (baddna.org) using established protocols at the University of New Mexico. We pooled toepad- and tissue-sourced libraries separately (10–15 toepad libraries per lane and 15–16 tissue libraries per lane) and sequenced them across 12 S4 PE-150 lanes of an Illumina NovaSeq 6000 at the Oklahoma Medical Research Foundation.

Bioinformatic processing

We trimmed demultiplexed raw reads with trimmomatic v0.39 (Bolger et al. 2014) and aligned cleaned reads to a Collared Kingfisher (*T. chloris collaris*) reference genome (Eliason et al. 2022) using BWA v0.7.17 (Li and Durbin 2009) and GNU Parallel (Tange 2021). We used MarkDuplicatesSpark, implemented in GATK v4.2.6.1 (McKenna et al. 2010; Van der Auwera and O'Connor 2020), to tag and remove duplicate reads. We assessed individual genome

summary statistics (i.e., depth) with Picard v2.26.11 (Broad Institute 2019) and samtools v.1.15 (Danecek et al. 2021). We used GATK v3.8.1 to identify and realign indels (RealignerTargetCreator, IndelRealigner) to produce final BAM files for extraction of different types of molecular markers for downstream phylogenetic analyses. Because the quality of toepad-derived samples varied across the four dataset types (e.g., number of UCEs extracted or whether the mitogenome was recovered), some samples were excluded from certain datasets. As a result, the number of tips differs slightly between datasets, as shown in Table S1. We also subsetting our dataset for some computationally intensive methods that aim to assess incomplete lineage sorting and or gene flow (site concordance factors, SNaQ, and ABBA-BABA tests; discussed below).

Extraction and analysis of Ultraconserved Elements (UCEs)

We used the Phyluce v1.7.0 (Faircloth 2016); described in full at <https://github.com/faircloth-lab/phyluce>) Python package to harvest thousands of UCE loci in silico (specifically following the phyluce Tutorial III: Harvesting UCE Loci From genomes). We used samtools to convert the final BAM file to fasta and then to 2.bit format using ftoTwoBit (Kuhn et al. 2013). Next, we aligned the tetrapods UCE 5k probe set to each genome and extracted loci with 500 bp flanking regions with “phyluce_probe_slice_sequence_from_genomes”. We then followed the typical bioinformatic steps implemented in the phyluce pipeline starting from “phyluce_assembly_get_match_counts.” We aligned each locus with MAFFT (Katoh and Standley 2013) without initially trimming the ends of UCE loci, instead trimming using TrimAL v1.4.rev15 (Capella-Gutiérrez et al. 2009) with the “-automated1” flag and degenerated_DNA matrix (available at

https://github.com/inab/trimAl/blob/trimAl/dataset/matrix.Degenerated_DNA) to allow for ambiguous bases.

During preliminary phylogenetic exploration, we determined that many of the toepad-sourced samples had exceptionally long branches (see below for phylogenetic analyses and Table S1 for these samples). Biologically unrealistic long branches such as these can contribute to long-branch attraction and therefore incorrect phylogenetic relationships (Felsenstein 1978); this issue has been shown as a byproduct of poor alignment trimming contributing to “dirty ends” of UCE loci sourced from historical samples, including those sourced from avian toepads (McCormack et al. 2015; Smith et al. 2020; Salter et al. 2022). We removed these artefactual “dirty ends” following the bioinformatic pipeline by Smith et al. (2020; see Appendix 2 and Table S2 for further information). Our final UCE dataset was a 90% complete matrix comprising multiple individuals for some taxa that had at least 105 of 117 samples present at each UCE locus (Table S3).

We used multispecies coalescent tree (MSC) and concatenated maximum likelihood (ML) methods to analyze UCE datasets. Because gene tree histories could conflict with the overall species tree, we used two species tree methods that account for gene tree heterogeneity (Kubatko and Knowles 2023). First, we used SVDQuartets (Chifman and Kubatko 2014) implemented in PAUP* v4.0a168 (Swofford 2003); this quartet-based method uses a concatenated alignment and site pattern frequencies of splits to estimate a species tree and has been shown to perform well for large multilocus datasets (Wascher and Kubatko 2021). To decrease computation time in PAUP*, we split up the 117-sample, 90% complete matrix into two, overlapping subsets of taxa (each with 69 samples). We split up the dataset in two sections with sampling focused on including all the representatives of the two major clades within

Todiramphus (outlined below, the ‘Oceanic Clade’ and the ‘Australasian Clade’) and balancing complete sampling for the other species complexes between datasets. For each subset, we analyzed all possible quartets and assessed support with 100 bootstrap support. Next, we used the summary-statistic method ASTRAL-III v.1.15.2.4 (Zhang et al. 2018; Rabiee et al. 2019) to estimate the species tree. This summary-statistic MSC method is sensitive to fragmentary data and depends on high quality gene trees (Mirarab 2023). Initial ASTRAL analyses inferred a clear artifactual pattern in which the toepad samples clustered at the base of clades to the exclusion of tissue-sourced genomes (Fig. S2), a known issue for ASTRAL that is caused by poor quality and/or uninformative gene trees (Mirarab 2023) and the inclusion of DNA from degraded sources (Smith et al. 2020). Therefore, we imposed different per-sample and per-locus filtering thresholds of our UCE loci (See Appendix 2 for more information on filtering steps). We first filtered individual samples from locus-specific alignments in the 90% complete matrix, dropping any sample from an alignment that contained both more than 25% of ambiguous nucleotides (N) and 70% of gaps. Next, we did model selection and inferred gene trees using IQ-TREE v2.1.4 (Chernomor et al. 2016; Minh et al. 2020b) and assessed support with 1,000 ultrafast bootstraps. From the resultant gene trees, we imposed two locus-filtering thresholds based on parsimony informative (PI) sites: one of >50 PI sites (resulting in 1,583 gene trees for ASTRAL analysis) and a second of >100 PI sites (125 gene trees; see Appendix 2 for more details). For ASTRAL, we increased the number of searches (-r) and subsampling (-s) from the default of 4 to 8. To estimate a concatenated ML phylogeny of the 90% complete matrix, we used RaxML-NG v1.2.0 (Kozlov et al. 2019), assuming a general time-reversible model of nucleotide substitution and gamma-distributed rates among all sites (GTR+G; Abadi et al. 2019) and evaluated support with the autoMRE function (set to 1000 BS). Finally, we inferred a partitioned maximum likelihood

phylogeny with IQ-TREE 2.1.4 (Chernomor et al. 2016; Minh et al. 2020b), automatically applying best-fit models selected by ModelFinder to partitions, and assessing support with 1,000 replicates of Ultrafast bootstraps (Hoang et al. 2018).

Processing and analysis of single-copy orthologous loci (BUSCOs)

Because of their evolutionary stability, single-copy orthologous genes (Benchmarking Universal Single-Copy Orthologs, BUSCOs; Simão et al. 2015) have been shown to be reliable molecular markers at both deep and shallow timescales (Waterhouse et al. 2018; Timilsena et al. 2022; Alaei Kakhki et al. 2023). Prior to extracting thousands of BUSCO loci for phylogenetic inference, we masked low coverage sites from the final BAM files. Generally, we calculated read depths with mosdepth 0.3.3 (Pedersen and Quinlan 2017), generated consensus sequences with bcftools 1.19 (Li 2011; Danecek and McCarthy 2017) implemented in a custom function in R 4.3.2 (R Development Core Team 2013) and used bedtools v2.31.1 (Quinlan and Hall 2010) to mask sites with less than five reads. We extracted thousands of BUSCO loci from the genomes using BUSCO 5.4.6 (Manni et al. 2021a, 2021b). During initial phylogenomic analysis, it became clear that extracting these data from the lower coverage toepad genomes yielded problematic alignments that contributed to an artificial pattern in which these low coverage toepad genomes grouped together rather than within the clades that matched those inferred with SNP and UCE datasets (Fig. S3). Because all of these data are aligned to the same reference, we instead ran BUSCO on the high quality *T. chloris collaris* reference genome and used BED coordinates of 8,337 BUSCO loci to extract these same regions from all of our samples. To do so, we converted the metaeuk output for our reference sample to gff3 coordinate format using the python script MetaeukToGff.py (<https://github.com/Andy-B-123/MetaeukToGff3>). With

GFFread v0.12.8 (Pertea and Pertea 2020), we extracted individual genes in amino acid (AA) format from all samples. We created locus-specific files with faSomeRecords (Kuhn et al. 2013) and removed short duplicates within loci with keep-longest.py (<https://gist.github.com/mkweskin/8869358>). Because all loci—regardless of whether adequate coverage of sequence data is present—are extracted based on this approach, we filtered out loci that were entirely composed of missing data or invariant sites as well as those that did not have PI sites to produce a matrix of 8,012 BUSCO loci for 109 samples.

To determine whether estimates of phylogeny based on protein-coding loci resemble those based on UCEs and SNPs, we also inferred phylogenies for the BUSCO loci with MSC and ML methods. Like how we treated UCE data, we performed additional steps to filter BUSCO loci for MSC analyses in order to produce high quality gene trees as input into ASTRAL. Though every sample in our dataset was present at each of these loci regardless of presence of data, many toepad samples were largely composed of unidentified amino acids (represented by the ambiguity code ‘X’). Therefore, we dropped individual samples from BUSCO alignments if 50% or more consisted of X’s using the custom python scripts (drop_fasta_X.py; available GitHub, see Data Availability section). We then did model selection for those within the Q.bird matrix, automatically applying best-fit models selected by ModelFinder, and inferred gene trees using IQ-TREE 2.1.4 and assessed support with 1,000 ultrafast bootstraps (See Appendix 2 for more information on per-sample and per-locus filtering steps). In a similar fashion as the UCE datasets, we filtered BUSCO gene trees by the number of PI sites in alignments. With a threshold of 20 PI AA sites (4,177 gene trees), a similar artefactual pattern of toepad-sourced samples cluster was apparent (Fig. S4) that disappeared with a threshold of 100 PI AA sites (470 gene trees). This effect was likely due to the removal of

shorter, less informative alignments. We increased the number of searches (-r) and subsampling (-s) to 8 for each ASTRAL analysis. Next, we inferred a maximum likelihood phylogeny for the full concatenated matrix of 8,012 loci with IQ-TREE v2.1.4, with best-fit models selected by ModelFinder, and assessed support with 1,000 ultrafast bootstraps. During model selection prior to tree inference, we confined substitution models to the Q.bird matrix and did not allow for partition merging or site-specific rate matrices (Chernomor et al. 2016; Kalyaanamoorthy et al. 2017; Minh et al. 2021).

Processing and analysis of Single Nucleotide Polymorphisms (SNPs)

We performed variant discovery and genotyping on realigned BAM files with UnifiedGenotyper in GATK 3 using a scatter-gather approach. Recent work has shown that the results of this program are comparable to HaplotypeCaller in GATK 4 and ANGSD (Korneliussen et al. 2014) for non-model organisms (Aguillon et al. 2021). With VCFtools, we initially filtered SNPs that were successfully genotyped in at least 90% of samples, had a minimum quality score of 30, minimum depth of 3, and a minor allele count of 3. Because toepad-sourced samples had significantly higher missing data, we removed samples that were missing at 55% or more sites in this initial dataset. This only affected poorly sequenced toepad-sourced samples in which we had several representatives per taxon. One sample of *T. n. nigrocyaneus* (AMNH 301866) fell marginally below this threshold, but since it had less missing data than our other *T. n. nigrocyaneus* sample, thus we still included it in the final VCF file (see Table S1). After dropping these six toepad samples, we then produced a SNP dataset in which all samples were successfully genotyped at all sites, as well as only keeping bi-allelic SNPs every 5,000 bp. Our final dataset comprised 85,156 SNPs from 119 samples representing all *Todiramphus* taxa.

Additionally, we calculated genome wide heterozygosity with pixy v1.2.10 (Korunes and Samuk 2021). We estimated average per-site heterozygosity (π) across 50 Kb windows from an all sites VCF. We calculated genome-wide π as the sum of pairwise differences between genotypes (count_diffs) across all windows divided by the sum of all non-missing pairwise comparisons (count_comparisons).

We implemented three different ML, MSC, and distance-based network methods for tree building using SNP data. First, we converted the VCF file to nexus format with nucleotide data using the ruby script convert_vcf_to_nexus.rb (available on Dryad). We used this alignment for ML inference in IQ-TREE, correcting for ascertainment bias (+ASC) to limit branch length overestimations and assessed support with 1,000 ultrafast BS replicates. Second, we analyzed the SNP alignment using all possible quartets with SVDQuartets and assessed support with 1,000 BS replicates. Third, we generated a phylogenetic network to visualize the genetic distances between all samples. We used R package StAMPP v1.6.3 (Pembleton et al. 2013; R Development Core Team 2013) to calculate Nei's D (Nei 1972) to quantify pairwise genetic divergence as input into SplitsTree4 v4.18.13 (Bryant and Moulton 2004; Huson and Bryant 2006) to produce a Neighbor-Net phylogram.

Extraction and analysis of mitochondrial genomes

We generated mitogenomes by mapping the trimmomatic cleaned reads to a reference mitogenome of *T. sanctus vagans* (GenBank: NC011712, (Pratt et al. 2009) using the singularity version of Mitofinder V1.4.1 (Allio et al. 2020). We checked these alignments by eye for incorrect internal stop codons and dropped spurious samples from gene alignments if initial phylogenetic analyses inferred them as outside of crown *Todiramphus* (suggesting an incorrectly

mapped NUMT sequence rather than true mitochondrial DNA; (Nacer and Raposo do Amaral 2017). We used IQ-TREE v2.2.2.6 to infer a partitioned maximum likelihood phylogeny of the 12 mtDNA genes, with best-fit models selected by ModelFinder (all were GTR+F), and assessed support with 1,000 ultrafast BS replicates.

Tests for incomplete lineage sorting and gene flow

To test for incomplete lineage sorting, we calculated gene and site concordance (gCFs and sCFs) factors for the BUSCO and 90% complete UCE matrix trees inferred with IQ-TREE. gCFs and sCFs provide complementary measures of topological support by quantifying the degree of discordance between gene trees and species tree in phylogenomic datasets. To focus on higher-level relationships within *Todiramphus*, we reduced each dataset to a subset of 34 tips. This allowed us to lower our conservative parsimony-informative (PI) thresholds, as these reduced datasets contained substantially fewer toepad samples, which typically contribute to lower-quality gene trees. To calculate gCFs, we used the more informative gene trees produced for ASTRAL with the superfluous tips not included in our 34-tip subset dropped ad hoc. We calculated cGFs from UCE-based gene trees inferred with >50 PIsites (1,583 gene trees) and BUSCO-based gene trees with >20 PI AA sites (4,155 gene trees). We calculated sCFs, using the ML implementation with --scfl flag (Minh et al. 2020a; Mo et al. 2023), from the pared down concatenated alignments.

We estimated the phylogenetic network for the UCE gene tree dataset (1,583 gene trees) with Species Networks applying Quartets (SNaQ; Solís-Lemus and Ané 2016) implemented in the *PhyloNetworks* package (Solís-Lemus et al. 2017) in Julia 1.11.3 (Bezanson et al. 2017). SNaQ is a maximum pseudolikelihood and coalescent approach that allows for reticulation

events. Using quartet concordance factors (Baum 2007), SNaQ estimates a species network with reticulation events and γ -values (inheritance probabilities of ancestral contributions to hybridization events). We counted quartets and calculated concordance factors (CFs) with the ‘countquartetsintrees’. SNaQ is computationally limited by number of tips in a tree and our initial 34-tip UCE gene tree dataset (discussed in the above paragraph) was too computationally intensive to analyze together, a similar problem faced by other recent empirical studies (Myers et al. 2024). Instead, we downsampled our CF set of four taxon trees to only include quartets for 19 tissue-sourced samples that represent the major clades of *Todiramphus* (3,876 total quartets). With the ML UCE (Fig. 1A) as the starting topology, we estimated the best network for a range of allowed hybridization events ($h_m = 0-7$) in SNaQ, with each analysis performing 10 independent runs (runs=10). We compared pseudolikelihood scores between each of the best networks found for each analysis (Table S4).

Mitochondrial data revealed discordant topologies for some *T. sacer* taxa and *T. colonus* and *T. sordidus* (discussed in detail in the Results section); to specifically test for gene flow between non-sister taxa, we used Dsuite v0.5 (Malinsky et al. 2021) to perform four-taxon ABBA-BABA tests. We used our 119-sample filtered SNP dataset, in which each sample was present at a given site and each SNP was at least 5,000 bp apart (85,156 SNPs) as input and used the *Dtrios* module for block Jackknifing of 20 SNP windows across the genome (4,256 SNPs per window) to calculate D and f_4 -ratio statistics (Durand et al. 2011; Patterson et al. 2012) for every possible quartet topology. We analyzed two different datasets: 1) a species-level dataset in which all subspecific taxa were lumped into their respective species’ tip, except for *T. sacer regina* (as it was not monophyletic with the rest of *T. sacer*; see Results) and 2) the same as #1 but pared down for fewer species and the treatment of five *T. sacer* taxa that were recovered within the

mitochondrial *T. sanctus* clade as separate tips: *T. sacer vicina* and four microendemics of Temotu Province, Solomon Islands, *T. s. regina*, *vicina*, *ornatus*, *utupuae*, and *brachyurus*. The remaining *T. sacer* taxa were grouped within a “Polynesian” and “Melanesian” tip based on the two clades recovered in the UCE IQ-TREE topology (Fig. 1). We incorporated a false discovery rate (FDR)-adjusted statistical significance threshold (Benjamini and Hochberg 1995), which is recommended by the developer when running more than one trio (Malinsky et al. 2021). Our FDR-adjusted *p*-threshold was 0.0000137 (3,654 pairwise tests for 29 tips in both datasets).

RESULTS

The average coverage of assembled genomes was 20X with differences between toepad (*n* = 66, average depth 10X with range of 4.6–27.9X) and tissue-sourced genomes (*n* = 47, average depth 34.8X, 11.9–98X; Table S1, Fig. S5). Tissue-sourced genomes were relatively complete, with an average 96.2% (standard deviation $\pm 0.72\%$) of the 8,338 single-copy BUSCO loci (Table S5, Figs. S6–7). Toepad-sourced genomes, on the other hand, averaged $55.9 \pm 33.7\%$ single-copy BUSCO loci, increasing to 88% (65–100%) in those with more than 10X coverage. Average depth for toepad-sourced genomes did not negatively scale with collection date; perhaps not surprisingly, the relative data quality from the datasets extracted from these genomes did scale with average depth (Fig. S7). Heterozygosity estimates from Pixy averaged lower for toepad-sourced than tissue-sourced samples (Tables S6–7, Fig. S8). Ten of the 127 genomes produced for this project, all sourced from toepad material, were not high enough in coverage to produce adequate data for inclusion in all the four genetic datasets (we highlight in which datasets samples were present in Table S1).

We extracted several datasets with varying numbers of samples for UCE, BUSCO, SNP, and mtDNA data (Table S3). Our 90% complete UCE matrix with 117 samples comprised 4,942 loci and 4,531,264 bp. Our BUSCO datasets, differing based on thresholds of within-locus PI AA sites, comprised 8,012 (>20 PI sites per locus threshold, total length 5,102,241 AA sites) with 108 samples. Our 100% complete SNP dataset, with one SNP per 5 kb, comprised 85,156 SNPs for 119 samples. We recovered complete or partial mitochondrial genomes for 111 samples.

Topological conflict between nuclear data types and tree-building methods

The backbone of the *Todiramphus* tree is characterized by many short internodes, suggesting rapid and successive speciation events early in the evolution of this group. We found phylogenetic conflict between datasets and methods due, in part, to these short internodes. When just considering species-level relationships, we did not find a single well-resolved topology that matched across any two datasets or tree-building methods (Fig. 2). The oldest divergences of the tree rarely varied across analyses, with Blue-black Kingfisher (*T. nigrocyaneus*), Rufous-lored Kingfisher (*T. winchelli*), and Sombre Kingfisher (*T. funebris*), respectively. Only in one analysis did we find *T. winchelli* fully supported as sister to all other *Todiramphus* instead of *T. nigrocyaneus* (UCE SVDQuartets tree; Fig. S9). We found conflicting phylogenetic signals for the next major divergence (Fig. 2), as we either recovered: 1) the Australian endemic Rufous-backed Kingfisher (*T. pyrrhopygius*; Figs. S10–11), 2) a small clade of four species as the next branch (referred to as the “*leucopygius* clade”; Figs. 1, S12–19), or 3) *T. pyrrhopygius* sister to the *leucopygius* clade (Fig. S9). Gene and site concordance factors for the UCE and BUSCO IQ-TREE-inferred topologies revealed that both datatypes strongly favored conflicting topologies:

76% of 1,583 best UCE gene trees and 59% of concatenated UCE alignment (4,531,264 bp in length) favored *T. pyrrhopygius* + (*leucopygius* clade + all other *Todiramphus*) topology whereas a similar percentage of the significantly larger BUSCO dataset (4,155 gene trees and 5,102,241 AA sites) favored the topology of the *leucopygius* clade + (*T. pyrrhopygius* + all other *Todiramphus*; Fig. 3). The Lesser Sundas endemic species, Cinnamon-banded Kingfisher (*T. australasia*) was always supported as sister to the clade comprising the bulk of diversity within the genus: the Vanuatu Kingfisher (*T. farquhari*) and all other species. We consistently found support for two major clades within *Todiramphus*: 1) an entirely oceanic island clade and 2) an Australasian clade (Fig. 1). We hereafter refer to these as the “Oceanic clade” and the “Australasian clade” even though some taxa within the Australasian clade also inhabit oceanic islands.

Within the Oceanic clade, we found support for three subclades: 1) a subclade of two microendemics in Micronesia, the Palau Kingfisher (*T. pelewensis*) and the extinct-in-the-wild Guam Kingfisher (*T. cinnamominus*), 2) a subclade of eastern Polynesian species (referred to hereafter as such, comprising *T. veneratus*, *T. gertrudae*, *T. tutus* etc.), and 3) a subclade comprising Flat-billed Kingfisher (*T. recurvirostris*), Pohnpei Kingfisher (*T. reichenbachii*), and *T. sacer* (i.e., the “*sacer* clade”) sister to the Polynesian subclade. The relationships between these subclades were largely consistent, even though sCF of the relationship between the east Polynesian clade and the *sacer* clade showed that alternative topologies were favored at nearly the same proportion as the inferred topologies for both BUSCO and UCE datasets (Fig. 3). However, most of the discordance between analyses and data types were mostly restricted to whether *T. recurvirostris* and *T. sacer regina* diverged earlier than *T. reichenbachii* and crown *T. sacer* (supported by UCE data; Figs. S9–12, 16) or not (supported by SNP and BUSCO data;

Figs. S14–15, 17). Whereas the placement of *T. sacer regina* (Wallis and Futuna), represented by two toepad-sourced genomes (6.8 and 14.5 average coverage), varied between different clades across analyses, we never inferred a topology in which *T. sacer regina* was within crown *T. sacer*. UCE ML analyses instead found *T. s. regina* sandwiched between two other microendemic species in a ladderized branching pattern: *T. recurvirostris* (Samoa), *T. s. regina*, and *T. reichenbachii* (Pohnpei I.; Figs. S1, S10–11). With some support, we also found *T. s. regina*: 1) sister to *T. recurvirostris* (Fig. S9), 2) branching prior to *T. recurvirostris* (Fig. S16), 3) as sister to the rest of the Oceanic clade (Fig. S15), or 4) as sister to the *T. sanctus* complex (Fig. S17). The unrooted network placed *T. sacer regina* as similarly distant from *T. sacer* as *T. recurvirostris* (Figs. 1C; S18).

Within the Australasian clade, eight species formed four subclades: three species complexes (Sacred Kingfisher *T. sanctus*, Torresian Kingfisher *T. sordidus*, and Collared Kingfisher *T. chloris*) and a clade comprising the largely oceanic island species (Islet Kingfisher *T. colonus*, Mariana Kingfisher *T. albicilla*, Beach Kingfisher *T. saurophagus*, and Melanesian Kingfisher *T. tristrami*). *Todiramphus sanctus*, one the few migratory species in the genus (though four of five subspecies are sedentary and endemic to Pacific Islands), was supported as the sister to all other taxa in the Australasian clade. Across the nuclear datasets, most of the species-level discordance between analyses centered on the second branch within the clade: whether it was *T. sordidus* (Figs. S9B, 15), *T. chloris* (Fig. S8A), a sister relationship between the two (Figs. S11, 17), or so poorly supported we considered it a polytomy with the *colonus* clade (Figs. S10, 12–14, 16).

Mitochondrial discordance and new cases of mtDNA discordance within Todiramphus

Compared to nuclear DNA, the mitochondrial data revealed a different picture of the evolutionary history of *Todiramphus* kingfishers in three major ways (Figs. 4, S20). First, the mtDNA-inferred topology matched the ML UCE data in which *pyrrhopygius* diverges prior to the “*leucopygius*” clade (Figs. S10–11, 19). Second, it was the only dataset to show the eastern Polynesian clade (i.e., *T. veneratus* et al.) sister to the rest of the Oceanic clade and Australasian clade. Third, it was the only phylogeny to recover a significantly different topology from all nuclear datasets: *T. colonus* sister to *T. sanctus* and *T. sordidus*. This relationship has been highlighted before (DeRaad et al. 2023) and was therefore expected. However, we recovered a strongly supported topology of five *T. sacer* taxa embedded within the *T. sanctus* clade, most closely associated with the migratory taxon *T. s. sanctus* and sedentary *T. sanctus macmillani* (endemic to Loyalty Islands, NE of New Caledonia). This group of *T. sacer* taxa with *T. sanctus* mitochondrial DNA included *T. sacer regina* and four allopatric microendemics of Temotu Province of Solomon Islands (*T. sacer ornatus*, *vicina*, *brachyurus*, and *utupuae*). Apart from our inability to determine the relationship of *T. s. regina* with nuclear data, these four other Temotu *T. sacer* taxa were either supported as sequentially diverging lineages sister to all other *T. sacer* (Figs. S10–11, 15–17) or had equivocal support values deeper in the *sacer* complex (Figs. S12, 15–16) across nuclear datasets. In the unrooted network, three of these five taxa were inferred to be independent lineages on par with splits shown in other species-level taxa (i.e., *T. recurvirostris* and *T. reichenbachii*; Figs. 1C, S18). We had sequenced multiple individuals of all these taxa ($n = 2\text{--}3$ samples) to confirm their curious placement as sequentially branching at the base of the *T. sacer* complex. Yet, we did not find that all individuals of each taxon had *T. sanctus* mtDNA: *T. sacer ornatus* and *T. sacer vicina* had at least one individual in *T. sanctus*

and *T. sacer* clades, whereas all samples for *T. sacer brachyurus*, *regina*, and *utupuae* were recovered within *T. sanctus*.

Patterns of gene flow

ABBA-BABA tests uncovered biologically plausible scenarios of gene flow across both subsets of data (species-level dataset and the pared down dataset to investigate gene flow between *T. sanctus* and *T. sacer* taxa that have *T. sanctus* mtDNA). Of the 3,544 calculated D-statistics, 858 and 887, respectively, were significant with a FDR-adjusted p value <0.000013 . The results show complex patterns highlighting gene flow between *T. sanctus* and mitochondrially discordant lineages, with elevated F4 ratios between *T. sanctus* and *T. colonus* ($F4 = 0.34$), *T. sordidus* ($F4 = 0.31$), *T. s. regina* ($F4 = 0.34$), and the four Temotu *T. sacer* taxa (range of $F4 = 0.12$ – 0.33 ; Figs. S20–21). Though the highest F4 ratios in the pared down dataset are between *T. sacer ornatus* and the Polynesian ($F4 = 0.51$) and Melanesian ($F4 = 0.66$) clades of *T. sacer*. With conservative interpretations of these tests by considering the lowest D values between multiple comparisons ($D_{\min}$), we still see moderate signals of gene flow between *T. sacer regina* and *T. sanctus* ($D_{\min} = 0.13$) and *T. sacer* (0.16) in the species-level dataset (Fig. S22). When *T. sacer* taxa that have *T. sanctus* mtDNA are treated as their own tips, we see statistically significant signatures of gene flow between *T. sanctus* and *T. sacer brachyurus* ($D_{\min} = 0.08$; Fig. S20) and between *T. sacer brachyurus* and *T. sacer ornatus* ($D_{\min} = 0.27$). Long swaths of statistically significant and high D-statistic values for every species comparison, such as those shown for *T. colonus*, members of the *leucopygius* and east Polynesian clades (Fig. S22), could reflect either ancient introgression (Fig. S19), incorrect topology, or substitution rate variation

caused by bottlenecked populations (see Table S7 for heterozygosity estimates; Frankel and Ané 2023; Koppetsch et al. 2024).

Network analyses with SNaQ also confirm the presence of hybrid lineages across *Todiramphus* and may explain topological discordance across datasets. The best network was one with four reticulation events and a topology different from its starting tree (UCE ML IQ-TREE), instead matching the BUSCO ML topology (Figs. 2, S19). When we allowed for more reticulation events (i.e., higher values of $h_{\max}$), pseudolikelihood scores did not measurably improve (Table S4) and the best networks for these analyses still only inferred the same four reticulation events with minor differences in γ -values (results not shown). Importantly, these four reticulation events associated with extinct lineages in areas of the tree that were discordant across other tree building analyses. These events had inheritance probabilities of ancestral contributions to hybridization events ranging from ~1–30% (Figs. 2, S19), suggesting that this unaccounted introgression led, in part, to the topological discordance of the strictly bifurcating phylogenies inferred across datasets and methods. The potential introgression event with the highest γ -value was between a ghost lineage sister to *T. australasia* into the ancestor of the *leucopygius* clade ($\gamma = 0.3$), which could have been a contributing factor for the erratic placement of *T. pyrrhopygius* across tree building analyses. We inferred potential reticulation between a ghost lineage closely associated with *T. tutus* (representing a subclade the eastern Polynesian species inclusive of *T. veneratus* and *T. gertrudae*; $\gamma = 0.25$). Additionally, we inferred two potential reticulation events within the Australasian clade: one from a ghost lineage sister to *T. albicilla* and *T. saurophagus* into *T. chloris* ($\gamma = 0.21$) and from a ghost lineage sister to one of the peripheral island isolates of the migratory *T. sanctus* (*canacorum*, $\gamma = 0.01$).

Relationships within species complexes

We found several cases in which *Todiramphus* species complexes do not accurately reflect taxonomic groupings. First, we found that the Talaud Kingfisher (*T. enigma*, endemic to the Talaud islands between Sulawesi and the Philippines), is consistently recovered within the Collared Kingfisher (*T. chloris*) clade. It was most frequently supported as sister to nominate *T. chloris* (*T. c. chloris*, endemic to Wallacea; Figs. 1, 4, S1, S9, S14, S17). Additionally, we consistently found that the two most northern taxa of the *T. sacer* complex, *T. sacer pavuvu* (Pavuvu I.) and *T. sacer mala* (Malita I.) of the central Solomon Islands, were embedded within *T. tristrami* and closely associated with their geographically closest neighbor, *T. tristrami alberti* (main chain of the Solomons Archipelago). We found that the two unnamed *T. sacer* taxa, those from Tucopia Island in the Temotu Province of the Solomon Islands and Anietyum Island in southern Vanuatu, did not group with their assumed subspecific assignment. We never recovered a sister relationship between samples from Tucopia and representatives from its long-assumed subspecies, *T. sacer torresianus*, or between samples from Anietyum and its presumed subspecies, *T. sacer erromangae* (Mayr 1931; Gill et al. 2024; Peters 1945).

DISCUSSION

As we can efficiently sequence larger and more thoroughly sampled phylogenomic datasets, it is increasingly clear that the evolutionary histories of rapid radiations are complex (Jarvis et al. 2014; Prum et al. 2015; Malinsky et al. 2018; Zink and Vázquez-Miranda 2019; Rota et al. 2022; Mirarab et al. 2024; Stiller et al. 2024, Berv et al. 2021). Here, we show that whole genome resequencing of a thoroughly sampled taxonomic dataset of all described forms of a genus of ‘Great Speciators’ has revealed evidence of pervasive gene flow that occurred throughout its

rapid radiation. We inferred deep reticulation events as well as more shallow cases of gene flow between both sympatric (*T. sanctus* and *T. sordidus*) and allopatric species (*T. sanctus* and *T. sacer*; Figs. 4, S19–23). This inferred gene flow, in concert with many rapid speciation events that precluded gene coalescence and may explain the topological discordance across the four data types used in this study (UCEs, BUSCOs, SNPs, and mtDNA).

Our results confirm past work showing mitochondrial discordance in the Australasian *Todiramphus* clade (DeRaad et al. 2023) and reveal novel signatures of gene flow with a larger and more comprehensive dataset (Figs. S20–23). Moreover, we uncovered new cases of mitochondrial discordance (Fig. 4) between *T. sanctus* and several *T. sacer* populations that nuclear data inferred as some of the earliest branches within *T. sacer*. Though our limited sampling of a single individual for most taxa precluded us from more detailed population-level analyses, we found signatures of gene flow between *T. sanctus* and *T. sacer* that have *T. sanctus* mtDNA (Figs. S20–23). Our inference of these hybrid *T. sacer* as a series sequentially branching and divergent lineages sister to other *T. sacer* likely does not reflect the true evolutionary relationships of these taxa but instead suggests that they follow the ‘artefactual branch effect’ (Chan et al. 2020b, 2023; Pyron et al. 2022). Our results suggest that there are numerous violations of the traditional bifurcating species tree model within *Todiramphus* kingfishers.

Gene flow within Todiramphus kingfishers

Genomic studies increasingly demonstrate that gene flow is common during periods of rapid diversification (Edelman et al. 2019; Taylor and Larson 2019; Guo et al. 2022; Ocampo et al. 2022; Jensen et al. 2023; Jiang et al. 2024; Stiller et al. 2024; Zhao et al. 2024). Here, we uncovered novel patterns of gene flow among *Todiramphus* kingfishers as they diversified over

the past 10 Ma. Previous molecular work on *Todiramphus* kingfishers, using either mitochondrial (O’Connell et al. 2019) or RAD-seq data (DeRaad et al. 2023), have reported no evidence of gene flow between *T. sanctus* and other members of the Australasian clade (*T. chloris*, *T. sordidus*, *T. colonus*, etc.). In contrast, though we detected the first evidence of gene flow between *T. sanctus* and other clade members, these signatures were much lower than those compared to other pairwise comparisons, such as between *T. sanctus* and *T. sacer* or within the *T. sacer* complex (Figs. S21–24). Network analyses inferred a very low inheritance probabilities of ancestral contributions to a hybridization event involving a ghost lineage of *T. sanctus* and the ancestor to the remaining members of the Australasian clade (Figs. 2, S19). This signal of gene flow likely went undetected in earlier studies because of limited genomic sampling (three mtDNA genes for O’Connell et al. 2019 vs. ~2,000 SNPs for Deraad et al. 2023 vs. >85,000 SNPs and thousands of gene trees in this study). Notably, a reticulation event between *T. sanctus* and *T. sacer* was not supported with SNaQ, even when more reticulation events were allowed and we included the exact *T. sacer* individual that were inferred to have a *T. sanctus* mitochondrial genome (Figs. S19–20).

We are not the first to uncover gene flow within Indo-Pacific kingfishers. Studies that employ phylogenomic data showed persistent gene flow but maintenance of species-boundaries between the two sympatric *Syma* species (sister genus to *Todiramphus*) across an elevational gradient in New Guinea (Linck et al. 2020) as well as across *Ceyx*, the other ‘Great Speciator’ kingfisher genus (Lim et al. 2010; Andersen et al. 2013; Shakya et al. 2023). Overall, our study fits into a larger picture of gene flow between island endemic avian lineages, including within Fijian groups such as honeyeaters and bush-warblers (Gyllenhaal et al. 2020; Mapel et al. 2021) and Indonesian monarch flycatchers (Andersen et al. 2021).

Many of the contemporary patterns of gene flow that we observed in this study involve one species in particular, the Sacred Kingfisher *T. sanctus*. Because we had limited sampling per taxon, we could not pursue more detailed tests of gene flow between *T. sanctus* and other species, such as Admixture (Alexander et al. 2009) or fastsimcoal2 (Excoffier et al. 2021). Nevertheless, several lines of evidence support gene flow between *T. sanctus* and other species. First, we observed mitochondrial discordance of five *T. sacer* taxa (*regina*, *ornatus*, *utupuae*, *vicina*, and *brachyurus*; Fig. 4). Second, ABBA-BABA tests revealed elevated $D_{\min}$ values between *T. sanctus* and *T. sacer* (Figs. S20, S22) confirms the presence of gene flow. Finally, one *T. sacer* lineage (*regina*) was fully supported within the *T. sanctus* clade in one phylogeny (BUSCO IQ-TREE; Fig. S17).

Todiramphus sanctus is unusual because it is one of two truly migratory *Todiramphus* species (alongside the Forest Kingfisher, *T. macleayii*; Woodall 2001). Moreover, only the nominate subspecies (*T. s. sanctus*) migrates, whereas the other four taxa within this complex are considered sedentary and endemic to isolated Pacific islands (Fig. S1). We also inferred gene flow between *T. sanctus* and the Torresian Kingfisher (*T. sordidus*), a species that also breeds in Australia. During the non-breeding season, however, *T. sanctus* occupies a wide swath of the Indo-Pacific: from as far west as Sumatra, across Wallacea, New Guinea, and northern Melanesia, and as far east as Makira in the Solomon Islands (Fry et al. 1992; Woodall 2001). As a result, non-breeding *T. sanctus* is sympatric with as many as 42 *Todiramphus* taxa (15 species), compared to only five taxa (3 species) during the breeding season. Paradoxically, the *T. sacer* taxa that have *T. sanctus* mtDNA are not sympatric with wintering *T. sanctus*. No contemporary records exist for *T. sanctus* in Temotu Province, Solomon Islands, and especially not as far as in Wallis and Futuna (*T. sacer regina*). Though there are brief mentions of *T.*

sanctus breeding outside of Australia (Dutson 2011), these are likely incorrect identifications of two species that can be difficult to diagnose in the field (see Appendix 2 for more details on these breeding records of *T. sanctus* outside of Australia). With two species whose non-breeding ranges barely overlap, we are left to consider a complicated history of island colonization, historical gene flow, and range contraction between these two species.

With no substantial breeding records of *T. sanctus* outside of Australia, we are left with one central question: why do we infer gene flow between *T. sanctus* and *T. sacer* (specifically *ornatus*, *utupuae*, *vicina*, *brachyurus*, and *regina*; Fig. 4)? Notably, sedentary *T. sanctus* occur only on islands that are conspicuously lacking *T. sacer*. The closest geographic distance between two breeding populations of both species is between *T. sanctus macmillani* (Loyalty Islands) and an undescribed *T. sacer* population on Anietyum, approximately ~220 km away. Interestingly, *T. sanctus macmillani* clusters with migratory *T. s. sanctus* and all five *T. sacer* lineages in the mitochondrial phylogeny (Fig. 4). This pattern of non-overlapping breeding ranges mirrors one described by Mayr (1932b) for Fijian Whistlers (*Pachycephala*; Gyllenhaal et al. 2025): one species colonized an archipelago that was later replaced by another, forming hybrid populations as the second wave of colonists swept through the archipelago. Because crown *T. sanctus* predates crown *T. sacer* (McCullough et al. 2019, McCullough et al. *in prep*), we hypothesize that *T. sanctus* once maintained widespread sedentary populations across the South Pacific. These may have been replaced following a back-colonization of the Oceanic clade from Eastern Polynesia into Melanesia. Such a scenario would explain the hybridization signals (Fig. 4) without requiring present-day sympatry between *T. sanctus* and the *T. sacer* lineages that carry *T. sanctus* mtDNA.

Other sources of topological discordance

In addition to the demonstrated gene flow across the *Todiramphus* radiation (Fig. 4), topological discordance could also be attributed to other biological and methodological factors. Incomplete lineage sorting (ILS) is a well-known and pervasive source of topological discordance, especially within rapid radiations (Suh et al. 2015; Lopes et al. 2020). However, teasing apart the relative contribution of gene flow versus ILS is difficult. DeRaad et al. (2023) suggested that mitonuclear discordance within the Australasian *Todiramphus* clade was driven largely by ILS rather than nuclear gene flow or mitochondrial capture, based on largely non-significant pairwise comparisons of the ABBA-BABA D-statistics. Here, gene and site concordance factors (gCF/sCF) between major *Todiramphus* topologies similarly suggest that ILS is likely a significant source of topological conflict across the entire genus (Fig. 3). However, ancient reticulation events consistently inferred in similar areas of the tree (Fig. S19) and significant pairwise D-statistic comparisons using our comprehensive SNP dataset (Figs. S21–24), together suggest that ongoing gene flow during diversification contributed to signals of genome-wide discordance in the Australasian clade (Figs. 2–3). While DeRaad et al. (2023) rejected mitochondrial capture within the Australasian *Todiramphus* clade, our expanded taxonomic sampling across the genus reveals additional cases of derived *T. sanctus* haplotypes in multiple *T. sacer* lineages, highlighting the overall complexity of the heterogeneous evolutionary processes simultaneously contributing to generate the patterns of relatedness we observe among extant *Todiramphus* lineages.

Alternatively, methodological explanations like the source (tissue or toepad) or type of DNA (exonic vs. intronic) could also explain some of the topological discordance among data types and tree building methods. Because our dataset relied heavily on toepad samples, we took

698 additional steps at all levels of this study to ameliorate the effects of degraded DNA on
699 topological inference. In addition to special wet lab processing of toepad-sourced genomes, we
700 performed additional UCE alignment cleaning (Smith et al. 2020) and novel methods of *in silico*
701 BUSCO extractions (see Appendix 2). Moreover, we explored filtering approaches for MSC tree
702 building methods. ASTRAL is known to perform poorly when input gene trees are built from
703 short alignments of uninformative loci (Mirarab 2023), a pervasive issue for datasets utilizing
704 degraded DNA samples from museum specimens (Andersen et al. 2019; Salter et al. 2019, 2022;
705 Smith et al. 2020; Roycroft et al. 2021; Huynh et al. 2023). For datasets that have a high degree
706 of ancient or historical samples, there is often an artefactual pattern in which high quality and
707 historical samples form distinct clusters (Fig. S2) rather than being uniformly distributed in the
708 species tree. Before filtering for parsimony informative (PI) sites, ASTRAL-inferred species
709 trees showed a clear artefactual pattern of toepad-sourced samples clustering at the base of their
710 respective species-complexes (Figs. S2, S4). This pattern disappeared when we analyzed smaller
711 sets of gene trees based on alignments with more PI sites (Figs. S12, S16). Although filtering
712 based on informativeness can introduce bias (Musher et al. 2019; Burbrink et al. 2020), the
713 approach has been used with success elsewhere (e.g., Chan et al. 2020a; Leite et al. 2021;
714 Forthman et al. 2022). We preferred it here because it is a general approach to deal with these
715 issues rather than clade-specific filtering approaches (Chen et al. 2018) or by dropping important
716 tips represented by toepads. Additionally, the clades that represented the most topological
717 discordance were from those represented by high-quality tissues (i.e., *T. farquhari*, *T.*
718 *pyrrhopygius*) or were in clades with relatively few toepad-sourced samples (i.e., the *leucopygius*
719 clade, *T. sordidus*; Fig. 2).

The type of DNA from which molecular markers are derived (i.e., exonic vs. intronic regions) could also contribute to conflicting topological patterns. UCEs are largely sourced from intronic and non-coding regions of the genome whereas BUSCOs are all exonic markers from coding regions. The difference in selective pressures and therefore rates of fixed mutations, has been shown to have a substantial impact in the overall topology inferred by these markers, such as in higher-level phylogenomic studies of all birds (Jarvis et al. 2014; Prum et al. 2015; Reddy et al. 2017). Yet, we generally find that these data types produce largely similar topologies (Figs. 2–3). Though less commonly used in species-level relationships of birds, these molecular markers are more widely used to infer phylogenies outside of birds, such as in plants (Timilsena et al. 2022; Walden and Schranz 2023), fungi (Kanzi et al. 2020), arthropods (Dias et al. 2020; Van Damme et al. 2022). A next step towards understanding interspecies relationships would be a sliding window approach to determine if particular genomic regions are disproportionately driving the levels of discordance observed here, as has been shown in higher-level divergences of Neoaves (Mirarab et al. 2024; Stiller et al. 2024).

Taxonomic recommendations

In line with a growing body of work that has uncovered unsuspected species-level diversity in geographic radiations across the Indo-Pacific (Andersen et al. 2013; Reeve et al. 2023; Pedersen et al. 2018; Irestedt et al. 2013), we too found that some taxa in our dataset require taxonomic revisions based on their novel systematic relationships (see Appendix 2 for further discussion). Roughly half of the *Todiramphus* diversity we sampled has never been included in a molecular phylogenetic analysis. Many newly added taxa fall within their presumed species groups, such as all the subspecific diversity within *T. tristrami* (Fig. 1), but there are some instances that require

taxonomic changes. When Ernst Mayr described geographic variation of kingfishers across the Pacific, he noted that two populations on Tucopia (Temotu Province, Solomon Islands) and Aneityum (Tafea Province, Vanuatu) islands were each phenotypically distinct from those on nearby islands, but he refrained from naming these as subspecies (Mayr 1931b). He wrote of the birds from Aneityum, they were “indistinguishable from typical *juliae*... only the distribution keeps me, for the present, from uniting it immediately with *juliae*” (Mayr 1931b, pg 4). To our eyes, Aneityum *sacer* are more similar to those in central Vanuatu (*T. sacer juliae*) with white underparts and collar rather than the buffy *T. s. tannensis* on Tanna Island. However, instead of considering this a separate taxon or grouping this population with the closest island (Tanna), Aneityum birds have long been considered as part of *T. sacer erromangae*, forming a curious leapfrog distribution of white-bellied birds (*erromangae* and the Aneityum form) sandwiching buffy-bellied birds (Tanna). We would expect that if Aneityum birds are indeed part of *T. s. erromangae* or *tannensis*, our genetic samples would be closely associated with one of these taxa. For the samples from Tucopia, Mayr refrained from naming these birds as a subspecific taxon because their plumages were “too worn” (Mayr 1931b), and they have been considered either a part of *T. s. torresianus* (Banks Is., Vanuatu) or *T. s. melanodera* (Vanikolo in Temotu Province). Whereas we sometimes found Aneityum *sacer* grouping in a subclade with *T. s. erromangae* or *tannensis* and Tucopia *sacer* (Fig. 1), we never recovered Aneityum *sacer* or Tucopia *sacer* as sister to either of their presumed subspecies. We suspect these could represent independent lineages from their long-presumed subspecies, but we defer naming these two populations as subspecies at this time.

CONCLUSIONS

Geographic radiations across the Indo-Pacific have been critical to the development of influential speciation theories, with genome-scale datasets providing new and accelerated insights into the complicated evolutionary histories of such rapidly diversifying clades. In this study we show that whole genome resequencing and complete sampling of a rapid radiation of mostly island kingfishers does not outright resolve the evolutionary relationships of the group. Instead, we found that four types of data (UCEs, BUSCOs, SNPs, and mtDNA) and tree building methods (ML, MSC, networks) did not infer a single well-supported and concordant species-level topology. Phylogenetic network analyses suggest that ancient introgression is likely the cause of these topological differences. The discovery of several *T. sacer* populations falling in the mitochondrial clade of a widespread and migratory taxon, *T. sanctus*, and the inference of gene flow between them ABBA-BABA tests, suggests a potential historical hybrid zone between these two species as islands were successively colonized. We were only able to pick up on these signals of hybridization because we thoroughly sampled all described diversity within the genus by relying on a sizable number of toepad-sourced data. Future studies that investigate rapid radiations in this region should incorporate widespread taxonomic and population level sampling, while also sampling large amounts of genetic data to tease apart the interacting effects of gene flow and incomplete lineage sorting on complex evolutionary histories.

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DATA AVAILABILITY

Supplementary material, including alignments, tree figures, and other information (supplementary methods, discussion, figures, and tables) are available in the Dryad data repository (<https://doi.org/10.5061/dryad.cfxpvnvg8>). Code is available on Github (<https://github.com/JennaMcCullough/TodiramphusWGS>). Raw read data sequenced for this project is available on Genbank (Bioproject PRJNA1174201).

APPENDICES

Appendix 1: Combined excel spreadsheet that includes seven supplementary tables.

Appendix 2: Combined PDF of supplementary methods, discussion, and 27 figures.

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FIGURE CAPTIONS

Figure 1. Ranges and evolutionary relationships of all *Todiramphus* kingfishers. A) Partitioned maximum likelihood phylogeny of 4,942 UCE loci from the 90% complete matrix inferred with IQ-TREE. Circles on nodes indicate support values less than 100 bootstrap support. B). Ranges of 29 species-level groups with diagonal lines showing sympatry and colors corresponding to tips. Letters corresponding to species ranges are as follows: A, *T. enigma*; B, *T. funebris*; C, *T. diops*; D, *T. lazuli*; E, *T. macleayii*; F, *T. colonus*; G, *T. albonotatus*. See Figure S1 with these ranges directly labeled with taxon names. C) Unrooted network based on pairwise divergence among all samples, produced from a complete set of 85,165 SNPs. Note that some branch lengths have been artificially shortened, denoted by double slashes. See Figure S17 for subspecific labels. Illustrations created by Jenna McCullough and names are as follows: i, *T. nigrocyaneus*; ii, *T. farquhari*; iii, *T. reichenbachii*; iv, *T. sacer*; v, *T. sanctus*; vi, *T. saurophagus*; vii, *T. tristrami*; and viii, *T. leucopygius*.

Figure 2. Simplified comparisons of trees from UCE, BUSCO, SNP, and mtDNA datasets with red branches highlighting differences from the UCE maximum likelihood IQ-TREE topology (panel A). We collapsed nodes with <85 bootstrap support and note those with 99–85 BS. In panel E, we show the SNaQ topology, which allows for reticulation edges (blue dotted lines have γ -values). We grouped lineages that were consistently inferred as a clade for simplicity: *T. sacer*

et al. includes *T.reichenbachii* and *T. recurvirostris*. Note that *T. pelewensis* and *T. cinnamominus* are considered a single tip (“*pelewensis* et al.”) except in Panels I and J. In Panel C, relationships are representative across two SVDQuartets analyses and differences are highlighted with an asterisk (*). Daggers (†) indicate samples sourced from toepad samples. *T. nigrocyaneus* is pruned for simplicity as its relationship to other *Todiramphus* is invariable across datasets and methods.

Figure 3. Site (sCF) and gene (gCF) concordance factors of UCE and BUSCO topologies show a high degree of ILS present in the evolutionary history of *Todiramphus* kingfishers. A) Partitioned 90% complete UCE matrix (4,942 loci, total 4,531,264 bp) inferred in IQ-TREE with gCFs calculated from gene trees of loci with at least 50 parsimony informative sites (PIs; 1,583 gene trees). B) Partitioned BUSCO topology (8,012 loci, total 5,102,241 amino acid sites) inferred in IQ-TREE with gCFs calculated from gene trees of loci with >50 PI amino acid sites (4,155 gene trees).

Figure 4. Evidence of gene flow and mitochondrial discordance within some Pacific Kingfisher (*T. sacer*) taxa and Sacred Kingfisher (*T. sanctus*). A) Partitioned IQ-TREE phylogenies inferred from the 90% complete UCE matrix and 13 mitochondrial genes. Note that the mtDNA phylogeny for the Australasian clade (*T. sanctus*, *T. tristrami*, and allies) is different from the UCE topology, which has been described previously (DeRaad et al. 2023). In the mtDNA phylogeny, there are two clades of *T. sanctus*: a clade of four of the five sedentary, island endemic *T. sanctus* taxa (a), which is sister to the clade comprising the migratory and nominate taxon *T. sanctus sanctus* (b), the five *T. sacer* taxa (connected between the phylogenies with

1411 colored lines), and the fifth island endemic sedentary taxon *T. sanctus macmillani* (c). See Fig.
1412 S20 for tip labels. B) Range map of both species, highlighting the subspecific ranges of the *T.*
1413 *sacer* taxa with *T. sanctus* mtDNA (see Fig. S1 for the subspecific ranges of all 22 *T. sacer* taxa).
1414 Jenna McCullough created the illustrations of kingfisher taxa; names are indicated by roman
1415 numerals next to illustrations and are as follows: i, *T. sacer brachyurus*; ii, *T. sacer vicina*; iii, *T.*
1416 *sacer ornatus*; iv, *T. sacer utupuae*; v, *T. sacer regina*; vi, *T. sanctus sanctus*; and vii, *T. sacer*
1417 *sacer* (endemic to Tonga). C) Pairwise results of ABBA-BABA tests from Dsuite, with values in
1418 comparisons with FDR-adjusted significant pairwise p values. Above the diagonal line is the
1419 most significant (Dmin) for any pairwise comparison and below are F4-ratio values. Only a
1420 subset of all comparisons is shown here, see Figs. S21–24 for the complete set.

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