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RESEARCH ARTICLE

Genomic and geographic diversification of a "great-speciator" (*Rhipidura rufifrons*)

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ABSTRACT

The radiation of so-called "great speciators" represents a paradox among the myriad of avian radiations endemic to the southwest Pacific. In such radiations, lineages otherwise capable of dispersing across vast distances of open ocean differentiate rapidly and frequently across relatively short geographic barriers. Here, we evaluate the phylogeography of the Rufous Fantail (*Rhipidura rufifrons*). Although a presumed "great-speciator", no formal investigations across its range have been performed. Moreover, delimitation of lineages within *R. rufifrons*, and the biogeographic implications of those relationships, remain unresolved. To investigate whether *R. rufifrons* represents a great speciator we identified thousands of single nucleotide polymorphisms for 89 individuals, representing 19 described taxa. Analyses recovered 7 divergent lineages and evidence of gene flow between geographically isolated populations. We also found plumage differences to be a poor proxy for evolutionary relationships. Given the relatively recent divergence dates for the clade (1.35–2.31 mya), rapid phenotypic differentiation, and evidence for multiple independent lineages within the species complex, we determine that *R. rufifrons* possesses the characteristics of a great speciator.

Keywords: avian, Indo-Pacific, phylogeography, RADSeq, rapid radiations, *Rhipidura rufifrons*, Rufous Fantail

LAY SUMMARY

- To study biodiversity, we must have a clear understanding of the differences between species, and how those differences came to be.
- We obtained tissue samples for nearly 100 Rufous Fantails for this study making sure to include birds with as many different coloration patterns and geographic locations as possible.
- We used DNA sequence data to identify distinct genetic groups within the Rufous Fantail complex, and subsequently to determine how similar those groups are to one another.
- We found strong support for seven genetically distinct groups that are all currently considered one species, the Rufous Fantail.
- We found evidence for interbreeding among groups, despite some having different coloration patterns and geographic ranges.
- Studying the Rufous Fantail shows us that groups of birds can look different from one another and/or be separated from each other by large distances, and still be similar genetically.

Diversificación genómica y geográfica de un "gran especiador" (*Rhipidura rufifrons*)

RESUMEN

La radiación de los llamados "grandes especiadores" representa una paradoja entre la miríada de radiaciones de aves endémicas del Pacífico suroeste. En tales radiaciones, los linajes que de otro modo serían capaces de dispersarse a lo largo de grandes distancias en mar abierto se diferencian rápida y frecuentemente a través de barreras geográficas relativamente cortas. Aquí, evaluamos la filogeografía de *Rhipidura rufifrons*. Aunque se presume que es un "gran especiador", no se han realizado investigaciones formales en todo su rango. Además, la delimitación de linajes dentro de *R. rufifrons* y las implicaciones biogeográficas de esas relaciones siguen sin resolverse. Para investigar si *R. rufifrons* representa un gran especiador, identificamos miles de polimorfismos de un solo nucleótido para 89 individuos, que representan 19 taxones descritos. Los análisis recuperaron 7 linajes divergentes y evidencia de flujo génico entre poblaciones geográficamente aisladas. También encontramos que las diferencias de plumaje son un mal indicador de las relaciones evolutivas. Dadas las fechas de divergencia relativamente recientes para el clado (1.35–2.31 millones de años), la rápida diferenciación fenotípica y la evidencia de múltiples linajes independientes dentro del complejo de especies, determinamos que *R. rufifrons* posee las características de un gran especiador.

Palabras clave: aviar, filogeografía, Indo-Pacífico, radiaciones rápidas, RADSeq, Rhipidura rufifrons

INTRODUCTION

Island systems have a long history of influencing the development of evolutionary theory (Mayr 1942, Darwin 1859, Wallace 1881). Islands vary in many aspects that are expected to impact biological diversification such as age, degree of isolation, size, elevation, and climate. Variation within and among islands and island archipelagos provides natural laboratories in which to test hypotheses of how geographic and ecological differences affect the process of speciation (MacArthur and Wilson 1967). Given the abundance of archipelagos and islands within the southwest Pacific, it is unsurprising that early speciation research focused extensively on terrestrial biodiversity in this region (e.g., Mayr 1942, Diamond 1974, Diamond et al. 1976, MacArthur and Wilson 1963, 1967, Mayr and Diamond, 2001).

"Great speciators" (Diamond et al. 1976) represent a particularly interesting evolutionary phenomenon in which avian species complexes appear to have diversified rapidly across the southwest Pacific (Moyle et al. 2009, Andersen et al. 2013, 2015, Irestedt et al. 2013, Pedersen et al. 2018). Rapid radiations are certainly not limited to the Pacific island systems (Losos et al. 1998, Rees et al. 2001, Koblmüller et al. 2010, Campagna et al. 2015), but because many rapid radiations in the southwest Pacific share broadly overlapping distributions, they naturally lend themselves to detailed investigations of diversification in a comparative framework. Avian radiations on Pacific islands present a paradoxical situation in which lineages have dispersed across hundreds of kilometers of ocean, but populations have also differentiated across small or even ephemeral barriers. For example, the white-eyes (family Zosteropidae) contain multiple examples of lineages evolving from ancestral populations that were capable of crossing substantial water barriers (i.e., 300–1,500 km), but which then differentiated across relatively narrow water barriers (i.e., <20 km) (Moyle et al. 2009, Manthey et al. 2020) or even within an island (Milá et al. 2010). In other scenarios, geographically proximate island populations of the same species complex are not closely related. For example, within *Pachycephala pectoralis* and despite the proximity of the Louisiade Archipelago to mainland Papua New Guinea, populations from each area were not closely related to each other; rather, the Louisiade Archipelago population was sister to the entire species complex, which spans the Australasian region (Andersen et al. 2014). Additionally, these radiations often comprise species complexes with unstable taxonomy and/or uncertain phylogenetic relationships (e.g., Andersen et al. 2015, Pedersen et al. 2018). These shortcomings hinder biogeographic inference.

Most studies of rapid radiations in the Indo-Pacific (e.g., Moyle et al. 2009, Andersen et al. 2013, 2015, Jønsson et al. 2014, Pedersen et al. 2018) have been based on relatively small genetic datasets (i.e., <10 loci and one or a few samples per population). Increasing sampling both in terms of number of individuals and number of sites across the genome can permit analyses of gene flow, allow for more effective estimates of genetic diversity, and increase resolution for estimating phylogenetic relationships. Therefore, in this study we leverage high-throughput sequencing of dense taxon sampling to enable exploration of a genome-wide dataset for a putative "great-speciator", the Rufous Fantail (*Rhipidura rufifrons*). Such data-rich approaches can help to resolve complex biogeographic relationships and population demographic histories that smaller genetic datasets are less likely to inform.

The Rufous Fantail is a phenotypically diverse species composed of 18 subspecies (Clements et al. 2021; Table 1) distributed throughout Melanesia, Micronesia, and Australia (Pratt 2010; Figure 1). Predominantly an understory species of lowlands and mountains, *R. rufifrons* uses a diversity of habitats including primary old-growth forests, secondary forests, riparian areas including mangroves, and disturbed habitats. The diet of *R. rufifrons* consists mostly of insects including Coleoptera, Diptera, Hymenoptera, and Lepidoptera (Boles and Christie 2019). Most populations of *R. rufifrons* are non-migratory, but individuals from southeast Australia migrate to southern New Guinea during the nonbreeding season (Boles and Christie 2019). Significantly, an initial morphological evaluation of the evolutionary history of *R. rufifrons* placed the species in a group of species that also contained *Rhipidura dryas* and *Rhipidura lepida* (Micronesia, Palau), among others (Mayr and Moynihan 1946; Figure 1). Molecular

TABLE 1. The 18 subspecies within the *R. rufifrons* complex, their distribution, and the number of samples included in this study.

Subspecies	Authority	Distribution	Sample size
R. r. rufifrons	Latham, 1802	Eastern Australia	3
R. r. intermedia	North, 1902	Northeastern Australia, PNG	9
R. r. louisiadensis	Hartert, 1899	Louisade and D'Entrecasteaux archipelagos	7
R. r. ugiensis	Mayr, 1931	Solomon Island (Ugi)	3
R. r. kuperi	Mayr, 1931	Solomon Island (Santa Ana)	3
R. r. russata	Tristram, 1879	Solomon Island (Makira)	6
R. r. granti	Hartert, 1918	Solomon Island (New Georgia Group)	10
R. r. brunnea	Mayr, 1931	Solomon Island (Malaita)	5
R. r. commoda	Hartert, 1918	Solomon Island (Bougainville, Choiseul, Isabel)	7
R. r. rufofronta	Ramsey EP, 1879	Solomon Island (Guadalcanal)	8
R. r. agilis	Mayr, 1931	Santa Cruz Island (Nendo)	3
R. r. melanolaema	Sharpe, 1879	Santa Cruz Island (Vanikoro)	0
R. r. utupuae	Mayr, 1931	Santa Cruz Island (Utupua)	0
R. r. saipanesis	Hartert, 1898	Northern Mariana Island (Saipan, Tinian, Aguijuan)	3
R. r. mariae	Baker RH, 1946	Northern Mariana Island (Rota)	1 [a]
R. r. uraniae	Oustalet, 1881	Guam (extinct)	0
R. r. torrida	Wallace, 1865	Molucca Island	0
R. r. versicolor	Hartlaub and Finsch, 1872	West Caroline Island (Yap)	0

[a] Sample was removed from the dataset after failing to adequately sequence.

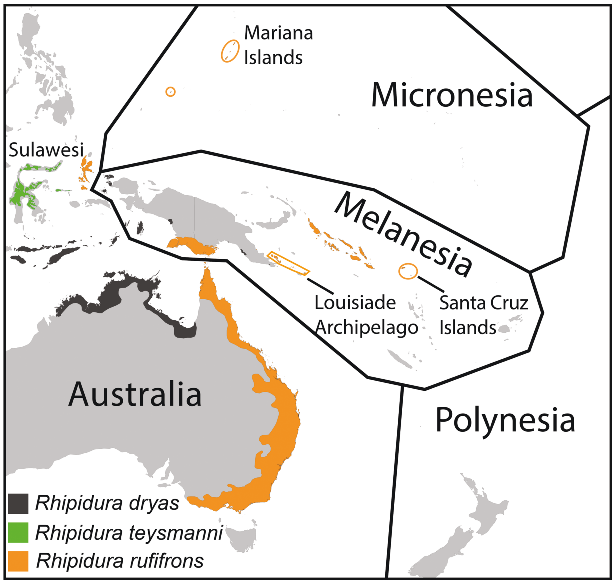

FIGURE 1. Map of the southwest Pacific. The distribution for *Rhipidura rufifrons* is shown in orange (Birdlife 2019) and extends east to the Santa Cruz Islands in Melanesia, north to the Northern Mariana Islands in Micronesia, and west to the Molucca Islands of Indonesia. The distribution for *Rhipidura dryas* includes north central Australia and the Lesser Sunda Islands and is shown in black on the map (Birdlife 2019). *Rhipidura teysmanni* is an endemic to Sulawesi and its distribution is shown in green (Birdlife 2019).

phylogenetic work using ~2,600 base pairs (bp) and 3 independent loci (2 nuclear, 2 mitochondrial DNA [mtDNA] loci) on Rhipiduridae also recovered a close relationship between *R. dryas and R. rufifrons* (Nyári et al. 2009); however, *R. lepida* was not included in that study, so the relationship between the 3 taxa remains equivocal.

Populations of *R. rufifrons* inhabit all major islands of the Solomon Islands, with some populations connected by land bridges during Pleistocene glacial maxima and others that remained geographically isolated (i.e., ~5–70 km). In addition, populations of *R. rufifrons* inhabit remote island archipelagos, such as the Santa Cruz Group and the Mariana Islands, that are isolated by hundreds or even thousands of kilometers of open ocean (Figure 1). Furthermore, subspecies of *R. rufifrons* display varied levels of morphological divergence (Pratt 2010). For example, *Rhipidura rufifrons saipanensis* exhibits little plumage differentiation compared to the nominate subspecies (Mayr and Moynihan 1946), despite being the most geographically isolated population. Conversely, *Rhipidura rufifrons ugiensis* differs distinctly from the rest of the *R. rufifrons* complex, being the only population with an all-black chin and throat (Mayr and Moynihan 1946), yet it is separated by <10 km from the nearest *R. rufifrons* population.

Given the wide geographic distribution of subspecies in this complex, their apparently rapid diversification, and their morphological variation, *R. rufifrons* is an ideal system in which to broaden our understanding of evolutionary processes during rapid radiations and address biogeographic hypotheses proposed by prior investigations. Here, we investigated the following questions for the *R. rufifrons* complex: 1 Does current taxonomy reflect the evolutionary history for *R. rufifrons*? For example, does the readily diagnosable (by plumage) *R. r. ugiensis* population also show clear genomic differentiation from sister lineages? 2 What insights can *R. rufifrons* reveal about the biogeography of Pacific lineages? Specifically, what role has the Louisiade Archipelago played in the diversification of Pacific lineages, and do we observe biogeographic patterns like those of *Pachycephala pectoralis* (Andersen et al. 2014, Jønsson et al. 2014)? Were remote islands colonized by a single dispersive ancestor or do we find evidence for multiple, long-distance dispersal events? Are Solomon Island lineages predicted by land-bridge connections via glacial cycling and how do these lineages compare to other radiations across the Solomon Islands?

METHODS

Sampling

Sampling included 94 individuals representing 19 named taxa from 5 species: *Rhipidura rufifrons* (12 taxa), *R. dryas* (4 taxa), *R. lepida*, *R. teysmanni*, and *R. dahli* with the last 3 species included as outgroups based on (Nyári et al. 2009) and preliminary mtDNA analyses (see below) (Table 2). Five described subspecies within *R. rufifrons* (*R. r. torrida*–Moluccas, *R. r. versicolor*–West Caroline Island, *R. r. melanolaema*–Vanikoro, *R. r. utupuae*–Utupua, and the extinct *R. r. uraniae*–formerly Guam) currently lack fresh tissue samples and are not represented in this study. Another taxon, *R. semirubra* of Manus Island, is sometimes treated as a subspecies of *R. rufifrons* (e.g., Mayr and Diamond 2001), but fresh tissue is lacking for this taxon and it was also not included in the study.

Sequencing and Bioinformatics

Nuclear genomic DNA. We extracted genomic DNA from blood or tissue samples using a QIAGEN DNeasy blood and tissue kit (Qiagen, Germantown, MD, USA) for all individuals, and quantified DNA concentrations with a Qubit Fluorometer 2.0 (Life Technologies, Fremont, CA, USA). We performed a single digest RAD-seq protocol (Miller et al. 2007) to obtain thousands of loci from across the *R. rufifrons* genome. We followed the procedures outlined by (Manthey et al. 2016) to generate the DNA libraries. We used NdeI, a restriction enzyme, to digest the genomic DNA and ligated custom barcoded adapters to permit the multiplexing of many individuals. We size selected fragments in a range between 450 and 600 bp using a Pippin Prep (Sage Science, Beverly, MA, USA) electrophoresis cassette (Andolfatto et al. 2011). Samples were sequenced using partial lanes of 3 different sequencing runs on an Illumina HiSeq2500 (Illumina, San Diego, CA, USA) and an Illumina NextSeq 550 for 100 bp single-end reads at the University of Kansas Genome Sequencing Core Facility.

We used the STACKS v2.3 (Catchen et al. 2011) pipeline to de novo assemble loci and produce a single nucleotide polymorphism (SNP) dataset from the sequencing data. Individuals were de-multiplexed and reads with an uncalled base and low-quality reads were removed using the *process_RADtags* script implementing the -c and -q flags, respectively. Following de-multiplexing, we ran the modules *ustacks*, *cstacks*, and *sstacks*. We used the *ustacks* module to identify loci within an individual initially using default parameters for number of mismatches allowed between stacks (*-M* 2) and the number of reads required to build a stack (*-m* 3). Next, we ran *cstacks* to combine individual loci into a catalogue of loci, permitting 3 mismatches (*-n* 3) across individuals. Then, we matched each individual's data to the catalogue with *sstacks* using default parameters. We transposed the dataset using *tsv2bam* and aligned and called SNPs using the *gstacks* module. Using the *populations* module within STACKS, we filtered out loci with a minor allele frequency below 0.05. We assumed loci with an observed heterozygosity above 0.5 was the result of assembling paralogous loci, thus we removed these loci. In order to examine possible influences of parameter choice on downstream analyses, we re-ran this protocol, iteratively modifying the parameters *M* (1–4), *m* (3, 5, 7), and *n* (1, 3, 5). Because sequence data for this project were amalgamated from three separate Illumina runs, we accounted for library specific loci by dropping loci present in fewer than 70% of individuals because no single library contributed more than 55% of the total individuals. Following quality control of our loci, we estimated nucleotide diversity (π) for islands by rerunning the *populations* module in STACKS with samples grouped by island. In addition to de novo assembly of RAD loci, we aligned the sequence data with BWA (Li and Durbin 2009) to the reference genome of the New Caledonia Crow (*Corvus moneduloides*: GCA_009650955.1) downloaded from GenBank. Individuals were genotyped for each locus with the STACKS module *gstacks* and loci were retained if they were present in at least 70% of individuals.

Mitochondrial DNA (mtDNA). We amplified the 1,041 bp of the NADH dehydrogenase subunit 2 (ND2) gene using the external primers L5215 (Edwards et al. 1991) and H6313 (Hackett 1996) and internal primers Mon590H and 500L (Filardi and Moyle 2005). Amplification of the ND2 gene was completed in 13 ml reactions using Promega GoTaq DNA polymerase. We used a touchdown protocol for polymerase chain reaction (PCR) of ND2 with annealing temperatures of 58°C, 54°C, and 50°C. We screened for successful amplification by running PCR products on a 2% agarose gel stained with GelRed. Successfully amplified samples were then purified with 10% Exo-Sap-It (GE Healthcare Bio-Sciences Corp.). Sequencing of the PCR products was then completed in both directions using an ABI Prism 3730 high-throughput capillary electrophoresis DNA analyzer.

TABLE 2. Samples included in the project. Individuals are ordered by clade membership in Figure 2. Given possible seasonal overlap of *R. dryas* and *R. rufifrons* on the western side of Cape York Peninsula, which is within the breeding range of *R. dryas*, we note that of several specimens listed here from that region, ANWC B57249 (collected in the austral winter, 8 July 2015) has been identified as *R. rufifrons intermedia* based on molecular data aligning it with that species and examination of specimens held at ANWC by LJ.

Genus	Species	Subspecies	Tissue #	Museum	Locality	Fig 2 Clade	Reads post QC	Cov. Median	Cov. Mean	Cov. St. Dev.
Rhipidura	*rufifrons*	*intermedia*	B31321	ANWC	Australia: Queensland	I	3,960,589	9	81.39	157.88
Rhipidura	*rufifrons*	*intermedia*	B31559	ANWC	Australia: Queensland	I	3,217,638	19	88.48	143.15
Rhipidura	*rufifrons*	*intermedia*	B43019	ANWC	Australia: Queensland	I	1,086,917	36	64.2	70.01
Rhipidura	*rufifrons*	*intermedia*	B57118	ANWC	Australia: Queensland	I	2,131,317	22	76.33	105.16
Rhipidura	*rufifrons*	*intermedia*	B57131	ANWC	Australia: Queensland	I	586,575	20	36.04	40.26
Rhipidura	*rufifrons*	*intermedia*	B57199	ANWC	Australia: Queensland	I	1,661,127	22	74.66	98.53
Rhipidura	*rufifrons*	*intermedia*	B56097	ANWC	Papua New Guinea: Western Province	I	1,286,979	15	57.36	76.81
Rhipidura	*rufifrons*	*intermedia*	B56405	ANWC	Papua New Guinea: Western Province	I	790,126	25	48.96	57.04
Rhipidura	*rufifrons*	*intermedia*	B57249	ANWC	Australia: Queensland, Dulhunty and Ducie Rivers ~67 km NNE Weipa	I	2,854,774	17	85.4	131.99
Rhipidura	*rufifrons*	*rufifrons*	B44315	ANWC	Australia: Queensland	I	922,775	29	56.15	64.42
Rhipidura	*rufifrons*	*rufifrons*	B46863	ANWC	Australia: New South Wales	I	2,891,189	24	95.87	137.88
Rhipidura	*rufifrons*	*rufifrons*	B49720	ANWC	Australia: New South Wales	I	2,629,858	17	85.41	128.59
Rhipidura	*rufifrons*	*louisiadensis*	97870	CAS	Papua New Guinea: Duchess Island	II	793,509	22	46.88	51.56
Rhipidura	*rufifrons*	*louisiadensis*	97887	CAS	Papua New Guinea: Panamoti Island	II	1,344,191	20	60.71	76.69
Rhipidura	*rufifrons*	*louisiadensis*	97970	CAS	Papua New Guinea: Panamoti Island	II	3,493,235	26	102.27	158.10
Rhipidura	*rufifrons*	*louisiadensis*	184548	BPBM	Papua New Guinea: Duchess Island	II	1,740,924	27	84.88	110.51
Rhipidura	*rufifrons*	*louisiadensis*	96782	CAS	Papua New Guinea: Panapompom Island	II	1,290,250	14	48.31	71.50
Rhipidura	*rufifrons*	*louisiadensis*	96783	CAS	Papua New Guinea: Haszard Island	II	1,758,740	11	47.7	80.97
Rhipidura	*rufifrons*	*louisiadensis*	96785	CAS	Papua New Guinea: Hummock Island	II	1,668,508	11	43.94	78.47
Rhipidura	*rufifrons*	*agilis*	19407	KUNHM	Solomon Island: Santa Cruz	III	895,692	15	45.47	60.39
Rhipidura	*rufifrons*	*agilis*	19408	KUNHM	Solomon Island: Santa Cruz	III	3,959,227	19	82.8	154.98
Rhipidura	*rufifrons*	*agilis*	19417	KUNHM	Solomon Island: Santa Cruz	III	1,234,707	14	50.04	74.74
Rhipidura	*rufifrons*	*saipanensis*	22578	KUNHM	Northern Mariana Island: Saipan	III	1,513,336	12	47.53	78.28
Rhipidura	*rufifrons*	*saipanensis*	22588	KUNHM	Northern Mariana Island: Saipan	III	1,611,507	13	57.77	93.61
Rhipidura	*rufifrons*	*saipanensis*	22597	KUNHM	Northern Mariana Island: Tinian	III	3,561,756	20	82.2	152.22
Rhipidura	*rufifrons*	*saipanensis*	22601	KUNHM	Northern Mariana Island: Tinian	III	689,131	11	32.56	45.26
Rhipidura	*rufifrons*	*ugiensis*	15928	KUNHM	Solomon Island: Ugi	V	926,692	12	39.73	57.87
Rhipidura	*rufifrons*	*ugiensis*	M007	U of Miami	Solomon Island: Ugi	V	3,216,729	17	75.92	143.45
Rhipidura	*rufifrons*	*ugiensis*	M008	U of Miami	Solomon Island: Ugi	V	2,805,477	18	84.45	145.97
Rhipidura	*rufifrons*	*kuperi*	M105	U of Miami	Solomon Island: Santa Catalina	V	1,950,950	15	62.05	100.85
Rhipidura	*rufifrons*	*kuperi*	M106	U of Miami	Solomon Island: Santa Catalina	V	5,448,399	21	98.46	195.66
Rhipidura	*rufifrons*	*kuperi*	M109	U of Miami	Solomon Island: Santa Catalina	V	2,630,954	17	74.68	126.75
Rhipidura	*rufifrons*	*russata*	M112	U of Miami	Solmon Island: Makira	V	1,693,946	16	59.41	92.93
Rhipidura	*rufifrons*	*russata*	M113	U of Miami	Solmon Island: Makira	V	3,815,039	17	67.51	135.12
Rhipidura	*rufifrons*	*russata*	12828	KUNHM	Solmon Island: Makira	V	661,948	15	37.72	46.86
Rhipidura	*rufifrons*	*russata*	12832	KUNHM	Solmon Island: Makira	V	774,385	13	39.27	52.88

TABLE 2. Continued.

Genus	Species	Subspecies	Tissue #	Museum	Locality	Fig 2 Clade	Reads post QC	Cov. Median	Cov. Mean	Cov. St. Dev.
Rhipidura	*rufifrons*	*russata*	13547	KUNHM	Solmon Island: Makira	V	639,724	9	25.75	36.10
Rhipidura	*rufifrons*	*russata*	15915	KUNHM	Solmon Island: Makira	V	675,950	10	29.78	42.82
Rhipidura	*rufifrons*	*granti*	32098	KUNHM	Solomon Island: Gizo	VI	740,113	12	36.03	49.29
Rhipidura	*rufifrons*	*granti*	32104	KUNHM	Solomon Island: Gizo	VI	935,143	8	27.43	45.69
Rhipidura	*rufifrons*	*granti*	33777	KUNHM	Solomon Island: Ranongga Island	VI	1,317,088	18	57.077	74.64
Rhipidura	*rufifrons*	*granti*	33786	KUNHM	Solomon Island: Ranongga Island	VI	6,060,119	12	88.35	166.02
Rhipidura	*rufifrons*	*granti*	33791	KUNHM	Solomon Island: Ranongga Island	VI	176,950	11	16.04	13.04
Rhipidura	*rufifrons*	*granti*	33862	KUNHM	Solomon Island: Vella Lavella	VI	13,321,108	13	96.72	192.56
Rhipidura	*rufifrons*	*granti*	33910	KUNHM	Solomon Island: Kolombangra	VI	2,849,754	10	68.24	118.72
Rhipidura	*rufifrons*	*granti*	33919	KUNHM	Solomon Island: Kolombangra	VI	12,780,508	10	74.05	157.82
Rhipidura	*rufifrons*	*granti*	Bu66046	UWBM	Solomon Island: New Georgia	VI	1,249,487	10	44.15	77.86
Rhipidura	*rufifrons*	*granti*	Bu66083	UWBM	Solomon Island: New Georgia	VI	458,788	9	21.52	26.47
Rhipidura	*rufifrons*	*brunnea*	32766	KUNHM	Solomon Island: Malaita	VII	667,794	9	25.35	34.94
Rhipidura	*rufifrons*	*brunnea*	32767	KUNHM	Solomon Island: Malaita	VII	923,712	13	34.08	45.94
Rhipidura	*rufifrons*	*brunnea*	32779	KUNHM	Solomon Island: Malaita	VII	1,413,435	19	70.98	94.09
Rhipidura	*rufifrons*	*brunnea*	32783	KUNHM	Solomon Island: Malaita	VII	1,038,579	12	42.14	60.96
Rhipidura	*rufifrons*	*brunnea*	32791	KUNHM	Solomon Island: Malaita	VII	2,014,330	14	62.76	101.59
Rhipidura	*rufifrons*	*commoda*	5282	KUNHM	Papua New Guinea: Bougainville	VII	507,790	7	13.8	18.39
Rhipidura	*rufifrons*	*commoda*	Bu63074	UWBM	Solomon Island: Choiseul	VII	2,624,511	14	62.04	116.93
Rhipidura	*rufifrons*	*commoda*	Bu63198	UWBM	Solomon Island: Choiseul	VII	187,338	8	13.28	12.82
Rhipidura	*rufifrons*	*commoda*	Bu58811	UWBM	Solomon Island: Isabel	VII	1,346,045	12	49.6	79.89
Rhipidura	*rufifrons*	*commoda*	Bu60315	UWBM	Solomon Island: Isabel	VII	138,410	8	12.06	10.38
Rhipidura	*rufifrons*	*commoda*	32061	KUNHM	Solomon Island: Shortland Island	VII	619,934	13	35.14	45.84
Rhipidura	*rufifrons*	*commoda*	32066	KUNHM	Solomon Island: Shortland Island	VII	1,428,900	11	47.7	75.88
Rhipidura	*rufifrons*	*rufofronta*	15904	KUNHM	Solomon Island: Guadalcanal	VII	575,676	12	31.76	40.81
Rhipidura	*rufifrons*	*rufofronta*	15910	KUNHM	Solomon Island: Guadalcanal	VII	2,771,728	15	68.5	128.46
Rhipidura	*rufifrons*	*rufofronta*	32807	KUNHM	Solomon Island: Guadalcanal	VII	1,311,981	9	39.55	66.06
Rhipidura	*rufifrons*	*rufofronta*	32809	KUNHM	Solomon Island: Guadalcanal	VII	1,271,126	15	44.36	62.75
Rhipidura	*rufifrons*	*rufofronta*	32810	KUNHM	Solomon Island: Guadalcanal	VII	1,382,894	11	37.41	59.62
Rhipidura	*rufifrons*	*rufofronta*	32823	KUNHM	Solomon Island: Guadalcanal	VII	840,711	27	57.93	66.35
Rhipidura	*rufifrons*	*rufofronta*	32854	KUNHM	Solomon Island: Guadalcanal	VII	962,325	18	32.03	36.52
Rhipidura	*rufifrons*	*rufofronta*	Bu60248	UWBM	Solomon Island: Guadalcanal	VII	835,126	13	40.56	57.73
Rhipidura	*dryas*	*dryas*	22743	KUNHM	Australia: Northern Territory		515,364	12	28.26	34.12
Rhipidura	*dryas*	*dryas*	B29495	ANWC	Australia: Queensland, Norman River, south of Karumba		2,702,340	11	67.79	113.64
Rhipidura	*dryas*	*dryas*	B29660	ANWC	Australia: Queensland, Staaten River, Inkerman		2,613,918	12	72.46	118.97
Rhipidura	*dryas*	*dryas*	B29869	ANWC	Australia: Queensland, Hey River, south of Weipa		226,833	10	17.56	17.25
Rhipidura	*dryas*	*dryas*	B32683	ANWC	Australia: Queensland, Leichhardt River, northeast of Burketown		2,568,336	11	69.19	115.48

TABLE 2. Continued.

Genus	Species	Subspecies	Tissue #	Museum	Locality	Fig 2 Clade	Reads post QC	Cov. Median	Cov. Mean	Cov. St. Dev.
Rhipidura	*dryas*	*dryas*	B33738	ANWC	Australia: Northern Territory, Koolpinyah Station, east of Darwin		3,125,113	7	54.71	112.98
Rhipidura	*dryas*	*dryas*	B48642	ANWC	Australia: Northern Territory, Goose Creek, Melville Island		2,312,421	9	57.7	100.21
Rhipidura	*dryas*	*dryas*	B55074	ANWC	Australia: Western Australia; Bindoola Creek, East Kimberley		981,126	11	41.58	54.18
Rhipidura	*dryas*	*semicollaris*	22704	WAM	Indonesia: Lesser Sundas		1,944,430	17	73.24	116.24
Rhipidura	*dryas*	*semicollaris*	23563	WAM	Indonesia: Lesser Sundas		1,864,656	16	62.52	98.57
Rhipidura	*dryas*	*semicollaris*	23884	WAM	Indonesia: Lesser Sundas		4,015,396	15	76.27	154.52
Rhipidura	*dryas*	*semicollaris*	24442	WAM	Indonesia: Lesser Sundas		1,026,765	11	44.04	67.77
Rhipidura	*dryas*	*semicollaris*	24503	WAM	Indonesia: Lesser Sundas		5,576,121	11	75.15	165.91
Rhipidura	*dryas*	*squamata*	24890	WAM	Indonesia: Banda Islands		1,415,653	11	49.58	82.97
Rhipidura	*dryas*	*sumbensis*	22842	WAM	Indonesia: Lesser Sundas		2,227,098	17	71.07	118.07
Rhipidura	*teysmanni*		DOT12566	AMNH	Indonesia: Sulawesi		882,896	13	41.94	58.40
Rhipidura	*lepida*		23628	KUNHM	Palau		797,225	13	36.05	48.98
Rhipidura	*lepida*		23660	KUNHM	Palau		798,799	15	42.09	56.33
Rhipidura	*lepida*		23623	KUNHM	Palau		3,875,182	18	97.57	159.28
Rhipidura	*dahli*		5305	KUNHM	Papua New Guinea: Bismarck Archipelago		3,446,318	15	80.17	133.71
Rhipidura	*dahli*		5313	KUNHM	Papua New Guinea: Bismarck Archipelago		437,175	9	20.78	24.29

Abbreviations: ANWC = Australian National Wildlife Collection, BPBM = Bernice P. Bishop Museum, CAS = California Academy of Sciences, KUNHM = University of Kansas Natural History Museum, UWBM = University of Washington Burke Museum, WAM = Western Australian Museum.

Following sequencing, we assembled sequence contigs in GENEIOUS v.5.6 (Biomatters, http://www.geneious.com) and manually checked alignments.

Analyses

Genomic DNA. We performed phylogenetic analyses on the concatenated dataset of SNPs using maximum likelihood (ML) and Bayesian approaches. Prior to concatenation, the alleles from each individual's SNPs were collapsed into a single consensus allele per locus, specifying ambiguity codes in the event of polymorphic sites. Loci were then concatenated for each individual and we used RAxML v8.0.19 (Stamatakis 2014) and BEAST v2.5.0 (Bouckaert et al. 2019) to identify phylogenetic relationships among individuals. Because the analysis omitted constant sites, we performed RAxML with an ascertainment bias correction (ASC_GTRGAMMA) and assessed support using 1,000 rapid bootstrap replicates. An input file for BEAST was created with BEAUTi v2.5.0 (Bouckaert et al. 2019) with a Markov chain Monte Carlo (MCMC) of 100,000,000 generations and sampling every 10,000. We identified a GTR + G model of sequence evolution to be the most appropriate using jModelTest v2.1.6 (Darriba et al. 2012) and was used for both ML and Bayesian analyses.

Population genetic structure was assessed with discriminate analysis of principle components (DAPC; Jombart et al. 2010), within the R package *adegenet* (Jombart 2008, Jombart and Ahmed 2011) and STRUCTURE v2.3.4 (Pritchard et al. 2000). STRUCTURE uses a predetermined number of populations (K) into which individuals are sorted. We used K values from 1 to 15 and completed 10 independent runs for each value of K. We ran STRUCTURE analyses for 550,000 generations per run, with the first 50,000 MCMC generations discarded as burn-in. We used likelihood scores and a ΔK calculation (Evanno et al. 2005) to determine the most likely number of populations. For DAPC, the most likely number of populations was determined based on the Bayesian Information Criterion. For both DAPC and STRUCTURE, we limited analyses to a single SNP per locus. In addition to analyzing the population genetic structure for all genomic loci, we analyzed sex-linked loci found on the Z chromosome separately with DAPC.

We assigned individuals to populations based on STRUCTURE and DAPC and inferred a species tree using TreeMix v1.13 (Pritchard et al. 2000), which allows for genetic exchange between populations that is not explained by the species tree alone. Specifically, we iteratively added migration events until these events explained 0.2% or less of the genetic variation (Pickrell and Pritchard 2012). We determined nodal support for the species tree by using 500 bootstrap replicates and accounted for possible linkage disequilibrium by completing independent runs using a bootstrapping block size (-k) of 100, 500, and 1,000 SNPs.

Mitochondrial DNA. We estimated a Bayesian mtDNA phylogeny using BEAST v1.8.1 (Drummond and Rambaut 2007). We used jModelTest v2.1.6 (Darriba et al. 2012) to determine the best-fit model of sequence evolution. We ran BEAST using the best-fit model (HKY+G+I) and partitioning by codon position. The MCMC was run for 100,000,000 generations sampling every 10,000 generations and we implemented a relaxed log-normal molecular clock with a substitution rate of 0.0145 (2.9% divergence my^{-1}) (Lerner et al. 2011). Log files were examined with TRACER v1.5 to determine convergence of model parameters and a maximum clade credibility tree was generated with TREEANNOTATER v1.5.4 (Drummond and Rambaut 2007) excluding the first 10% of phylogenies as burn-in.

RESULTS

Single Nucleotide Polymorphism (SNP) Data

After removing low-quality reads, we retained a total of 180,955,081 reads from 93 samples (data are available Klicka et al. 2022). The lowest coverage individual, UWBM 85583 *R. r. mariae* (Mariana Islands - Rota), had only 35,743 reads and, therefore, this sample and 3 other low-coverage samples (BPBM 184607, BPBM 18478, KUNHM 33896) were not included in subsequent analyses, bringing the total number of individuals down to 89 (Table 2). The 89 remaining samples had a mean of 2,032,801 reads per individual (range: 138,410–13,321,108; SD = 2,101,273). We determined that no significant differences existed in population differentiation or population relationships between the different data matrices produced by altering the parameters (*-M*, *-m*, *-n*) within the STACKS pipeline (Supplementary Material Figure 1). Therefore, we present only the results from the 70% complete matrix using the parameters *-M* 2, *-m* 3, and *-n* 3 (which contained 5,625 loci). For analyses that assume marker independence (i.e., STRUCTURE, TreeMix) a single SNP was retained per locus.

Phylogeny

Using 11,340 concatenated SNPs from 5,625 loci for 89 individuals, we recovered concordant phylogenies for both Bayesian and ML analyses with generally high nodal support. For clarity, we only discuss the ML phylogeny further, but the Bayesian tree can be found in Supplementary Material Figure 2. We rooted the phylogeny using *R. dahli* (Nyári et. al. 2009), and we identified 7 well-supported lineages within the *R. rufifrons* complex (Figure 2). *Rhipidura dryas* contained 2 independent lineages that together formed the sister group to the *R. rufifrons* complex. The oldest relationship in the *R. rufifrons* complex was hypothesized to be between the Australian *R. rufifrons* populations (Clade I; *R. r. rufifrons* and *R. r. intermedia*) and all other *R. rufifrons* lineages. Clade II was composed

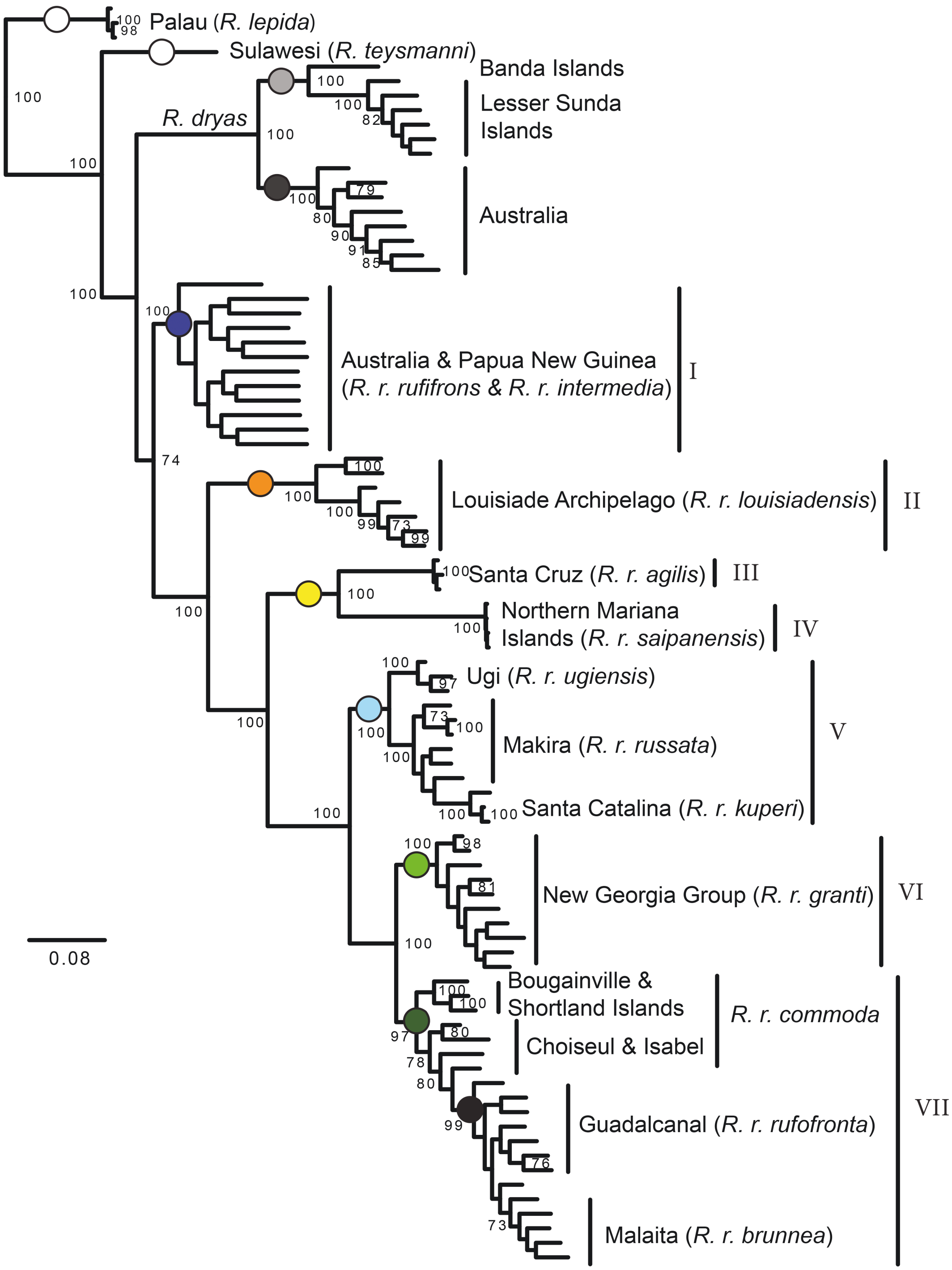

FIGURE 2. Maximum likelihood phylogeny obtained using RAxML for the 70% minimum representation SNP dataset with node support determined by rapid bootstrapping and only shown for relationships receiving BS > 70. The outgroup *R. dahli* has been removed from the phylogeny. Lineages currently described as *R. rufifrons* are labeled as Clades I–VII.

of individuals from across the Louisiade Archipelago (*R. r. louisiadensis*), and it shares a most recent common ancestor with the remaining 5 well-supported lineages (Clades III–VIII). Two isolated island taxa, *R. r. agilis* (Clade III; Santa Cruz) and *R. r. saipanensis* (Clade IV; Northern Mariana Islands), are sister taxa and together share a most recent common ancestor with all taxa from the Solomon Islands (Clades V–VII). The individuals of the southern Solomon Islands (Clade V; Ugi, Makira, Santa Catalina) have a sister relationship with individuals from the northern Solomon

Islands (Clades VI and VII). Within the northern Solomon Islands, New Georgia Group individuals (Clade VI) were sister to individuals from Bougainville, Shortland Islands, Choiseul, Isabel, Guadalcanal, and Malaita (Clade VII). The dated mtDNA phylogeny identified few well-supported nodes within *R. rufifrons*, but estimated a divergence age from *R. dryas* of 1.81 mya (95% highest posterior density [HPD]: 1.35–2.31 mya) (Supplementary Material Figure 3). In addition, the mtDNA phylogeny produced conflicting relationships relative to the SNP phylogeny. Most notably, mtDNA recovered individuals from the Northern Mariana Islands embedded within a clade containing samples from the northern Solomon Islands.

Population Genetics

Comparison of independent STRUCTURE runs using $K = 1–15$ (Figure 3) for only *R. rufifrons* individuals, yielded the highest likelihood score at $K = 5$. A calculation of ΔK identified $K = 2$ as the best population model; however, a second peak for ΔK was found for the 5-population model (i.e., $K = 5$) (Supplementary Material Figure 4). The 5-population model for STRUCTURE recovered the following populations: Australia (1), Louisiade Archipelago (2), Northern Mariana Islands (3), Greater Bukida (Bougainville, Shortland Islands, Choiseul, and Isabel), plus Guadalcanal, Malaita, and the New Georgia Group (4), and southern Solomon Islands (Santa Catalina, Makira, Ugi) (5). The individuals from Santa Cruz shared a genomic background with those from the Northern Mariana Islands and southern Solomon Island populations (Figure 3B). Hereafter, Solomon Islands will be used to refer to the geographic region of the Solomon Archipelago (i.e., Bougainville, Choisel, Isabel, Malaita, Guadalcanal, Makira, etc.), to the exclusion of the Santa Cruz Islands despite being politically part of the Solomon Islands.

STRUCTURE analyses using only samples from the Solomon Islands supported 3 populations ($K = 3$) as the preferred model based on ΔK values and raw likelihood scores (Figure 3C). The 3-population model placed the individuals from Makira, Ugi, and Santa Catalina into a cluster. Individuals from Malaita and Guadalcanal formed a second genetic cluster, and individuals from the New Georgia Group formed a third. The Greater Bukida individuals (i.e., those from Bougainville, Shortland Islands, Choiseul, and Isabel) showed varying levels of admixture between the second and third clusters (Figure 3C). A similar result was recovered in the 7-population model ($K = 7$) using the full dataset (Figure 3B).

DAPC analyses of genomic and z-linked loci converged on the same result and discriminated more population clusters (7) than STRUCTURE (5) when analyzing all of the *R. rufifrons* taxa jointly. The additional clusters identified by DAPC split Santa Cruz and the North Mariana Islands into distinct clusters, and individuals from the New Georgia Group were recognized as a single population to the exclusion of all other Solomon Island populations (Supplementary Material Figure 5).

Nucleotide diversity (π) within the Solomon Islands ranged from 0.037 to 0.063 nucleotide differences per site, with the majority of the genetic diversity represented by shared polymorphisms (Figure 4). Despite the small size of Ugi and the Santa Catalina Islands, each population from these islands contained similar genetic diversity estimates relative to the other Solomon Island populations (Figure 4). By contrast, nucleotide diversity of small but isolated island populations (e.g., Northern Mariana Islands and Santa Cruz) was comparatively low, even with equivalent sample sizes (i.e., Choiseul, Isabel, Santa Catalina, Ugi, and Bougainville) (Figure 4). Importantly, because the methods used to generate these diversity estimates were limited to variable genomic regions, they are likely overestimates of genetic diversity and comparisons should be limited to populations within this study.

Introgression

The species tree produced by TreeMix was topologically consistent with the RAxML phylogeny when zero migration edges were permitted. However, with the addition of migration to the TreeMix analyses, the New Georgia Group (Clade VI; *Rhipidura rufifrons granti*) was recovered as sister to Clades V and VII (Figure 5). With no migration edges, the species tree explained 97.58% of the variation in the SNP data. We added migration edges until they explained <0.2% of the data, resulting in 4 migration events. The first migration edge indicated gene flow between the Santa Cruz population and the ancestor of the populations on Makira (*R. r. russata*), Ugi (*R. r. ugiensis*), and Santa Catalina (*R. r. kuperi*; Figure 5), a result also supported in STRUCTURE analyses (Figure 1) The second migration edge paired the Australian populations of *R. dryas* and the Louisiade Archipelago (*R. r. louisiadensis*) population. The third migration edge also involved the Louisiade Archipelago population, but this time showing gene flow between *R. r. louisiadensis* and *R. teysmanni* (Sulawesi). The last migration edge indicated potential introgression between *R. teysmanni* (Sulawesi) and Clade V (Makira and Santa Catalina).

DISCUSSION

We examined relationships among 12 *R. rufifrons* subspecies in an explicit phylogenetic context. We found variable amounts of genomic divergence for the 12 named subspecies, and support for 7 lineages across analyses. We estimated *R. rufifrons* to be a recent radiation (1.35–2.31 mya), similar to the broadly sympatric radiation of white-eyes (*Zosterops*) (1.40–1.89 mya; Moyle et al. 2009), and it

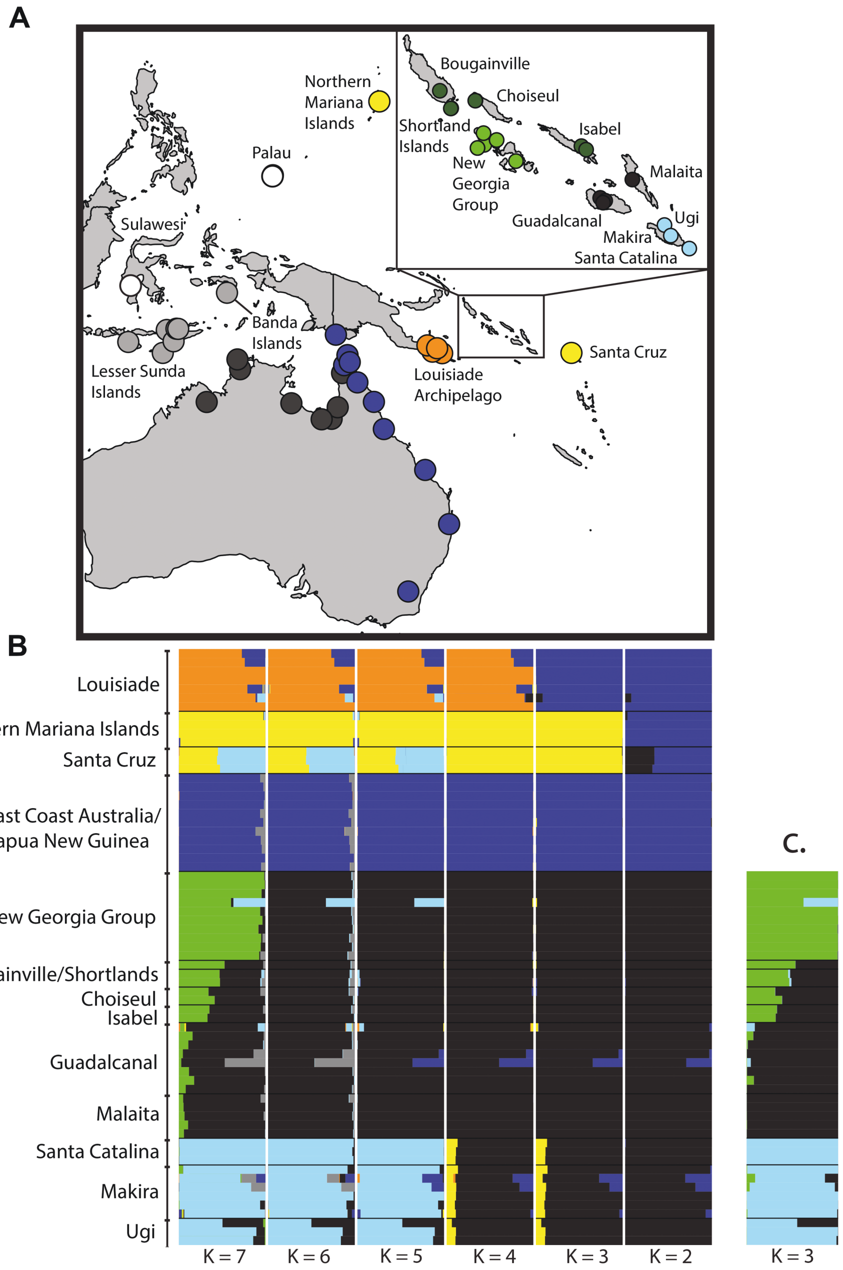

FIGURE 3. Sampling and genetic structure of the *Rhipidura rufifrons* species complex. (A) Sampling locations. Samples of *R. rufifrons* are colored according to their population assignment for the K = 7 STRUCTURE analysis. (B) STRUCTURE results for K = 2–7 using the 70% minimum representation SNP dataset with the outgroup samples removed. (C) STRUCTURE results for population model of K = 3 for Solomon Island individuals.

appears to be older than the diversification of Chestnut-bellied Monarchs (*Monarcha castaneiventris*) (0.40–0.98 mya; Uy et al. 2019).

Taxonomy

Six named subspecies within *R. rufifrons* were monophyletic in phylogenetic analyses with strong support (BS = 100: *R. r. louisiadensis*, *R. r. agilis*, *R. r. saipanensis*, *R. r. ugiensis*, *R. r. kuperi*, and *R. r. granti*). A seventh subspecies, *R. r. brunnea*, received only minimal support as a clade (BS = 73), but it is possible this was a result of sampling bias because all five samples were collected from the same site during the same field season. The remaining 5 subspecies did not form independent clades (*R. r. rufifrons*, *R. r. intermedia*, *R. r. russata*, *R. r. commoda*, and *R. r. rufofronta*). In the case of the Australian and Papua New Guinea taxa (Clade 1: *R. r. rufifrons* and *R. r. intermedia*), not a single node within Clade 1 received BS support above

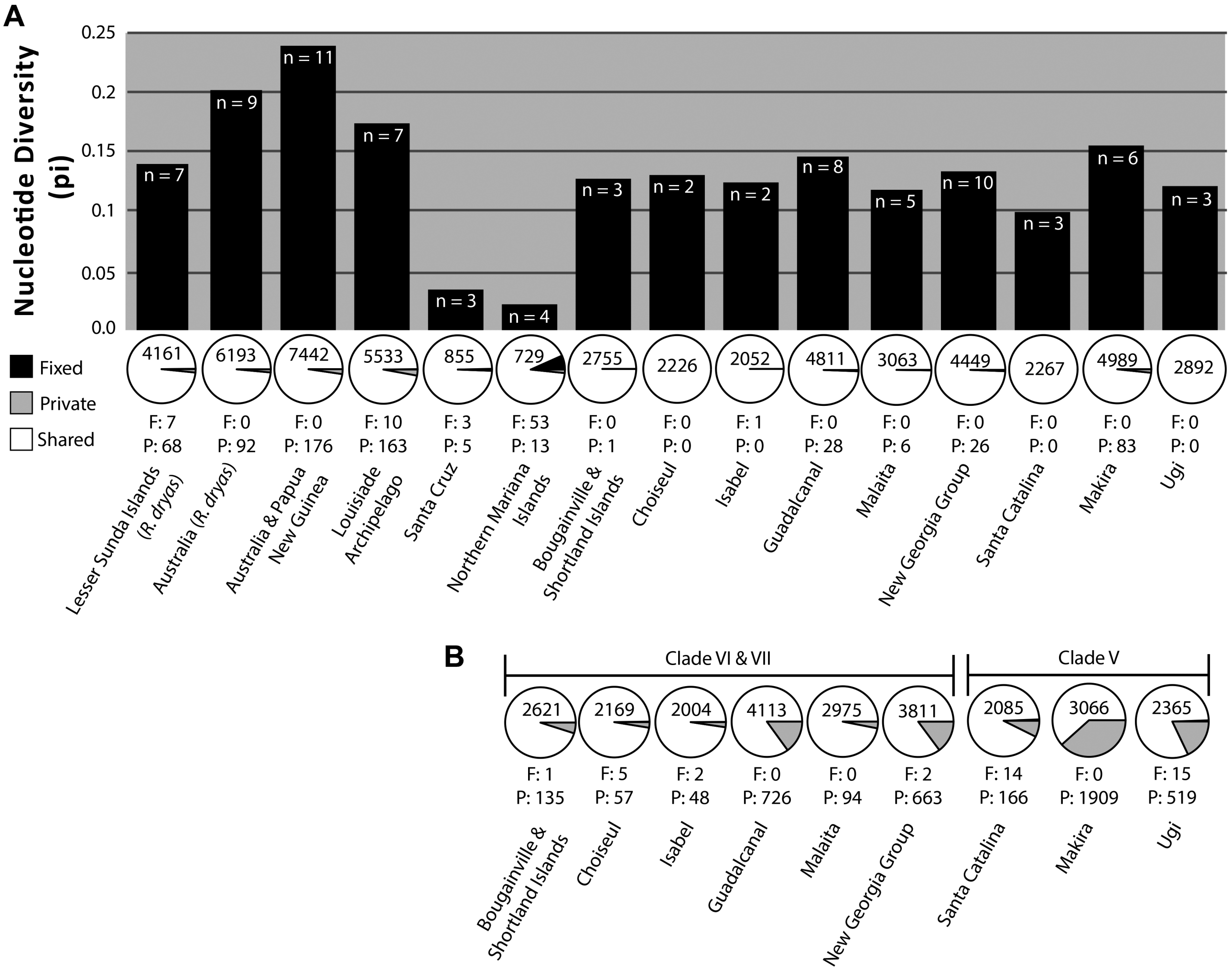

FIGURE 4. Genetic diversity for *Rhipidura rufifrons* and *R. dryas* populations. (A) Nucleotide diversity for each population is shown by the bar graph with sample sizes (*n*). Proportion of fixed differences (black), private alleles (gray), and shared polymorphisms (white) are represented as pie charts. Numbers within the pie chart represent number of shared polymorphisms, while numbers below represent counts of fixed differences (F) and private alleles (P) alleles. (B) Pie charts depicting the same values within Clades VI + VII and Clade V, separately.

31 in the RAxML analysis, suggestive of panmixia, and that these populations are more appropriately treated as one evolutionary unit. Genomic analyses indicated that *R. r. russata*, *R. r. rufofronta*, and *R. r. commoda* are paraphyletic designations, but individuals from Bougainville and Shortland islands were reciprocally monophyletic with the rest of Clade VII and could warrant consideration as an evolutionarily distinct taxon.

Louisiade Archipelago

The Louisiade Archipelago, located southeast of Papua New Guinea, harbors a diverse set of endemic taxa (e.g., Allison and Leisz 2009, Polhemus et al. 2004, Lavery et al. 2016, Linck et al. 2016), and recent phylogenetic studies (e.g., Kearns et al. 2013, Oliver et al. 2013, Andersen et al. 2014, 2015, Pedersen et al. 2018, Tu et al. 2018, McCullough et al. 2021) have supported the independence of endemic lineages with genetic data. In the most dramatic examples (e.g., Andersen et al. 2014), the Louisiade Archipelago populations are highly divergent and sister to species complexes that span the Australasian region. Similar to these studies, we recovered a deep phylogenetic split between *R. r. louisiadensis* and all other non-Australian subspecies of *R. rufifrons* (Figure 2). However, unlike *Pachycephala pectoralis* (Andersen et al. 2014), we recovered a pattern more consistent with the Louisiade Archipelago acting as an early stepping stone in the colonization of Melanesian and Micronesian islands. Regardless, the growing body of evidence across taxonomic groups (Colgan and Soheili 2008, Andersen et al. 2014, 2015, Shashank et al. 2014, Oliver et al. 2017), including our study, indicates a potentially important role for the Louisiade

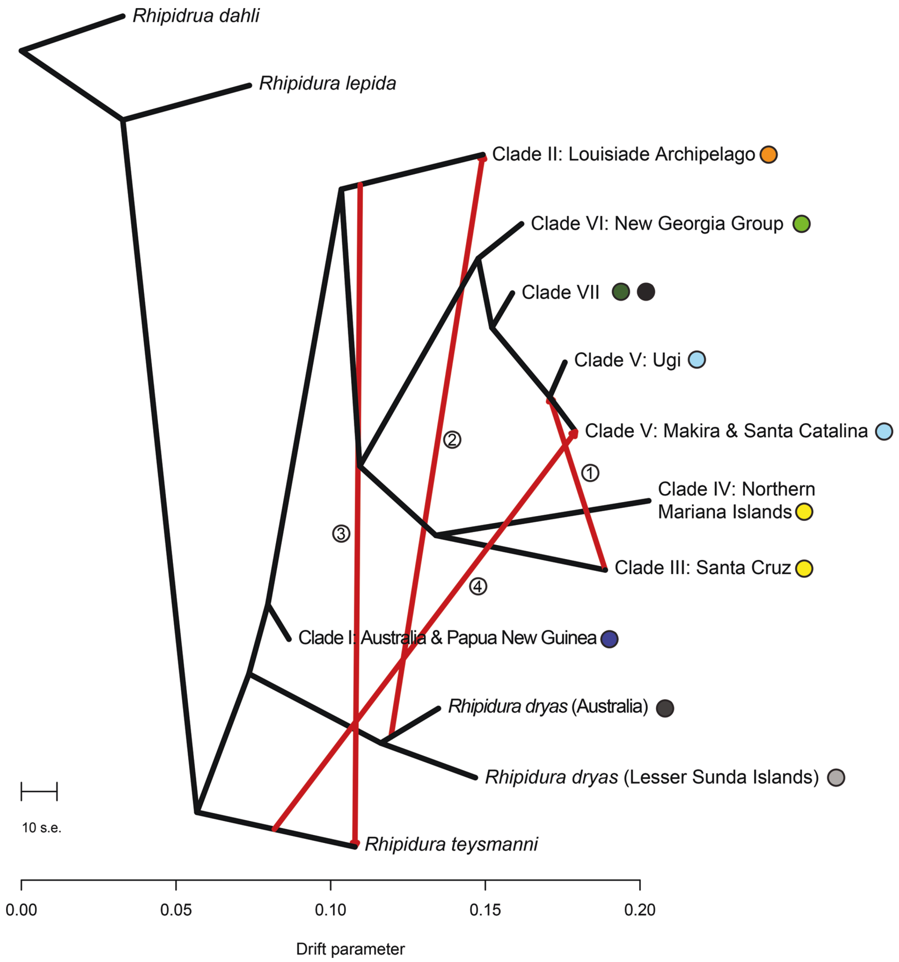

FIGURE 5. Species tree estimated in TreeMix for the *Rhipidura rufifrons* species complex using the 70% minimum representation dataset of SNPs (5,625 SNPs). Migration edges are numbered in the order that they were added and explain 0.73%, 0.466%, 0.345%, and 0.399% of the variation in the SNP data, respectively. Tips are labeled with geographic locations and clade assignments in accordance with Figure 2. Migration edges 2–4 should be interpreted with caution. The placement of these migration edges would likely be influenced by the inclusion of potentially independent ingroup lineages such as *R. r. torrida* (Molucca Islands) or *R. r. versicolor* (West Caroline Island; Yap).

Archipelago in the early diversification of lineages across the Southwest Pacific.

Geographically proximate to the Louisiade Archipelago, the island of New Guinea has played a significant role in diversification within the genus *Rhipidura*. New Guinea contains both highland and lowland species from across the *Rhipidura* phylogeny and New Guinea holds more species than any other geographic location (Nyári et al. 2009). However, New Guinea is conspicuously absent from the breeding distribution of the otherwise widespread *R. rufifrons* complex. The absence of *R. rufifrons* on New Guinea could be a consequence of many closely related species already inhabiting the island (i.e., competitive exclusion), in particular *R. rufidorsa* and *R. brachyrhyncha*, which are members of the same *Rhipidura* subclade as *R. rufifrons* (Nyári et al. 2009). However, while competitive exclusion is a compelling hypothesis for these abutting ranges, we do not have sufficient data to address it confidently. Of note, *Pachycephala pectoralis* sensu lato not only shares the biogeographic pattern of individuals from the Louisiade Archipelago sister to a radiation of Pacific lineages, but it is also absent from New Guinea despite its otherwise broad distribution. Therefore, this pattern of the Louisiade Archipelago playing a prominent role in the diversification of Pacific lineages may be limited to taxa that are otherwise absent from New Guinea.

Remote Island Populations

The two most geographically remote taxa in our dataset, *R. r. saipanensis* (Northern Mariana Islands) and *R. r. agilis* (Santa Cruz), are separated from the nearest sampled *R. rufifrons* population by over 2,600 km and 400 km, respectively. Furthermore, they are separated from one another by a distance of over 3,600 km of open ocean, and yet were recovered as sister lineages in our analysis of genomic SNPs. In contrast, phylogenetic analysis of the mtDNA (ND2) supported individuals from the Northern Mariana Islands embedded within a clade containing the Solomon Island taxa rather than sister to individuals from Santa Cruz. Discordance between nuclear and mitochondrial genomes is not uncommon (Toews and Brelsford 2012, Campillo et al. 2018), and explanations for incongruence include incomplete lineage sorting, sex-biased hybridization, sex-biased dispersal, and selection. However, explicit tests for gene flow (see below) did not identify any involving the Mariana Islands population, but instead supported gene flow between Santa Cruz Island and Solomon Island populations. Although explanations that invoke introgression cannot be excluded, we did not find genomic evidence for gene flow between the Solomon Islands and the Northern Mariana Islands. Furthermore, in a situation with several short internodes, as is the case for *R. rufifrons*, we expect the number of incongruent gene trees to increase and the probability of any one locus reflecting the true species tree to decrease. On average, we expect mtDNA to coalesce faster than a nuclear marker because of the smaller effective population size. However, when examining several thousand independent and putatively neutral loci we expect some of those loci to coalesce faster than mtDNA and potentially provide phylogenetic resolution. Therefore, we find the most likely cause for mito-nuclear discordance within *R. rufifrons* to be incomplete lineage sorting in mtDNA.

The sister relationship of Northern Mariana and Santa Cruz lineages supported by the genomic data suggests that a single dispersive ancestor may have quickly colonized archipelagos across the Pacific Ocean. Unfortunately, because of incomplete sampling (see Introduction for details on which taxa were excluded) it is difficult to determine the relative importance of multiple colonization events or in situ diversification in the evolutionary history of the *R. rufifrons* complex. In other avian systems with isolated island archipelago populations, researchers have shown that co-occurring lineages often are not sister taxa (Cibois et al. 2007, 2011, Ryan et al. 2013). Further, it is becoming increasingly clear that lineages on the Mariana Islands have unexpected evolutionary relationships. For example, Cibois et al. (2011) found that populations of reed-warblers (genus *Acrocephalus*) on the Mariana Islands were not monophyletic, and instead the result of multiple colonization events. In other, non-avian systems, populations on the Northern Mariana Islands were undifferentiated from the other island isolates of Micronesia (Tonione et al. 2016), or were undifferentiated across Micronesia, Polynesia, and Melanesia (Klein et al. 2016). Here, we find support for a deeply divergent lineage on the Mariana Islands having a sister relationship to another remote island population. More complete sampling of Pacific lineages, however, would enable a more robust reconstruction of the biogeographic history for this part of the *R. rufifrons* complex.

Solomon Islands

Currently 7 taxa are recognized within the *R. rufifrons* species complex in the Solomon Islands: *R. r. ugiensis*, *R. r. russata*, *R. r. kuperi*, *R. r. granti*, *R. r. commoda*, *R. r. rufofronta*, and *R. r. brunnea*. However, we found genetic evidence for only 3 genomic backgrounds (Figure 3B, C) pertaining to the New Georgia Group, Malaita and Guadalcanal, and Makira, Ugi, and Santa Catalina populations. Furthermore, only subtle genetic structure existed between populations from Malaita (*R. r. brunnea*) and Guadalcanal (*R. r. rufofronta*). Although Malaita is an oceanic island that hosts many endemic bird species (Mayr and Diamond 2001), we did not find strong or consistent evidence for a distinct Malaitan taxon, a pattern common to mammalian systems in the region (Lavery et al. 2016). One explanation could be that *R. rufifrons* may have recently colonized Malaita without sufficient time for genetic differentiation. If colonization was recent, we would expect Malaitan populations to exhibit lower genetic diversity compared to other islands, contrary to our results (Figure 4). Alternatively, recent or ongoing gene flow between Guadalcanal and Malaita may have prevented genetic divergence between the two populations while maintaining relatively high genetic diversity. In fact, STRUCTURE suggested a broader pattern of isolation by distance (see Gene Flow section below) that not only included all the populations from Clade VII (Figure 3C) but also the New Georgia Group individuals that form Clade VI. Glacial cycling in the Pleistocene created numerous land bridge connections within the Solomon Islands (Mayr and Diamond 2001) and is likely a cause for the close association between avifaunas on some islands. However, the pattern for *R. rufifrons* cannot be explained simply by Pleistocene glacial cycles. That is, despite Bougainville, Choiseul, and Isabel having been most likely connected by land bridges to form the Greater Bukida Islands, Guadalcanal was likely never physically connected to this group, although the water barrier was perhaps less than 2 km (Neall and Trewick 2008, Becker et al. 2009). Furthermore, Malaita and the New Georgia Group are surrounded by deep water and remained isolated from other islands by channels ranging in size of 20–50 km.

Populations from the island of Makira (*R. r. russata*) and its satellites Ugi (*R. r. ugiensis*) and Santa Catalina (*R. r. kuperi*) in the southeastern part of the Solomon Archipelago form another well-supported clade. *Rhipidura r. ugiensis* is an isolated taxon on a small island with distinct melanistic plumage along the throat and chin. This likely adds to several well-documented examples of the evolution of melanism on small islands in this region (Uy et al. 2009, 2016, Uy and Vargas-Castro 2015). *Rhipidura r. ugiensis* along with *Monarcha castaneiventris ugiensis* and *Symposiachrus vidua squamulatus* form a trio of avian subspecies on Ugi that are easily identified by plumage. Despite the distinct phenotype for *R. r. ugiensis* individuals, we did not consistently observe genomic differentiation between the Makira and Ugi populations across all analyses. A similar pattern of distinct plumage but limited genetic differentiation was recovered for *M. castaneiventris ugiensis* (Cooper and Uy 2017). Furthermore, a lack of genetic divergence for Ugi populations was also found for the arboreal skink, *Corucia zebrata*, despite diversification among, and even within, other Solomon Islands (Hagen et al. 2012).

In contrast to *R. r. ugiensis*, the Makira (*R. r. russata*) and Santa Catalina (*R. r. kuperi*) populations were not recovered as reciprocally monophyletic with respect to each other. Instead, Santa Catalina individuals formed a clade embedded within a paraphyletic group from Makira (Figure 5, Clade V). These results suggest that *R. r. kuperi* is a result of recent colonization of Santa Catalina by the Makira population, and that there has been insufficient time for complete lineage sorting.

Gene Flow

Although we recovered phylogenetic structure among many closely related allopatric populations, we also found evidence of possible gene flow between allopatric taxa across vast geographic distances. For example, TreeMix indicated gene flow between *R. r. agilis* (Santa Cruz, Clade III) and the common ancestor of Clade V (Ugi, Makira, and Santa Ana). The migration edge between *R. r. agilis* and Clade V accounted for 0.73% of the variance in the genomic dataset. In addition to TreeMix analyses, STRUCTURE analyses for all values of *K* indicated a shared genomic background for Santa Cruz individuals and individuals from Ugi, Makira, and Santa Catalina. Therefore, despite nearly 400 km of open ocean between them, these populations have maintained shared genomic variation.

The placement of the first migration edge discussed above was within a region of the phylogeny with thorough sampling, and thus we are confident in its reality. However, the interpretation of the other 3 inferred migration edges is less straightforward. This is because the three additional migration edges involved outgroup taxa. Placement of these migration edges would likely be influenced by the inclusion of potentially independent ingroup lineages such as *R. r. torrida* (Molucca Islands) or *R. rufifrons* individuals from Rossel Island (Louisiade Archipelago). Unfortunately, modern sampling was not available for Indonesian taxa like *R. r. torrida*, and the sample from Rossel Island that we sampled did not produce enough useable data to be included in our final dataset. Thus, while we find support for gene flow between Santa Cruz and Clade V, we caution against over-interpretation of the other three migration events inferred by TreeMix until more complete sampling for *R. dryas* and *R. rufifrons* is available.

Although individuals from Bougainville, Shortland Islands, Choiseul, and Isabel (Clade VII) shared 30% or more of their genomic background with New Georgia Group (Clade VI) samples in a $K = 3$ population model for Solomon Island samples (Figure 3C), none of the 4 migration events inferred by TreeMix involved either of these clades. Phylogenetic analyses recovered the monophyly of Clade VI and the monophyly of the Bougainville and Shortland Island individuals with strong support, but both groups contained few fixed genetic differences (Figure 4). Considering the contrasting results recovered by clustering, phylogeny, and species tree analyses, populations from the northern Solomon Islands clearly warrant further investigation.

Conclusions

In this study, we find that current taxonomy aligns with genetic clades for *R. r. louisiadensis*, *R. r. agilis*, *R. r. saipanensis*, *R. r. ugiensis*, and *R. r. granti*. In other instances, continued recognition of taxa, such as *R. r. kuperi* or *R. r. brunnea*, will render other named subspecies as paraphyletic, which is perhaps expected in lineages, like *R. rufifrons*, that have recently diversified.

Furthermore, we identified several biogeographic patterns of broad interest. First, the Louisiade Archipelago contains a distinct population of the *R. rufifrons* complex that is sister to all remaining Pacific lineages. In combination with similar patterns in other taxonomic groups, our results indicate that this small island archipelago has been important in the early diversification of *R. rufifrons* and other terrestrial lineages. We also discovered that individuals from the Northern Mariana Islands (*R. r. saipanensis*) formed a sister relationship with individuals from the Santa Cruz group, again highlighting a common pattern whereby birds from the Mariana Islands do not form sister relationships with the nearest sampled conspecific population (Cibois et al. 2011, Andersen et al. 2015). Within the Solomon Islands, Malaita, the New Georgia Group, and Makira remained isolated from other major Solomon Islands during the Pleistocene, yet *R. r. brunnea* from Malaita was not supported as an independent lineage. In addition, we uncovered evidence of gene flow between populations that are distantly isolated from one another (i.e., separated by ~400 km of open ocean). This research adds to the growing body of literature for systems exhibiting rapid phenotypic evolution despite recent or ongoing gene flow in some situations. Furthermore, despite varied life histories and dispersal ability between taxa representing rapid radiations, convergent patterns of diversification in the Indo-Pacific are beginning to emerge.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithology* online.

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Data Availability: Analysis reported in this article can be reproduced using the data provided by Klicka et al. (2022).

LITERATURE CITED

Allison, A., and S. Leisz (2009). Analysis of the Impacts of Climate Change on the Herpetofauna of the Papuan Region (New Guinea to the Solomon Islands). Bishop Museum, Honolulu, HI, USA.

Andersen, M. J., Á. S. Nyári, I. Mason, L. Joseph, J. P. Dumbacher, C. E. Filardi, and R. G. Moyle (2014). Molecular systematics of the world's most polytypic bird: The *Pachycephala pectoralis/melanura* (Aves: Pachycephalidae) species complex. Zoological Journal of the Linnean Society 170:566–588.

Andersen, M. J., C. H. Oliveros, C. E. Filardi, and R. G. Moyle (2013). Phylogeography of the Variable Dwarf-Kingfisher *Ceyx Lepidus* (Aves: Alcedinidae) inferred from mitochondrial and nuclear DNA sequences. The Auk: Ornithological Advances 130:118–131.

Andersen, M. J., H. T. Shult, A. Cibois, J. C. Thibault, C. E. Filardi, and R. G. Moyle (2015). Rapid diversification and secondary sympatry in Australo-Pacific kingfishers (Aves: Alcedinidae: *Todiramphus*). Royal Society Open Science 2:140375.

Andolfatto, P., D. Davison, D. Erezyilmaz, T. T. Hu, J. Mast, T. Sunayama-Morita, and D. L. Stern (2011). Multiplexed shotgun genotyping for rapid and efficient genetic mapping. Genome Research 21:610–617.

Becker, J. J., D. T. Sandwell, W. H. F. Smith, J. Braud, B. Binder, J. L. Depner, D. Fabre, J. Factor, S. Ingalls, S. H. Kim, et al. (2009). Global bathymetry and elevation data at 30 arc seconds resolution: SRTM30_PLUS. Marine Geodesy 32:355–371.

Birdlife International and Handbook of the Birds of the World (2019). Bird Species Distribution Maps of the World, Version 2019.1. http://datazone.birdlife.org/species/requestdis

Boles, W., and D. Christie (2019). Rufous Fantail (*Rhipidura rufifrons*). In Handbook of the Birds of the World Alive (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana, Editors). Lynx Edicions, Barcelona, Spain.

Bouckaert, R., T. G. Vaughan, J. Barido-Sottani, S. Duchêne, M. Fourment, A. Gavryushkina, J. Heled, G. Jones, D. Kühnert, N. De Maio, et al. (2019). BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. PLoS Computational Biology 15:e1006650.

Campagna, L., I. Gronau, L. F. Silveira, A. Siepel, and I. J. Lovette (2015). Distinguishing noise from signal in patterns of genomic divergence in a highly polymorphic avian radiation. Molecular Ecology 24:4238–4251.

Campillo, L. C., C. H. Oliveros, F. H. Sheldon, and R. G. Moyle (2018). Genomic data resolve gene tree discordance in spiderhunters (Nectariniidae, Arachnothera). Molecular Phylogenetics and Evolution 120:151–157.

Catchen, J. M., A. Amores, P. Hohenlohe, W. Cresko, and J. H. Postlethwait (2011). Stacks: building and genotyping loci de novo from short-read sequences. G3: Genes, Genomes, Genetics 1:171–182.

Cibois, A., J. S. Beadell, G. R. Graves, E. Pasquet, B. Slikas, S. A. Sonsthagen, J. C. Thibault, and R. C. Fleischer (2011). Charting the course of reed-warblers across the Pacific islands. Journal of Biogeography 38:1963–1975.

Cibois, A., J. C. Thibault, and E. Pasquet (2007). Uniform phenotype conceals double colonization by reed-warblers of a remote Pacific archipelago. Journal of Biogeography 34:1150–1166.

Clements, J. F., T. S. Schulenberg, M. J. Iliff, S. M. Billerman, T. A. Fredericks, J. A. Gerbracht, D. Lepage, B. L. Sullivan, and C. L. Wood (2021). The eBird/Clements Checklist of Birds of the World: v2021. http://www.birds.cornell.edu/clementschecklist/download/.

Colgan, D. J., and S. Soheili (2008). Evolutionary Lineages in *Emballonura* and *Mosia* Bats (Mammalia: Microchiroptera) from the Southwestern Pacific. Pacific Science 62:219–232.

Cooper, E. A., and J. A. C. Uy (2017). Genomic evidence for convergent evolution of a key trait underlying divergence in island birds. Molecular Ecology 26:3760–3774.

Darriba, D., G. L. Taboada, R. Doallo, and D. Posada (2012). jModelTest 2: More models, new heuristics and parallel computing. Nature Methods 9:772–772.

Darwin, C. (1859). On the Origin of Species. John Murray, London, UK.

Diamond, J. M. (1974). Colonization of exploded volcanic islands by birds: The supertramp strategy. Science 184:803–806.

Diamond, J. M., M. E. Gilpin, and E. Mayr (1976). Species-distance relation for birds of the Solomon Archipelago, and the paradox of the great speciators. Proceedings of the National Academy of Sciences USA 73:2160–2164.

Drummond, A. J., and A. Rambaut (2007). BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evolutionary Biology 7:214.

Edwards, S. V., P. Arctander, and A. C. Wilson (1991). Mitochondrial resolution of a deep branch in the genealogical tree for perching birds. Proceedings of the Royal Society of London B: Biological Sciences 243:99–107.

Evanno, G., S. Regnaut, and J. Goudet (2005). Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Molecular Ecology 14:2611–2620.

Filardi, C. E., and R. G. Moyle (2005). Single origin of a pan-Pacific bird group and upstream colonization of Australasia. Nature 438:216–219.

Hackett, S. J. (1996). Molecular phylogenetics and biogeography of tanagers in the genus *Ramphocelus* (Aves). Molecular Phylogenetics and Evolution 5:368–382.

Hagen, I. J., S. C., Donnellan, C. M. Bull (2012). Phylogeography of the prehensile-tailed skink *Corucia zebrata* on the Solomon Archipelago. Ecology and Evolution 2:1220–1234.

Irestedt, M., P. H. Fabre, H. Batalha-Filho, K. A. Jønsson, C. S. Roselaar, G. Sangster, and P. G. Ericson (2013). The spatio-temporal colonization and diversification across the Indo-Pacific by a "great speciator"(Aves, *Erythropitta erythrogaster*). Proceedings of the Royal Society of London B: Biological Sciences 280:20130309.

Jombart, T. (2008). adegenet: a R package for the multivariate analysis of genetic markers. Bioinformatics 24:1403–1405.

Jombart, T., and I. Ahmed (2011). adegenet 1.3-1: New tools for the analysis of genome-wide SNP data. Bioinformatics 27:3070–3071.

Jombart, T., S. Devillard, and F. Balloux (2010). Discriminant analysis of principal components: A new method for the analysis of genetically structured populations. BMC Genetics 11:94.

Jønsson, K. A., M. Irestedt, L. Christidis, S. M. Clegg, B. G. Holt, and J. Fjeldså (2014). Evidence of taxon cycles in an Indo-Pacific passerine bird radiation (Aves: *Pachycephala*). Proceedings of the Royal Society of London B: Biological Sciences 281:20131727.

Kearns, A. M., L. Joseph, and L. G. Cook (2013). A multilocus coalescent analysis of the speciational history of the Australo-Papuan butcherbirds and their allies. Molecular Phylogenetics and Evolution 66:941–952.

Klein, E. R., R. B. Harris, R. N. Fisher, and T. W. Reeder (2016). Biogeographical history and coalescent species delimitation of Pacific island skinks (Squamata: Scincidae: *Emoia cyanura* species group). Journal of Biogeography 43:1917–1929.

Klicka, L. B., L. C. Campillo, J. D. Manthey, M. J. Andersen, J. P. Dumbacher, C. E. Filardi, L. Joseph, J. A. C. Uy, D. E. Weidemann, and R. G. Moyle (2022). Data from: Genomic and geographic diversification of a "great-speciator" (Rhipidura rufifrons). Ornithology 140:ukac049. doi:10.5061/dryad.1wstqjxx

Koblmüller, S., B. Egger, C. Sturmbauer, and K. M. Sefc (2010). Rapid radiation, ancient incomplete lineage sorting and ancient hybridization in the endemic Lake Tanganyika cichlid tribe *Tropheini*. Molecular Phylogenetics and Evolution 55:318–334.

Lavery, T. H., A. D. Olds, J. M. Seddon, and L. K. P. Leung (2016). The mammals of northern Melanesia: Speciation, ecology, and biogeography. Mammal Review 46:60–76.

Lerner, H. R. L., M. Meyer, H. F. James, M. Hofreiter, and R. C. Fleischer (2011). Multilocus resolution of phylogeny and timescale in the extant adaptive radiation of Hawaiian Honeycreepers. Current Biology 21:1838–1844.

Li, H., and R. Durbin (2009). Fast and accurate short read alignment with Burrows–Wheeler transform. Bioinformatics 25:1754–1760.

Linck, E., S. Schaack, and J. P. Dumbacher (2016). Genetic differentiation within a widespread "supertramp" taxon: Molecular phylogenetics of the Louisiade White-eye (*Zosterops griseotinctus*). Molecular Phylogenetics and Evolution 94:113–121.

Losos, J. B., T. R. Jackman, A. Larson, K. D. Queiroz, and L. Rodríguez-Schettino (1998). Contingency and determinism in replicated adaptive radiations of island lizards. Science 279:2115–2118.

MacArthur, R. H., and E. O. Wilson (1963). An equilibrium theory of insular zoogeography. Evolution 17:373–387.

MacArthur, R. H., and E. O. Wilson (1967). The Theory of Island Biogeography. Princeton University Press, Princeton, NJ, USA.

Manthey, J. D., L. C. Campillo, K. J. Burns, and R. G. Moyle (2016). Comparison of target-capture and restriction-site associated DNA sequencing for phylogenomics: A test in Cardinalid Tanagers (Aves, Genus: *Piranga*). Systematic Biology 65:640–650.

Manthey, J. D., C. H. Oliveros, M. J. Andersen, C. E. Filardi, and R. G. Moyle (2020). Gene flow and rapid differentation characterize a rapid insular radiation in the southwest Pacific (Aves: Zosterops). Evolution 74:1788–1803.

Mayr, E. (1942). Systematics and The Origin of Species: From The Viewpoint of A Zoologist. Harvard University Press, Cambridge, MA, USA.

Mayr, E., and J. Diamond (2001). The Birds of Northern Melanesia: Speciation, Ecology, and Biogeography. Oxford Universiy Press, New York, NY, USA.

Mayr, E., and M. Moynihan (1946). Evolution in the *Rhipidura rufifrons* group. American Museum Novitates 1321:1–21.

McCullough, J. M., E. F. Gyllenhaal, X. M. Mapel, M. J. Andersen, and L. Joseph (2021). Taxonomic implications of recent molecular analyses of Spectacled (*Symposiachrus trivirgatus*) and Spotted (S. *guttula*) Monarch flycatchers (Passeriformes: Monarchidae). Emu–Austral Ornithology 121:365–371.

Milá, B., B. H. Warren, P. Heeb, and C. Thébaud (2010). The geographic scale of diversification on islands: Genetic and morphological divergence at a very small spatial scale in the

Mascarene grey white-eye (Aves: *Zosterops borbonicus*). BMC Evolutionary Biology 10:1–13.

Miller, M. R., J. P. Dunham, A. Amores, W. A. Cresko, and E. A. Johnson (2007). Rapid and cost-effective polymorphism identification and genotyping using restriction site associated DNA (RAD) markers. Genome Research 17:240–248.

Moyle, R. G., C. E. Filardi, C. E. Smith, and J. Diamond (2009). Explosive Pleistocene diversification and hemispheric expansion of a "great speciator". Proceedings of the National Academy of Sciences USA 106:1863–1868.

Neall, V. E., and S. A. Trewick (2008). The age and origin of the Pacific islands: A geological overview. Philosophical Transactions of the Royal Society B: Biological Sciences 363:3293–3308.

Nyári, Á. S., B. W. Benz, K. A. Jønsson, J. Fjeldså, and R. G. Moyle (2009). Phylogenetic relationships of fantails (Aves: Rhipiduridae). Zoologica Scripta 38:553–561.

Oliver, L. A., E. N. Rittmeyer, F. Kraus, S. J. Richards, and C. C. Austin (2013). Phylogeny and phylogeography of *Mantophryne* (Anura: Microhylidae) reveals cryptic diversity in New Guinea. Molecular Phylogenetics and Evolution 67:600–607.

Oliver, P. M., S. L. Travers, J. Q. Richmond, P. Pikacha, and R. N. Fisher (2017). At the end of the line: independent overwater colonizations of the Solomon Islands by a hyperdiverse trans-Wallacean lizard lineage (*Cyrtodactylus*: Gekkota: Squamata). Zoological Journal of the Linnean Society 182:681–694.

Pedersen, M. P., M. Irestedt, L. Joseph, C. Rahbek, and K. A. Jønsson (2018). Phylogeography of a "great speciator" (Aves: *Edolisoma tenuirostre*) reveals complex dispersal and diversification dynamics across the Indo-Pacific. Journal of Biogeography 45:826–837.

Pickrell, J., and J. Pritchard (2012). Inference of population splits and mixtures from genome-wide allele frequency data. PLoS Genetics 8:e1002967.

Polhemus, D. A., G. R. Allen, and R. A. Englund (2004). Freshwater Biotas of New Guinea and Nearby Islands: An Analysis of Endemism, Richness, and Threats. Vol. 31. Bishop Museum, Washington, D.C., USA.

Pratt, H. D. (2010). Revisiting species and subspecies of island birds for a better assessment of biodiversity. In Avian Subspecies (K. Winker and S. M. Haig, Editors). Ornithological Monographs 67:78–89.

Pritchard, J. K., M. Stephens, and P. Donnelly (2000). Inference of population structure using multilocus genotype data. Genetics 155:945–959.

Rees, D. J., B. C. Emerson, P. Oromí, and G. M. Hewitt (2001). The diversification of the genus *Nesotes* (Coleoptera: Tenebrionidae) in the Canary Islands: Evidence from mtDNA. Molecular Phylogenetics and Evolution 21:321–326.

Ryan, P. G., L. B. Klicka, K. F. Barker, and K. J. Burns (2013). The origin of finches on Tristan da Cunha and Gough Island, central South Atlantic Ocean. Molecular Phylogenetics and Evolution 69:299–305.

Shashank, P., A. Chakravarthy, B. Raju, and K. Bhanu (2014). DNA barcoding reveals the occurrence of cryptic species in host-associated population of *Conogethes punctiferalis* (Lepidoptera: Crambidae). Applied Entomology and Zoology 49:283–295.

Stamatakis, A. (2014). RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30:1312–1313.

Toews, D. P., and A. Brelsford (2012). The biogeography of mitochondrial and nuclear discordance in animals. Molecular Ecology 21:3907–3930.

Tonione, M. A., R. N. Fisher, C. Zhu, and C. Moritz (2016). Deep divergence and structure in the Tropical Oceanic Pacific: A multilocus phylogeography of a widespread gekkonid lizard (Squamata: Gekkonidae: *Gehyra oceanica*). Journal of Biogeography 43:268–278.

Tu, N., M. Yang, D. Liang, and P. Zhang (2018). A large-scale phylogeny of Microhylidae inferred from a combined dataset of 121 genes and 427 taxa. Molecular Phylogenetics and Evolution 126:85–91.

Uy, J. A. C., E. A. Cooper, and J. A. Chaves (2019). Convergent melanism in populations of a Solomon Island flycatcher is mediated by unique genetic mechanisms. Emu-Austral Ornithology 119:242–250.

Uy, J. A. C., E. A. Cooper, S. Cutie, M. R. Concannon, J. W. Poelstra, R. G. Moyle, and C. E. Filardi (2016). Mutations in different pigmentation genes are associated with parallel melanism in island flycatchers. Proceedings of the Royal Society B: Biological Sciences 283:20160731.

Uy, J. A. C., R. G. Moyle, C. E. Filardi, and Z. A. Cheviron (2009). Difference in plumage color used in species recognition between incipient species is linked to a single amino acid substitution in the melanocortin-1 receptor. The American Naturalist 174:244–254.

Uy, J. A. C., and L. E. Vargas-Castro (2015). Island size predicts the frequency of melanic birds in the color-polymorphic flycatcher *Monarcha castaneiventris* of the Solomon Islands. The Auk: Ornithological Advances 132:787–794.

Wallace, A. (1881). Island Life. Harper and Brothers, New York, NY, USA.