Molecular Phylogenetics and Evolution 166 (2022) 107333

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

Population connectivity across a highly fragmented distribution: Phylogeography of the *Chalcophaps* doves

Devon A. DeRaad [a,*], Joseph D. Manthey [b], Emily N. Ostrow [a], Lucas H. DeCicco [a], Michael J. Andersen [c], Peter A. Hosner [d], Hannah T. Shult [a], Leo Joseph [e], John P. Dumbacher [f], Robert G. Moyle [a]

[a] Biodiversity Institute and Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS 66045, USA
[b] Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409, USA
[c] Department of Biology and Museum of Southwestern Biology, University of New Mexico, Albuquerque, NM 87106, USA
[d] Natural History Museum of Denmark and Center for Global Mountain Biodiversity, University of Copenhagen, Copenhagen, Denmark
[e] Australian National Wildlife Collection, CSIRO National Research Collections Australia, GPO Box 1700, Canberra, ACT 2601, Australia
[f] California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118, USA

ARTICLE INFO

Keywords:
Phylogeography
Evolution
Isolation by distance
Mitonuclear discordance
Phylogenetics
Chalcophaps

ABSTRACT

Chalcophaps is a morphologically conserved genus of ground-walking doves distributed from India to mainland China, south to Australia, and across the western Pacific to Vanuatu. Here, we reconstruct the evolutionary history of this genus using DNA sequence data from two nuclear genes and one mitochondrial gene, sampled from throughout the geographic range of *Chalcophaps*. We find support for three major evolutionary lineages in our phylogenetic reconstruction, each corresponding to the three currently recognized *Chalcophaps* species. Despite this general concordance, we identify discordant mitochondrial and nuclear ancestries in the subspecies *C. longirostris timorensis,* raising further questions about the evolutionary history of this Timor endemic population. Within each of the three species, we find evidence for isolation by distance or hierarchical population structure, indicating an important role for geography in the diversification of this genus. Despite being distributed broadly across a highly fragmented geographic region known as a hotspot for avian diversification, the *Chalcophaps* doves show modest levels of phenotypic and genetic diversity, a pattern potentially explained by strong population connectivity owing to high overwater dispersal capability.

1. Introduction

Evolutionary biology has long sought to understand the processes generating patterns of biodiversity seen on earth today (MacArthur and Wilson, 1967; Mayr, 1942; Moyle et al., 2016; Smith et al., 2014). New lineages are generated when the diversifying forces of drift and local adaptation overwhelm the homogenizing forces of migration and gene flow (Slatkin, 1987). Populations separated by biogeographic barriers will not exchange migrants, resulting in the gradual accumulation of differences. Conversely, interconnected populations continue to exchange migrants in a single pool of shared genetic diversity that prevents the development of private, locally adapted variants that might eventually lead to speciation (Coyne, 1992; Slatkin, 1987). By studying DNA sequence data from natural populations, investigators can begin to understand how this process of isolation and diversification is affected by the interaction between extrinsic biogeographic variables and the intrinsic biology of a given taxon.

Current understanding of how geography impacts lineage diversification has been developed in part via studies of avian biodiversity across the globe (Campagna et al., 2015; Irwin et al., 2018; Lovette, 2005; Manthey et al., 2011; Moyle et al., 2009). One key region for studying avian biogeography has been the western Pacific, which, due to its highly fragmented geography, generates ample opportunity for isolation and divergence between incipient lineages (Mayr and Diamond, 2001). Molecular biogeographic studies have regularly revealed cryptic genetic diversity throughout the complex island geography of the western

Abbreviations: IBD, isolation by distance; ND2, NADH dehydrogenase subunit 2; IQGAP2, IQ Motif Containing GTPase Activating Protein 2; GPBP, Goodpasture Antigen-binding Protein; MCMC, Markov chain Monte Carlo; mtDNA, mitochondrial DNA; PNG, Papua New Guinea.

* Corresponding author.
E-mail address: devonderaad@gmail.com (D.A. DeRaad).

https://doi.org/10.1016/j.ympev.2021.107333
Received 29 July 2021; Received in revised form 15 October 2021; Accepted 19 October 2021
Available online 21 October 2021

Pacific (Andersen et al., 2017; Hosner et al., 2018; Kyriazis et al., 2018; Lohman et al., 2010; Manthey et al., 2017). In the most extreme cases, iconic taxa such as white-eyes (*Zosterops*) are hyperdiverse and comprise dozens of species across the region, including island endemic species separated by as little as two kilometers of open ocean (Manthey et al., 2020; Moyle et al., 2009). In contrast, other taxa such as emerald doves (*Chalcophaps*) comprise only a handful of species, despite being distributed broadly throughout the western Pacific. Studying taxa on both ends of this spectrum of lineage diversity is crucial to understanding how a single biogeographic region can give rise to the disparate patterns of diversification observable among extant taxa.

Chalcophaps is a genus of ground-dwelling rainforest doves that are found from tropical latitudes of southern Asia through the Australo-Papuan region to Vanuatu (Baptista et al., 2020a; Baptista et al., 2020b; del Hoyo et al., 2020). It represents a biogeographic conundrum. Despite its broad geographic distribution throughout the western Pacific, the entire genus comprises only three currently recognized species: *C. stephani*, *C. indica*, and *C. longirostris* (Baptista et al., 2020a; Baptista et al., 2020b; del Hoyo et al., 2020). Within these species, populations can be separated by thousands of kilometers of open ocean, seemingly an ideal recipe for isolation leading to repeated divergence and speciation. Considering this biogeographic context, the conserved phenotype and limited species diversity across the expansive range of *Chalcophaps* is surprising.

Previously, diversity in *Chalcophaps* has been evaluated via phenotypic analyses of museum specimens and limited genetic sampling (Goodwin, 1983; Khan and Arif, 2013). Here, we use dense geographic sampling from throughout the *Chalcophaps* distribution to investigate phylogeographic patterns within the genus using DNA sequence data from three genes (two nuclear, one mitochondrial). We sample multiple geographic regions where described species come into secondary contact and evaluate support for current species boundaries based on available data. Additionally, we test for isolation by distance (IBD) to determine whether populations within each species are well described by a linear relationship between genetic divergence and geographic distance. Finally, we speculate on the intrinsic life-history traits of *Chalcophaps* doves that may contribute to their marked lack of lineage diversity across a biogeographic region known as a hotspot for avian diversification.

2. Methods

2.1. Laboratory protocols

We used a QIAGEN (Hilden, Germany) DNEasy Blood and Tissue Kit following the manufacturer's protocol to extract genomic data from 84 ingroup samples, 76 of which were vouchered tissue samples deposited in natural history museum collections, whereas eight were blood samples (Table 1). We also extracted genomic DNA from two outgroup samples, *Turtur brehmeri* and *Turtur abyssinicus*. We PCR amplified the mitochondrial gene NADH dehydrogenase subunit 2 (ND2), and portions of the nuclear gene IQ Motif Containing GTPase Activating Protein 2 (IQGAP2), and the nuclear gene Goodpasture Antigen-binding Protein (GPBP) for each sample. DNA amplifications were completed in 25 μL reactions under the following conditions: 95.0 °C for 2 min followed by: 95 °C for 20 s, 60.0 °C for 15 s, 70.0 °C for 30 s repeated 10 times; 95.0 °C for 20 s, 56.0 °C for 15 s, 70.0 °C for 30 s repeated 8 times; 95.0 °C for 20 s, 50.0 °C for 15 s, 70.0 °C for 30 s repeated 35 times. A 4-min extension was completed at 70.0 °C and a final holding temperature of 4.0 °C.

2.2. Inferring genetic relationships

We used *Geneious* v.8.1.9 (Kearse et al., 2012) to assemble and trim samples, and used *MUSCLE* (Edgar, 2004) to align each gene. After trimming, we retained a 1009-bp alignment for ND2, a 477-bp alignment for GPBP, and a 207-bp alignment for IQGAP2, for a total concatenated alignment of 1693 bp. We used *PopART* v.1.7 (Leigh and Bryant, 2015) to make a haplotype network for the ND2 gene using the minimum spanning algorithm, separately for each of the three species in our dataset. Additionally, for the two nuclear genes that we sequenced, we used *PHASE* v.2.1.1 (Stephens and Scheet, 2005) implemented via the SEQPHASE web interface (Flot, 2010) to generate phased haplotype sequences for each sample. We then generated haplotype networks for each gene with all species included using *PopART* to visualize potential sharing of haplotypes between species in both nuclear and mitochondrial DNA. To visualize our sampling localities from each species in a geographic context, we used R v.3.5.1 (R Core Team 2019) and the *ggplot2* package (Wickham et al., 2020) to download a world map, crop it to the relevant regions of interest, and color code our sampling localities according to species (corresponding R script available at: github.com/DevonDeRaad/Chalcophaps.Sanger/blob/master/haplotype.networks/haplotype.network.maps.R). For each species, the range map for the entire distribution was adapted directly from the BirdLife International IUCN Red List for birds (BirdLife International, 2021)

We used *PartitionFinder2* v.2.1.1 (Lanfear et al., 2012) for determining the best model of sequence evolution for a concatenated alignment of all three gene sequences using IUPAC ambiguity codes to represent heterozygous sites, specifying separate partitions for each codon position and each gene. The most highly supported model of sequence evolution was TRN + I, with all genes and codons combined in a single partition. We used the TRN + I substitution model in *BEAST2* v.2.5.2 (Bouckaert et al., 2014) and varied the clock model (strict versus relaxed log normal) and tree priors (yule versus coalescent with constant population size). For each parameterization, we ran the MCMC for 10 million generations, discarded the first 1 million generations as burn-in, and stored every 1,000th generation. For all trees, we confirmed that chain convergence and effective sample sizes were $>$ 200 for all estimated parameters using *Tracer* v.1.7.1 (Rambaut et al., 2018). Overall, the parameterization of the clock model and tree priors had little effect on tree shape, nor the evolutionary relationships recovered, therefore we used the default strict clock model and yule tree prior. Because we have both intra- and interspecies sampling included in our phylogenetic reconstruction, we have made the reconstruction using both a coalescent constant tree prior (which may be favorable for reconstructing intraspecies relationships), and a yule tree prior, available in NEXUS format in the following repository: (github.com/DevonDeRaad/Chalcophaps.Sanger/tree/master/beast.tree). Using *TreeAnnotator* (Bouckaert et al., 2014), we summarized the 9,000 trees stored from the nine million post-burn-in generations as the maximum credibility tree. We used the R package *ggtree* (Yu et al., 2017) to visualize phylogeny and node support, annotate the tree, and prune the two outgroup samples used to root *Chalcophaps* in the phylogenetic tree (corresponding R script available at: https://github.com/DevonDeRaad/Chalcophaps.Sanger/blob/master/beast.tree/fig1.R).

2.3. Testing isolation by distance

We used the R package *phangorn* (Schliep, 2011) to calculate pairwise, uncorrected P distances between all individuals within each species using our 1693-bp concatenated alignment. We then used the R package *geosphere* (Hijmans et al., 2017) to calculate pairwise geodesic distance between the geographic sampling coordinates within each of the three species and converted the values to kilometers. To test the statistical significance of isolation-by-distance within each species, we used a Mantel test via the function mantel.randtest() from the R package *Ade4* (Dray et al. 2020) to calculate Pearson's r, quantifying the strength of the linear correlation between the genetic and geographic distance matrices for each species. We performed 1000 randomizations of the input matrices for each Mantel test and used the randomized test statistic values as a null distribution, from which we assessed the degree of significance of the observed Pearson's r in each species. For each linear

Table 1
List of *Chalcophaps indica*, *C. stephani*, and *C. longirostris* samples used in this study. Museum acronyms are as follows: Australian National Wildlife Collection (ANWC), California Academy of Sciences (CAS), Louisiana State University Museum of Natural Science (LSU), University of Kansas Biodiversity Institute (KU), Western Australia Museum (WAM).

Subspecies	Type	Museum	Tissue number	Specimen number	Prep number	IQGAP2 genbank accession	GPBP genabank accession	ND2 genbank accession	Country	Lat	Long
C. i. indica	voucher	ANWC	B44351	B44351	–	MZ618541	MZ618457	MZ618373	Malaysia	3.5	101.67
C. i. indica	voucher	KU	10088	93309	AN 422	MZ618563	MZ618479	MZ618395	China	23.12	105.96
C. i. indica	voucher	KU	10411	96422	TJD 6267	MZ618564	MZ618480	MZ618396	China	21.84	107.88
C. i. indica	voucher	KU	12404	111270	RGM 858	MZ618565	MZ618481	MZ618397	Malaysia	2.94	113.03
C. i. indica	voucher	KU	12439	99039	CHO-B-135	MZ618566	MZ618482	MZ618398	Philippines	18.9	121.91
C. i. indica	voucher	KU	12629	99082	CHO-B-274	MZ618567	MZ618483	MZ618399	Philippines	9.84	118.64
C. i. indica	voucher	KU	12673	99083	CHO-B-309	MZ618568	MZ618484	MZ618400	Philippines	9.84	118.64
C. i. indica	voucher	KU	12823	99084	REF 43	MZ618569	MZ618485	MZ618401	Philippines	8.75	117.69
C. i. indica	voucher	KU	12947	110341	REF 156	MZ618570	MZ618486	MZ618402	Philippines	9.18	124.72
C. i. indica	voucher	KU	14008	110429	REF 258	MZ618571	MZ618487	MZ618403	Philippines	9.19	124.71
C. i. indica	voucher	KU	14078	110610	REF 327	MZ618572	MZ618488	MZ618404	Philippines	10.34	125.62
C. i. indica	voucher	KU	14295	110773	REF 513	MZ618573	MZ618489	MZ618405	Philippines	10.74	124.84
C. i. indica	voucher	KU	14321	110439	REF 51	MZ618574	MZ618490	MZ618406	Philippines	9.18	124.72
C. i. indica	voucher	KU	14451	111386	CHO-B-374	MZ618575	MZ618491	MZ618407	Philippines	12.61	122.05
C. i. indica	voucher	KU	14470	113082	CHO-B-393	MZ618576	MZ618492	MZ618408	Philippines	12.61	122.05
C. i. indica	voucher	KU	15262	98729	CHO-B-2	MZ618577	MZ618493	MZ618409	Philippines	19.1	121.22
C. i. indica	voucher	KU	15263	98730	CHO-B-3	MZ618578	MZ618494	MZ618410	Philippines	19.1	121.22
C. i. indica	voucher	KU	15278	98695	CHO-B-18	MZ618579	MZ618495	MZ618411	Philippines	10.81	122.18
C. i. indica	voucher	KU	17898	113056	CHO 477	MZ618580	MZ618496	MZ618412	Philippines	20.47	121.99
C. i. indica	voucher	KU	17914	112380	CHO 493	MZ618581	MZ618497	MZ618413	Philippines	20.29	121.87
C. i. indica	voucher	KU	17928	112381	CHO 507	MZ618582	MZ618498	MZ618414	Philippines	20.29	121.87
C. i. indica	voucher	KU	17941	112364	CHO 520	MZ618583	MZ618499	MZ618415	Philippines	20.38	121.93
C. i. indica	voucher	KU	18107	112434	PAH 473	MZ618584	MZ618500	MZ618416	Philippines	6.98	122.07
C. i. indica	voucher	KU	19307	116433	CHO 1049	MZ618585	MZ618501	MZ618417	Philippines	13.8	120.16
C. i. indica	voucher	KU	19362	116432	CHO 1104	MZ618586	MZ618502	MZ618418	Philippines	13.8	120.16
C. i. indica	voucher	KU	19398	116642	CHO 1140	MZ618587	MZ618503	MZ618419	Philippines	10.67	123.19
C. i. indica	voucher	KU	20978	114482	CHO 1358	MZ618589	MZ618505	MZ618421	Philippines	9.76	124.28
C. i. indica	voucher	KU	23260	116768	NHR 2717	MZ618590	MZ618506	MZ618422	Vietnam	11.38	107.06
C. i. natalis	voucher	ANWC	B27974	B27974	–	MZ618528	MZ618444	MZ618360	Australia	−10.5	105.58
C. i. natalis	voucher	WAM	A36166	A36166	–	MZ618594	MZ618510	MZ618426	Australia	−10.58	105.67
C. i. natalis	voucher	WAM	A36642	A36642	–	MZ618595	MZ618511	MZ618427	Australia	−10.58	105.67
C. i. natalis	voucher	WAM	A38624	A38624	–	MZ618596	MZ618512	MZ618428	Australia	−10.5	105.67
C. l. longirostris	voucher	ANWC	B34022	B34022	–	MZ618535	MZ618451	MZ618367	Australia	−12.83	131.65
C. l. rogersi	voucher	ANWC	B28894	B28894	–	MZ618529	MZ618445	MZ618361	Australia	−26.68	153.05
C. l. rogersi	voucher	ANWC	B29959	B29959	–	MZ618530	MZ618446	MZ618362	Australia	−17.35	145.67
C. l. rogersi	voucher	ANWC	B31543	B31543	–	MZ618531	MZ618447	MZ618363	Australia	−15.79	145.23
C. l. rogersi	voucher	ANWC	B32557	B32557	–	MZ618532	MZ618448	MZ618364	Australia	−16.62	145.33
C. l. rogersi	voucher	ANWC	B32626	B32626	–	MZ618533	MZ618449	MZ618365	Australia	−16.62	145.33
C. l. rogersi	voucher	ANWC	B32641	B32641	–	MZ618534	MZ618450	MZ618366	Australia	−16.62	145.33
C. l. rogersi	voucher	ANWC	B34429	B34429	–	MZ618536	MZ618452	MZ618368	Australia	−17.35	145.67
C. l. rogersi	voucher	ANWC	B34582	B34582	–	MZ618537	MZ618453	MZ618369	Australia	−17.35	145.67

(*continued on next page*)

Table 1 (*continued*)

Subspecies	Type	Museum	Tissue number	Specimen number	Prep number	IQGAP2 genbank accession	GPBP genabank accession	ND2 genbank accession	Country	Lat	Long
C. l. rogersi	voucher	ANWC	B42894	B42894	–	MZ618538	MZ618454	MZ618370	Australia	−13.83	143.46
C. l. rogersi	voucher	ANWC	B43702	B43702	–	MZ618539	MZ618455	MZ618371	Australia	–22.8	150.6
C. l. rogersi	voucher	ANWC	B43703	B43703	–	MZ618540	MZ618456	MZ618372	Australia	–22.8	150.6
C. l. rogersi	voucher	ANWC	B46354	B46354	–	MZ618542	MZ618458	MZ618374	Australia	–32.22	151.42
C. l. rogersi	voucher	ANWC	B49763	B49763	–	MZ618543	MZ618459	MZ618375	Australia	−26.68	153.05
C. l. rogersi	voucher	ANWC	B55964	B55964	–	MZ618544	MZ618460	MZ618376	Papua New Guinea	−8.71	146.53
C. l. rogersi	voucher	ANWC	B56040	B56040	–	MZ618545	MZ618461	MZ618377	Papua New Guinea	−9	146.8
C. l. rogersi	blood	CAS	DPM506	–	DPM506	MZ618546	MZ618462	MZ618378	Papua New Guinea	−10.6	151.38
C. l. rogersi	blood	CAS	DPM530	–	DPM530	MZ618547	MZ618463	MZ618379	Papua New Guinea	−10.76	152.39
C. l. rogersi	blood	CAS	DPM536	–	DPM536	MZ618548	MZ618464	MZ618380	Papua New Guinea	−10.76	152.39
C. l. rogersi	voucher	CAS	97849	97849	JF3019	MZ618549	MZ618465	MZ618381	Papua New Guinea	−10.03	150.98
C. l. rogersi	blood	CAS	JF3031	–	JF3031	MZ618550	MZ618466	MZ618382	Papua New Guinea	−9.24	150.9
C. l. rogersi	voucher	CAS	97896	97896	JF3083	MZ618551	MZ618467	MZ618383	Papua New Guinea	−9.3	153.69
C. l. rogersi	voucher	CAS	97897	97897	JF3084	MZ618552	MZ618468	MZ618384	Papua New Guinea	−9.29	152.83
C. l. rogersi	voucher	CAS	97905	97905	JF3097	MZ618553	MZ618469	MZ618385	Papua New Guinea	−9.27	151.9
C. l. rogersi	voucher	CAS	97910	97910	JF3110	MZ618554	MZ618470	MZ618386	Papua New Guinea	−8.8	151.91
C. l. rogersi	voucher	CAS	97913	97913	JF3115	MZ618555	MZ618471	MZ618387	Papua New Guinea	−8.63	151.31
C. l. rogersi	voucher	CAS	97915	97915	JF3117	MZ618556	MZ618472	MZ618388	Papua New Guinea	−8.63	151.31
C. l. rogersi	voucher	CAS	97918	97918	JF3126	MZ618557	MZ618473	MZ618389	Papua New Guinea	−8.83	151.15
C. l. rogersi	blood	CAS	JPD453	–	JPD453	MZ618558	MZ618474	MZ618390	Papua New Guinea	−10.6	151.38
C. l. rogersi	blood	CAS	JPD522	–	JPD522	MZ618559	MZ618475	MZ618391	Papua New Guinea	−11.13	152.69
C. l. rogersi	voucher	CAS	99398	99398	JPD526	MZ618560	MZ618476	MZ618392	Papua New Guinea	−11.13	152.69
C. l. rogersi	blood	CAS	JPD777	–	JPD777	MZ618561	MZ618477	MZ618393	Papua New Guinea	−9.57	150.51
C. l. rogersi	blood	CAS	JPD782	–	JPD782	MZ618562	MZ618478	MZ618394	Papua New Guinea	−9.57	150.51
C. l. sandwichensis	voucher	KU	19419	113187	RGM 1163	MZ618588	MZ618504	MZ618420	Solomon Islands	−10.78	165.85
C. l. sandwichensis	voucher	LSUMNH	45432	–	–	MZ618591	MZ618507	MZ618423	Vanuatu	−15.34	166.93
C. l. sandwichensis	voucher	LSUMNH	45458	–	–	MZ618592	MZ618508	MZ618424	Vanuatu	−15.34	166.93
C. l. timorensis	voucher	WAM	A22924	A22924	–	MZ618593	MZ618509	MZ618425	Indonesia	−9.97	124
C. s. mortoni	voucher	KU	15887	111337	RGM 988	MZ618600	MZ618516	MZ618432	Solomon Islands	−9.5	159.98
C. s. mortoni	voucher	KU	15912	114974	RGM 1013	MZ618601	MZ618517	MZ618433	Solomon Islands	−9.5	159.98
C. s. mortoni	voucher	KU	15919	111370	RGM 1020	MZ618602	MZ618518	MZ618434	Solomon Islands	−10.25	161.76
C. s. mortoni	voucher	KU	15934	111368	RGM 1035	MZ618603	MZ618519	MZ618435	Solomon Islands	−8.26	157.15
C. s. mortoni	voucher	KU	19423	126055	RGM 1167	MZ618604	MZ618520	MZ618436	Solomon Islands	−8.4	160.59
C. s. mortoni	voucher	KU	19425	113196	RGM 1169	MZ618605	MZ618521	MZ618437	Solomon Islands	−8.4	160.59
C. s. stephani	voucher	CAS	97883	97883	JF3048	MZ618597	MZ618513	MZ618429	Papua New Guinea	−10.42	150.4
C. s. stephani	voucher	CAS	98019	98019	ZRH857	MZ618598	MZ618514	MZ618430	Papua New Guinea	−10.42	150.4
C. s. stephani	voucher	KU	12228	111677	BWB 1197	MZ618599	MZ618515	MZ618431	Papua New Guinea	−4.71	145.4
C. s. stephani	voucher	KU	5304	92002	ALM 1196	MZ618606	MZ618522	MZ618438	Papua New Guinea	−5.37	151.1
C. s. stephani	voucher	KU	5577	97887	ALM 1527	MZ618607	MZ618523	MZ618439	Papua New Guinea	−6.92	144.96
C. s. stephani	voucher	KU	6891	97025	SEA 323	MZ618608	MZ618524	MZ618440	Papua New Guinea	−9.55	149.07
C. s. stephani	voucher	KU	6905	97026	BWB 641	MZ618609	MZ618525	MZ618441	Papua New Guinea	−9.55	149.07
C. s. stephani	voucher	KU	7146	97823	ALM 1679	MZ618610	MZ618526	MZ618442	Papua New Guinea	−4.48	145.03
C. s. stephani	voucher	KU	7287	97890	ALM 1821	MZ618611	MZ618527	MZ618443	Papua New Guinea	−4.48	145.03

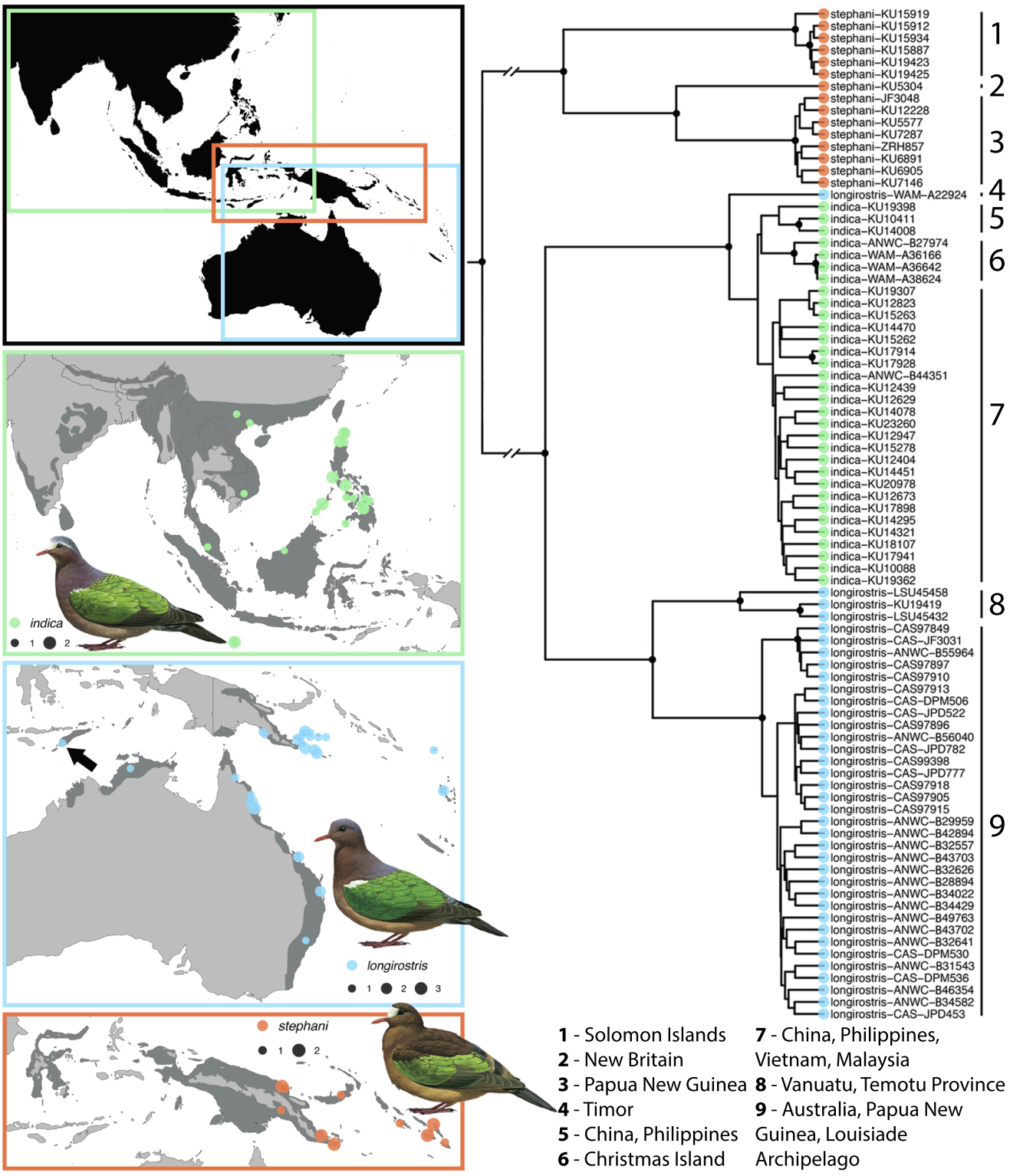

Fig. 1. Map showing the entire distribution of each *Chalcophaps* species shown in dark gray. Sampling localities sizes are scaled according to number of samples and colored according to species assignment: *C. indica* (green), *C. longirostris* (blue), and *C. stephani* (orange). A black arrow highlights the discordantly placed sample from Timor on *C. longirostris* distribution map. On the right, a Bayesian phylogenetic reconstruction generated using all three genes (ND2, IQGAP2, and GPBP) concatenated as a single partition. Branch length for the first split in the tree is artificially shortened, as indicated by double hash marks. Nodes for which posterior probabilities were > 0.95 are denoted by an enlarged dot. Clades on the tree are labeled corresponding to geography. Illustrations reproduced by permission of Lynx Edicions. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

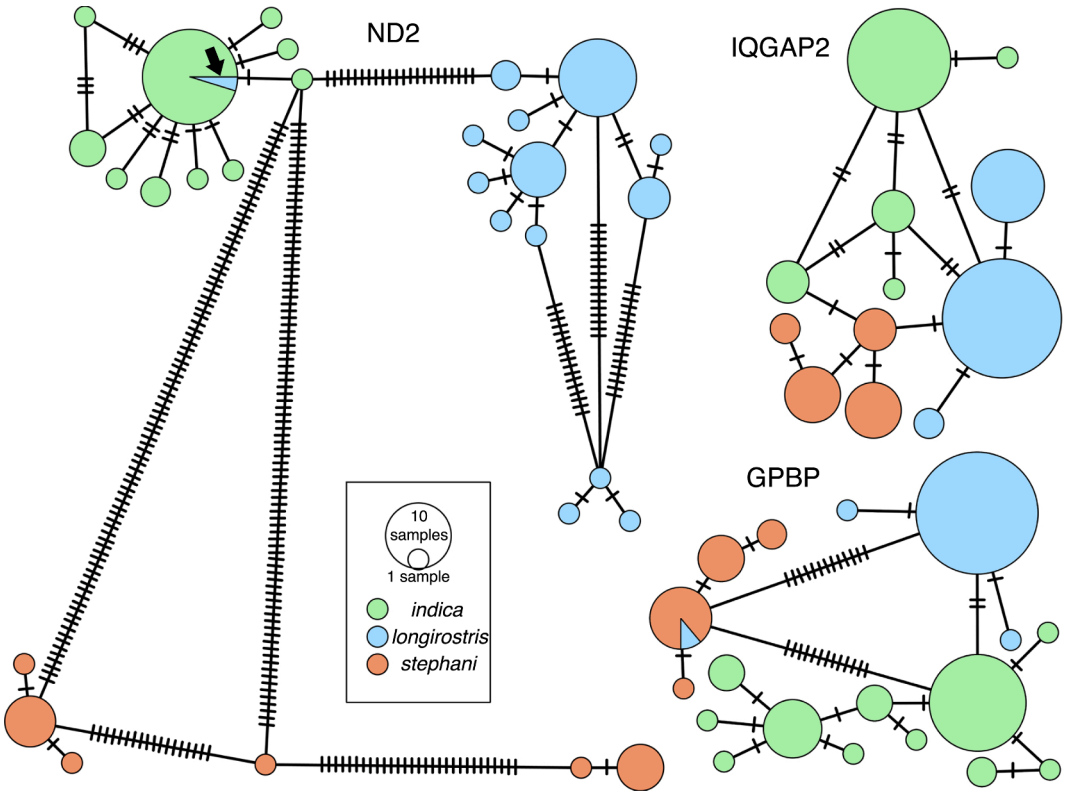

Fig. 2. Haplotype networks for each of the three sequenced genes (ND2, GPBP, and IQGAP2). Circle size corresponds to number of individuals, and each sample is color-coded based on species assignment. Arrow indicates sample from Timor for which ND2 haplotype identity does not match species assignment.

model, we then calculated the residuals and plotted them against the independent variable (geographic distance) in order to visually assess the fit of a continuous linear model to these data (corresponding R script available at: github.com/DevonDeRaad/Chalcophaps.Sanger/blob/master/ibd/test.ibd.plot.allspecies.together.R).

3. Results

Our phylogenetic reconstruction based on concatenated sequence data from three genes (two nuclear and one mitochondrial) shows three distinct lineages within *Chalcophaps*, corresponding to the three recognized species, *C. stephani*, *C. indica*, and *C. longirostris* (Fig. 1). *Chalcophaps stephani* is the most genetically divergent species in the genus, differing from its congeners by ~8% in mtDNA. The sister species *C. longirostris* and *C. indica* are 2.4% divergent in mtDNA, and, except for the *C. longirostris* sample from Timor, are reciprocally monophyletic (Fig. 1). This sample from Timor Island shares the most common *C. indica* mitochondrial haplotype, despite clustering as expected with *C. longirostris* in haplotype networks of each nuclear gene (Fig. 2). The haplotype network for the gene GPBP reveals additional interspecies haplotype sharing, including one *C. longirostris* sample from Vanuatu that shared the most common *C. stephani* haplotype (Fig. 2).

Within both *C. stephani* and *C. longirostris*, our phylogenetic reconstruction reveals well supported splits between geographically isolated populations. Within *C. stephani*, we recover well-supported splits between samples from Papua New Guinea (PNG), the Bismarck Archipelago, and the Solomon Islands (Fig. 1). A haplotype network for the gene ND2 indicates that between 10 and 18 substitutions separate these three geographically isolated clades, amounting to 1–1.8% uncorrected pairwise divergence in mtDNA (Fig. 3). Within *C. longirostris*, we confidently recover all samples from Vanuatu and Temotu Province, Solomon Islands as a clade, which is sister to the rest of the species' distribution across Australia and PNG (Fig. 1). Our ND2 haplotype network indicates that the Vanuatu and Temotu Province mitochondrial haplotypes are separated by 12–13 substitutions, amounting to 1.2–1.3% raw divergence in mtDNA from the most common mitochondrial haplotype shared by samples from Australia and PNG (Fig. 3).

We tested explicitly whether the three major lineages recovered in our phylogenetic reconstruction show correlations between geographic and genetic distance. We found a significant correlation between geographic and genetic distance in all three species, although the strength of relationship varied greatly: *C. indica* ($r = 0.373$, $p = 0.002$), *C. longirostris* ($r = 0.583$, $p = 0.001$), and *C. stephani* ($r = 0.841$, $p = 0.001$) (Fig. 4). Plots of the residuals of each linear model indicate a generally linear relationship between geographic and genetic distance in each species, although a continuous model of isolation by distance is poorly fit in *C. longirostris* and *C. stephani*, each of which show discretely related geographic clusters in plots of model residuals (Fig. 4). This heterogenous pattern of intraspecies divergence—the strongest relationship was between genetic and geographic differentiation in *C. stephani*, whereas the weakest was in *C. indica*—is consistent with the phylogenetic signal from all genes concatenated, and with the mtDNA haplotype networks of each species.

4. Discussion

Here we present the first molecular phylogeographic investigation of *Chalcophaps* doves. We find that the three currently recognized species, identified based on phenotype and geography, tightly correspond to the three major phylogenetic groups in our reconstruction. Despite this overall congruence, we uncover discordance between nuclear and mitochondrial DNA ancestry on Timor where *C. indica* and *C. longirostris* come into contact, which is concordant with evidence of phenotypic intermediacy on this island (Johnstone et al., 2014). Additionally, we find evidence for hierarchical population structure within *C. stephani* and *C. longirostris*, indicating the early stages of ongoing diversification

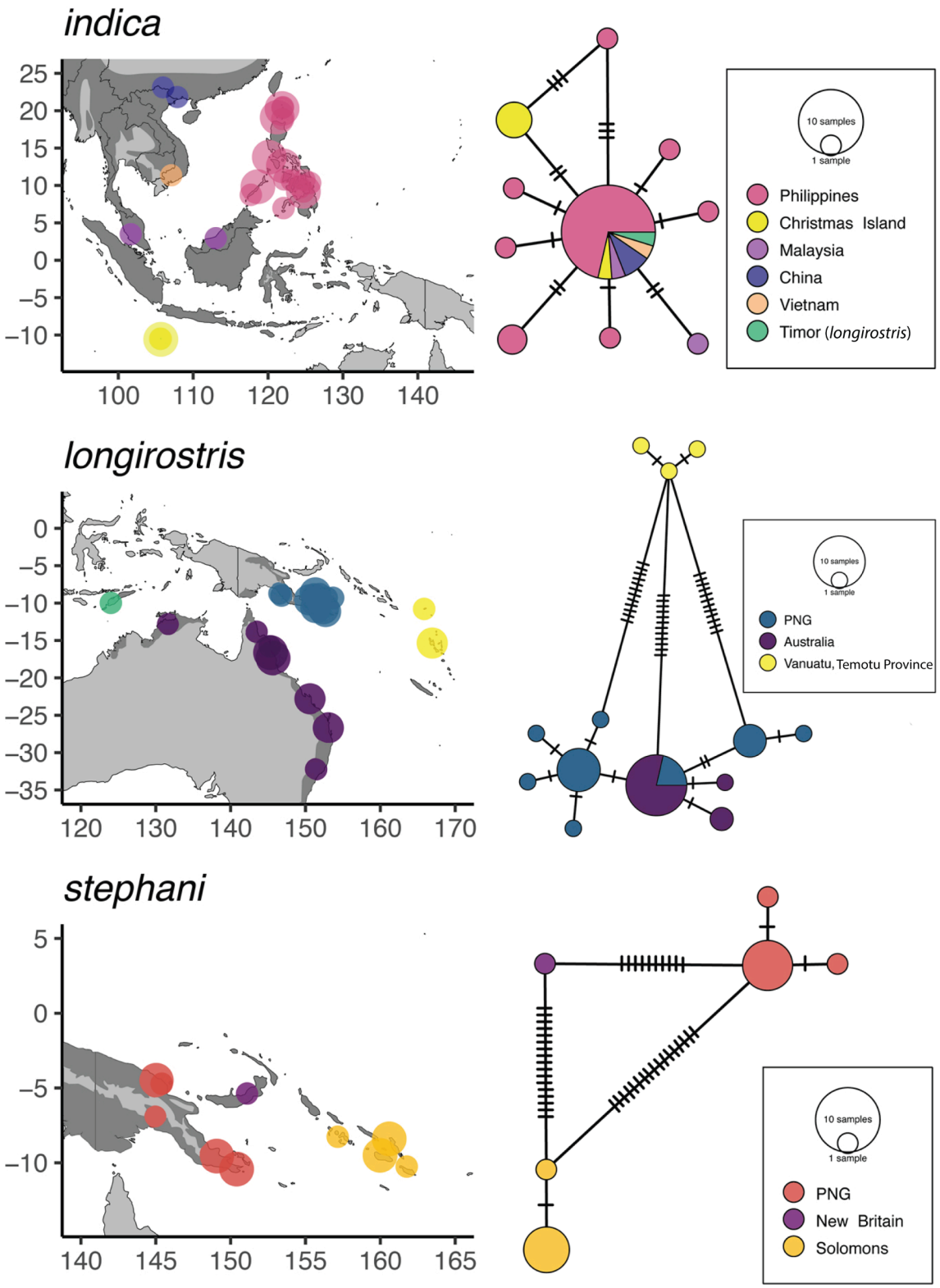

Fig. 3. ND2 Haplotype networks for each species. Number of substitutions separating haplotypes are shown on branches as tick marks. Each sample is color-coded based on sampling locality in each map and in each corresponding haplotype network. Range map for each species shown in dark gray on each map. Our single sample from the subspecies *C. longirostris timorensis* is shown on the *longirostris* range map, but is included in the *indica* haplotype network.

within each species. Despite uncovering these cases of ongoing lineage diversification deserving further investigation, we find limited evidence for species-level genetic divergences, in concert with the phenotypic stasis observed throughout the large geographic range of *Chalcophaps*.

4.1. Phylogeography

The degree of genetic differentiation among allopatric populations varies within each of the three *Chalcophaps* species. The most geographically structured species is *C. stephani*, in which the

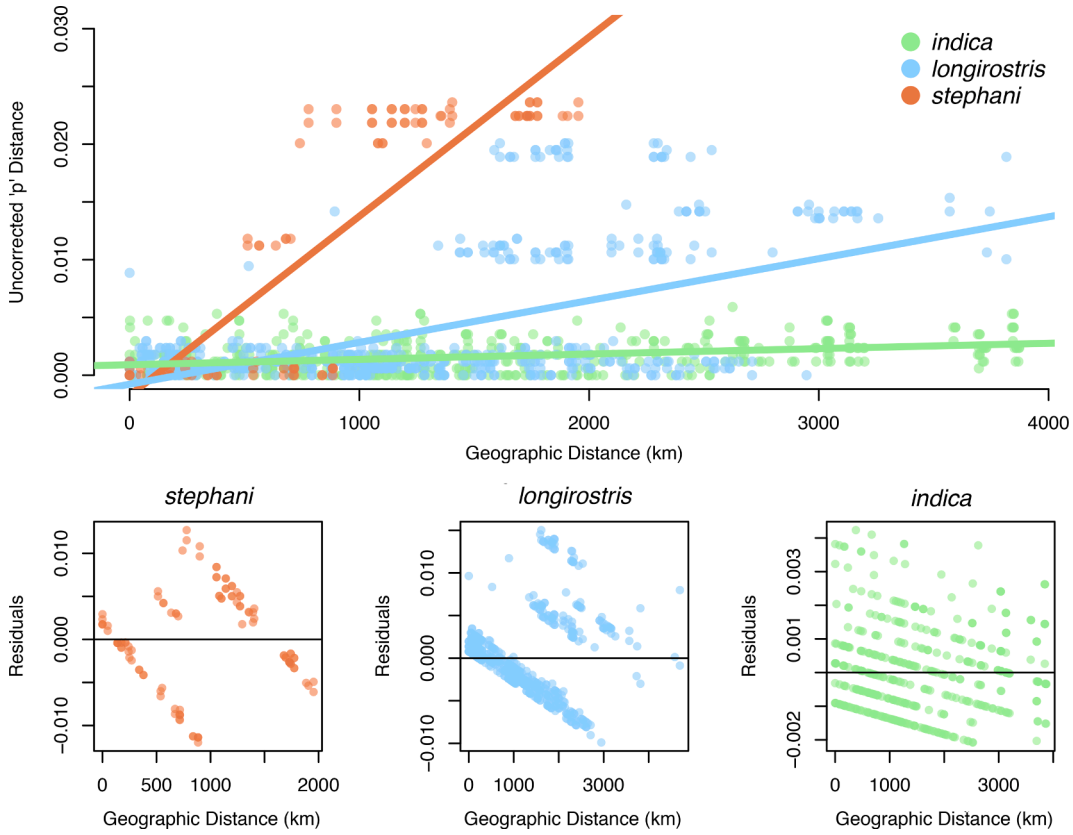

Fig. 4. Scatter plot showing the correlation between all possible pairwise comparisons of geographic distance and uncorrected P distance across 1693 concatenated bp within each species. Mantel tests confirmed significant correlations between geographic and genetic distance in *C. indica* (r = 0.373, $p = 0.002$), *C. longirostris* (r = 0.583, $p = 0.001$), and *C. stephani* (r = 0.841, $p = 0.001$). Below, plots show the residuals of the linear regression model for each species plotted against the independent variable (geographic distance).

geographically proximate samples from PNG, New Britain Island, and the Solomon Islands each have unique, moderately divergent mtDNA haplotypes (Fig. 2). We interpret the highly structured pattern of divergence within *C. stephani* as resulting from sequential colonization from New Guinea to the Bismarck Archipelago, and subsequently into the Solomon Islands. This west-to-east linear pattern of colonization sequence is thought to be common in Melanesian birds (Mayr and Diamond, 2001). Within *C. longirostris*, we find shared haplotypes between samples from Australia and PNG, but a deep phylogeographic break between the Australo-Papuan populations and the isolated populations on Vanuatu and Temotu Province (Fig. 2). We currently lack sampling of *C. longirostris* from New Caledonia, but morphological evidence suggests that this population shares ancestry with the nearby Vanuatu and Temotu Province populations. These three populations together comprise the subspecies, *C. l. sandwichensis* (del Hoyo et al., 2020). These populations have likely diverged genetically due to geographic isolation, as *C. longirostris* on Vanuatu and Temotu Province are separated by more than 1500 km of open ocean from the Australo-Papuan populations included in our sampling. Meanwhile, *C. indica* is the least geographically structured *Chalcophaps* species, and we find mtDNA haplotype sharing across nearly every geographic sampling location (Fig. 3). The *C. indica* population on Christmas Island has been identified as an endemic subspecies, *C. i. natalis*, and the three *C. i. natalis* samples included in our analysis share a unique haplotype that is separated by two substitutions from the most common *C. indica* haplotype. Yet the fourth *C. i. natalis* sample shares a common haplotype with samples from China and the Philippines (Fig. 3). This indicates that although *C. i. natalis* has developed unique alleles during a period of divergence in isolation, genetic variation from nearby populations is still segregating within this Christmas Island population, due to incomplete lineage sorting or ongoing gene flow (Slatkin, 1987).

This relative paucity of species-level diversity is surprising given the extensive distribution of these doves across the western Pacific, a region known as a hotspot for avian diversification (Mayr and Diamond, 2001). Across similar geographic distributions in the western Pacific, closely related groups show much greater levels of diversity, for example, *Macropygia* cuckoo-doves, which include 15 species, or *Ducula* imperial-pigeons, which include 39 species (Gibbs and Barnes, 2001). One potential explanation for the lack of comparative genetic and phenotypic diversity within *Chalcophaps* is the dispersal capability of these doves. For instance, occurrence data from India indicate that populations of *C. indica* move extensively throughout the year, tracking food sources associated with monsoonal patterns (Jayson and Mathew, 2000). Additionally, *C. longirostris* is known to wander locally, often showing up in suburban areas in PNG and has been observed actively crossing open ocean on the Torres Strait (del Hoyo et al., 2020). Anecdotally, an individual *C. stephani* was found trapped in ice at an elevation of 4350 m on the Carstensz Masiff in New Guinea, roughly 3000 m above the known distributional limit of the species (Beehler and Pratt, 2016; Schodde et al., 1975). Finally, *C. stephani* was recently documented on Rennell Island, Solomon Islands (Lavery et al. 2021). Given that the Whitney South Sea Expedition did not record it there (Mayr 1931), it is possible that it is a recent colonist to Rennell. These accounts of the dispersal potential of *Chalcophaps* doves support the hypothesis that the overall lack of diversification we documented within this genus could be explained by occasional migration between geographically isolated island populations. Both empirical and theoretical population genetic studies have established that rare, long-distance dispersal events can have an outsized effect in preventing differentiation and maintaining shared genetic diversity among geographically isolated populations

(Lourenço et al., 2019; Mallet, 1999). Further studies integrating ecology and evolutionary genetics are warranted to test the hypothesis that strong overwater dispersal capability maintains long-distance genetic connectivity within *Chalcophaps*.

4.2. Secondary contact

There are three regions of secondary contact (sympatry or parapatry) among the three species of *Chalcophaps* ground-doves: *C. stephani* and *C. longirostris* co-occur in southeastern New Guinea, *C. stephani* and *C. indica* co-occur on the island of Sulawesi, and the abutting distributions of *C. longirostris* and *C. indica* in the Lesser Sunda Islands of Indonesia. In southeastern PNG, *C. stephani* and *C. longirostris* occur in sympatry, although the species are known to segregate ecologically, with *Chalcophaps longirostris* occurring in secondary growth and edge habitat, whereas *C. stephani* is generally restricted to interior forest (Diamond, 1970). We find no haplotype sharing between the two species despite extensive sampling of both species from the same localities in southeastern PNG (Fig. 2). In contrast, despite no known geographic overlap in distribution, a *C. longirostris* sample from Vanuatu shares the most common *C. stephani* haplotype for the gene GPBP (Fig. 2). Due to our limited character sampling, we cannot determine decisively whether this represents a case of incomplete lineage sorting or gene flow; the deep mitochondrial divergence between these species (~8% uncorrected P distance) indicates ample evolutionary time for allele sorting within derived populations, supporting the potential role of interspecies gene flow in driving this pattern. Nonetheless, the sympatric co-occurrence of these species in PNG without evidence for genetic introgression indicates that these species have achieved reproductive isolation, at least in this region of secondary sympatry. Further study using genome-wide markers is warranted to determine whether reproductive isolation effectively prevents introgression throughout the ranges of these divergent congeners.

The more closely related sister species, *C. longirostris* and *C. indica* (2.4% divergent in mtDNA), occur in the islands of the Lesser Sundas, Indonesia—*C. longirostris* (ssp. *timorensis*) occurrs in the eastern Lesser Sundas west to Roti, Timor, and Wetar, whereas *C. indica* (ssp. *indica*) occurrs in the western Lesser Sundas east to Sumba and Alor (Coates and Bishop, 1997; Mayr, 1944). However, Johnstone et al. (2014) added considerable detail to this area of contact, suggesting that there is not a clean break between these taxa but a broader zone of phenotypic intergradation. From their work on Timor, Roti, Semau, and Sabu, Johnstone et al. (2014) concluded that *C. longirostris* and *C. indica* form a broad intergradation zone with intermediate phenotypes occurring on Sabu, Sumau, and Timor islands, and introgression extending as far as Lembata Island. Our single genetic sample from Timor shares nuclear haplotypes with *C. longirostris* samples from Australia and PNG and a mitochondrial haplotype with *C. indica* samples from Malaysia, China, and the Philippines (Fig. 3), supporting the findings of Johnstone et al. (2014) that the Timor population possesses a mixture of genetic ancestry from *C. longirostris* and *C. indica*. Phasing of each of the two nuclear loci revealed no detectable heterozygosity within this sample, indicating that this sample is not likely to be a recent hybrid. This case of mitochondrial mismatch without an indication of nuclear gene flow is instead suggestive of a complex history of gene flow including potential mitochondrial capture events (Andersen et al., 2021). Subspecies within *C. longirostris* are morphologically variable, and del Hoyo et al. (2020) considers subspecies *timorensis* to be smaller with a grayer nape and mantle than the nominate subspecies, further suggesting that it may share some phenotypic characteristics with *C. indica*. The phenotypic intermediacy of this subspecies, combined with this genetic evidence of introgression, raise ongoing questions about the evolutionary history of the *Chalcophaps* population on Timor, which should be further investigated with larger sample sizes and genome-wide sequence data.

Chalcophaps stephani (in ssp. *wallacei*) and the nominate form of *C. indica* occur on the large island of Sulawesi where they may segregate by habitat with *C. stephani* occurring in more forested areas than *C. indica* (Coates and Bishop, 1997). Unfortunately, our lack of sampling from this interesting area of secondary contact does not allow us to comment on any genetic patterns.

4.3. Isolation by distance

Isolation by distance is a biogeographic pattern that arises between populations due to geographically restricted gene flow (Wright, 1938). As two populations become more geographically distant, they will exchange fewer migrants and genetic drift will increase within populations, eventually resulting in a correlation between genetic and geographic distance (Wright, 1940, 1938). Some of the key factors in generating patterns of IBD, like mutation rate and dispersal ability, show strong phylogenetic signal across birds, and we expect these traits are highly conserved among species of *Chalcophaps* (Jetz et al., 2008; Losos, 2008; Phillimore et al., 2006). However, the signal of IBD varies greatly between *Chalcophaps* species ($r = 0.365–0.842$) (Fig. 4). This difference is likely attributable to hierarchical population structure, which is known to generate signals of IBD even in cases where gene flow is not geographically restricted within each structured population (Meirmans, 2012). Within both *C. longirostris* and *C. stephani*, the characteristic stepping-stone pattern in the relationship between genetic and geographic distance indicates that there are multiple hierarchically structured subpopulations present within each species (Fig. 4). Plots of the residuals of the linear model fit to each of these species indicate that although the relationships between geographic and genetic distance are generally linear, the relationships are driven by discretely clustering groups of samples, which do not conform to a continuous model of IBD. In contrast, *C. indica* is well fit by a model of IBD, which may indicate that the species has only recently achieved its current distributional extent and has not had sufficient time for population structure to develop (Avise et al., 1998; Hewitt, 1996). Meanwhile, *C. stephani* and *C. longirostris* may have maintained more temporally stable distributional patterns, allowing the gradual accumulation of differences between geographically isolated island populations to develop into hierarchical population structure. Despite this heterogeneity among species, these data strongly support that migration between geographically proximate populations has shaped the current genetic diversity within *Chalcophaps*.

4.4. Conclusions

Overall, current taxonomy of *Chalcophaps* nicely outlines the evolutionary history of the group but belies multiple circumstances of ongoing intrigue. Despite genetic connectivity between *Chalcophaps* populations, we find evidence for hierarchical population structure within *C. longirostris* and *C. stephani*. Geographically isolated populations within each species show substantial (1.2–1.8%) mtDNA divergence, but this geographic isolation precludes the analysis of potential reproductive isolation upon secondary contact. Although this hierarchical population structure may indicate incipient speciation, the role of geography as an isolating barrier makes it difficult to place these populations along the “speciation continuum” under the General Lineage Species Concept (De Queiroz, 2007). Furthermore, the three areas of secondary sympatry within the genus, only one of which is well-sampled, warrant future work to assess levels of isolation using both denser sampling and genomic-scale genetic data. Future work testing for introgression between *C. indica* and *C. longirostris* on Timor and quantifying genomic divergence amongst isolated island populations within species will enhance our understanding of the evolutionary history of *Chalcophaps*.

CRediT authorship contribution statement

Devon A. DeRaad: Methodology, Formal analysis, Data curation,

Writing – original draft, Writing – review & editing, Visualization. **Joseph D. Manthey:** Conceptualization, Methodology, Investigation, Resources, Data curation, Writing – review & editing. **Emily N. Ostrow:** Methodology, Data curation, Writing – review & editing. **Lucas H. DeCicco:** Methodology, Data curation, Writing – review & editing. **Michael J. Andersen:** Conceptualization, Investigation, Writing – review & editing. **Peter A. Hosner:** Conceptualization, Investigation, Writing – review & editing. **Hannah Shult:** Investigation, Writing – review & editing. **Leo Joseph:** Resources, Writing – review & editing. **John P. Dumbacher:** Resources, Writing – review & editing. **Robert G. Moyle:** Conceptualization, Methodology, Resources, Writing – review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank the Western Australian Museum, Australian National Wildlife Collection, the California Academy of Sciences, Florida Museum of Natural History, Louisiana State University Museum of Natural History, for providing tissue and blood samples to make this project possible. For field work in the Solomon Islands we thank the Solomon Islands Ministry of Environment, Climate Change, Disaster Management, and Meteorology; numerous provincial governments; and the chiefs, landowners, and communities that allowed access to customary land. We would also like to thank the PNG Department of Environment and Conservation and Milne Bay Provincial government for permission to work in Papua New Guinea, and Bulisa Iova and the PNG National Museum and Art Gallery for assistance in the field. This work was supported by National Science Foundation grants to RGM (DEB-1557053) and MJA (DEB-1557051). PAH acknowledges the support of the VILLUM FONDEN for the Center for Global Mountain Biodiversity (grant no. 25925). DAD was supported by the Madison & Lila Self Graduate Fellowship for the duration of this project. ENO was supported by the NSF GRFP for the duration of this project.

Data Accessibility

All individual gene sequences analyzed here have been uploaded to GenBank (Table 1). Sequence data in fasta format and all scripts used for data analysis can be found at the following GitHub repository: github.com/DevonDeRaad/Chalcophaps.Sanger. The entire repository including raw sequence data and all scripts to perform analyses is stably archived and available for download at: https://doi.org/10.5061/dryad.x3ffbg7kz

References

Andersen, M.J., Manthey, J.D., Naikatini, A., Moyle, R.G., 2017. Conservation genomics of the silktail (Aves: *Lamprolia victoriae*) suggests the need for increased protection of native forest on the Natewa Peninsula. Fiji. Conserv. Genet. 18 (6), 1277–1285. https://doi.org/10.1007/s10592-017-0979-x.

Andersen, M.J., McCullough, J.M., Gyllenhaal, E.F., Mapel, X.M., Haryoko, T., Jønsson, K.A., Joseph, L., 2021. Complex histories of gene flow and a mitochondrial capture event in a nonsister pair of birds. Mol. Ecol. 30 (9), 2087–2103. https://doi.org/10.1111/mec.v30.910.1111/mec.15856.

Avise, J.C., Walker, DeEtte, Johns, G.C., 1998. Speciation durations and Pleistocene effects on vertebrate phylogeography. Proc. R. Soc. Lond. B Biol. Sci. 265 (1407), 1707–1712. https://doi.org/10.1098/rspb.1998.0492.

Baptista, L.F., Trail, P.W., Horblit, H.M., Kirwan, G.M., 2020a. Stephan's Dove (*Chalcophaps stephani*), version 1.0. In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A., de Juana, E. (Eds.), Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.stedov1.01.

Baptista, L.F., Trail, P.W., Horblit, H.M., Kirwan, G.M., Garcia, E.F.J., Boesman, P.F.D., 2020b. Asian Emerald Dove (*Chalcophaps indica*), version 1.0. In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A., de Juana, E. (Eds.), Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.emedov2.01.

Beehler, B.M., Pratt, T.K., 2016. Birds of new guinea: distribution, taxonomy, and systematics. Princeton University Press.

BirdLife International, 2021. IUCN Red List for birds. Downloaded from http://www.birdlife.org on 25/6/2021.

Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C.-H., Xie, D., Suchard, M.A., Rambaut, A., Drummond, A.J., Prlic, A., 2014. Beast 2: a software platform for Bayesian evolutionary analysis. PLoS Comput. Biol. 10 (4), e1003537. https://doi.org/10.1371/journal.pcbi.1003537.

Campagna, L., Gronau, I., Silveira, L.F., Siepel, A., Lovette, I.J., 2015. Distinguishing noise from signal in patterns of genomic divergence in a highly polymorphic avian radiation. Mol. Ecol. 24 (16), 4238–4251. https://doi.org/10.1111/mec.13314.

Coates, B., Bishop, K.D., 1997. A guide to the birds of Wallacea. Dove Publications, Australia.

Coyne, J.A., 1992. Genetics and speciation. Nature 355 (6360), 511–515. https://doi.org/10.1038/355511a0.

De Queiroz, K., 2007. Species concepts and species delimitation. Syst. Biol. 56 (6), 879–886. https://doi.org/10.1080/10635150701701083.

del Hoyo, J., Collar, N., Kirwan, G.M., Garcia, E.F.J., 2020. Pacific Emerald Dove (*Chalcophaps longirostris*), version 1.0. In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A., de Juana, E. (Eds.), Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.emedov3.01.

Diamond, J.M., 1970. Ecological consequences of island colonization by southwest Pacific birds, II. The effect of species diversity on total population density. Proc. Natl. Acad. Sci. 67 (4), 1715–1721.

Dray, S., Dufour, A.-B., Thioulouse, and J., Jombart, with contributions from T., Pavoine, S., Lobry, J.R., Ollier, S., Borcard, D., Legendre, P., Chessel, S.B. and A.S.B. on earlier work by D., 2020. Ade4: analysis of ecological data: exploratory and Euclidean methods in environmental sciences.

Edgar, R.C., 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucl. Acids Res. 32 (5), 1792–1797. https://doi.org/10.1093/nar/gkh340.

Flot, J.-F., 2010. seqphase: a web tool for interconverting phase input/output files and fasta sequence alignments. Mol. Ecol. Resour. 10 (1), 162–166. https://doi.org/10.1111/j.1755-0998.2009.02732.x.

Gibbs, D., Barnes, E., 2001. Pigeons and Doves: A Guide to Pigeons and Doves of the World. Yale University Press, New Haven, Connecticut.

Goodwin, D., 1983. Pigeons and doves of the world, third ed. Cornell Univ. Press, Ithaca, NY.

Hewitt, G.M., 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. Biol. J. Linn. Soc. 58, 247–276. https://doi.org/10.1111/j.1095-8312.1996.tb01434.x.

Hijmans, R.J., Williams, E., Vennes, C., Hijmans, M.R.J., 2017. Package "geosphere". Spherical Trigonometry 1, 7.

Hosner, Peter A., Campillo, Luke C., Andersen, Michael J., Sánchez-González, Luis A., Oliveros, Carl H., Urriza, Rolly C., Moyle, Robert G., 2018. An integrative species delimitation approach reveals fine-scale endemism and substantial unrecognized avian diversity in the Philippine Archipelago. Conserv. Genet. 19 (5), 1153–1168. https://doi.org/10.1007/s10592-018-1085-4.

Irwin, D.E., Milá, B., Toews, D.P.L., Brelsford, A., Kenyon, H.L., Porter, A.N., Grossen, C., Delmore, K.E., Alcaide, M., Irwin, J.H., 2018. A comparison of genomic islands of differentiation across three young avian species pairs. Mol. Ecol. 27 (23) https://doi.org/10.1111/mec.14858.

Jayson, E.A., Mathew, D., 2000. Seasonal changes of tropical forest birds in the Southern Western Ghats. J. Bombay Nat. Hist. Soc. 97, 52–61.

Jetz, Walter, Freckleton, Robert P., McKechnie, Andrew E., Chave, Jerome, 2008. Environment, migratory tendency, phylogeny and basal metabolic rate in birds. PLoS ONE 3 (9), e3261. https://doi.org/10.1371/journal.pone.0003261.

Johnstone, R.E., Hidayat, O., Darnell, J.C., Trainor, C.R., 2014. The avifauna of Semau Island, Lesser Sundas, Indonesia: Ecology, taxonomy and conservation. West. Aust. Nat. 29, 162–221.

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Meintjes, P., Drummond, A., 2012. Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28 (12), 1647–1649. https://doi.org/10.1093/bioinformatics/bts199.

Khan, Haseeb Ahmad, Arif, Ibrahim Abdulwahid, 2013. COI barcodes and phylogeny of doves (*Columbidae* family). Mitochondrial DNA 24 (6), 689–696. https://doi.org/10.3109/19401736.2013.773319.

Kyriazis, Christopher C., Alam, Bushra, Wjodyla, Mark, Hackett, Shannon, Hosner, Peter, Mays, Herman L., Heaney, Lawrence R., Reddy, Sushma, 2018. Colonization and diversification of the White-browed Shortwing (Aves: Muscicapidae: *Brachypteryx montana*) in the Philippines. Mol. Phylogenet. Evol. 121, 121–131. https://doi.org/10.1016/j.ympev.2017.12.025.

Lanfear, R., Calcott, B., Ho, S.Y.W., Guindon, S., 2012. Partitionfinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Mol. Biol. Evol. 29 (6), 1695–1701. https://doi.org/10.1093/molbev/mss020.

Lavery, T.H., DeCicco, L.H., Richmond, J.Q., Tigulu, I.G., Andersen, M.J., Boseto, D., Moyle, R.G., 2021. New faunal records from a World Heritage Site in danger: Rennell Island, Solomon Islands. Pac. Sci. 75 (3), 407–420. https://doi.org/10.2984/75.3.8.

Leigh, J.W., Bryant, D., 2015. popart: full-feature software for haplotype network construction. Methods Ecol. Evol. 6 (9), 1110–1116. https://doi.org/10.1111/2041-210X.12410.

Lohman, David J., Ingram, Krista K., Prawiradilaga, Dewi M., Winker, Kevin, Sheldon, Frederick H., Moyle, Robert G., Ng, Peter K.L., Ong, Perry S., Wang, Luan

Keng, Braile, Thomas M., Astuti, Dwi, Meier, Rudolf, 2010. Cryptic genetic diversity in "widespread" Southeast Asian bird species suggests that Philippine avian endemism is gravely underestimated. Biol. Conserv. 143 (8), 1885–1890. https://doi.org/10.1016/j.biocon.2010.04.042.

Losos, J.B., 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. Ecol. Lett. 11, 995–1003. https://doi.org/10.1111/j.1461-0248.2008.01229.x.

Lourenço, André, Gonçalves, João, Carvalho, Filipe, Wang, Ian J., Velo-Antón, Guillermo, 2019. Comparative landscape genetics reveals the evolution of viviparity reduces genetic connectivity in fire salamanders. Mol. Ecol. 28 (20), 4573–4591. https://doi.org/10.1111/mec.v28.2010.1111/mec.15249.

Lovette, I, 2005. Glacial cycles and the tempo of avian speciation. Trends Ecol. Evol. 20 (2), 57–59. https://doi.org/10.1016/j.tree.2004.11.011.

MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press.

Mallet, J., 1999. Gene flow. In: Symposium-Royal Entomological Society of London.

Manthey, J.D., Klicka, J., Spellman, G.M., 2011. Isolation-driven divergence: speciation in a widespread North American songbird (Aves: *Certhiidae*). Mol. Ecol. 20 (20), 4371–4384. https://doi.org/10.1111/j.1365-294X.2011.05270.x.

Manthey, Joseph D., Moyle, Robert G., Gawin, Dency F., Rahman, Mustafa Abdul, Ramji, Mohamad Fizl Sidq, Sheldon, Frederick H., 2017. Genomic phylogeography of the endemic Mountain Black-eye of Borneo (*Chlorocharis emiliae*): montane and lowland populations differ in patterns of Pleistocene diversification. J. Biogeogr. 44 (10), 2272–2283. https://doi.org/10.1111/jbi.2017.44.issue-1010.1111/jbi.13028.

Manthey, Joseph D., Oliveros, Carl H., Andersen, Michael J., Filardi, Christopher E., Moyle, Robert G., 2020. Gene flow and rapid differentiation characterize a rapid insular radiation in the southwest Pacific (Aves: *Zosterops*). Evolution 74 (8), 1788–1803. https://doi.org/10.1111/evo.v74.810.1111/evo.14043.

Mayr, E., 1944. The birds of Timor and Sumba. Bull. Am. Mus. Nat. Hist. 83, 126–194.

Mayr, E., 1942. Systematics and the origin of species. Columbia University Press. Columbia University Press., New York, New York.

Mayr, E., 1931. A systematic list of the birds of Rennell Island with description of new species and subspecies. Am. Mus. Novit. 486, 1–29.

Mayr, E., Diamond, J., 2001. The birds of Northern Melanesia: speciation, ecology & biogeography. Oxford University Press.

Meirmans, P.G., 2012. The trouble with isolation by distance. Mol. Ecol. 21 (12), 2839–2846. https://doi.org/10.1111/j.1365-294X.2012.05578.x.

Moyle, Robert G., Filardi, Christopher E., Smith, Catherine E., Diamond, Jared, 2009. Explosive Pleistocene diversification and hemispheric expansion of a "great speciator". Proc. Natl. Acad. Sci. 106 (6), 1863–1868.

Moyle, R.G., Oliveros, C.H., Andersen, M.J., Hosner, P.A., Benz, B.W., Manthey, J.D., Travers, S.L., Brown, R.M., Faircloth, B.C., 2016. Tectonic collision and uplift of Wallacea triggered the global songbird radiation. Nat. Commun. 7, 12709. https://doi.org/10.1038/ncomms12709.

Phillimore, A.B., Freckleton, R.P., Orme, C.D.L., Owens, I.P.F., 2006. Ecology predicts large-scale patterns of phylogenetic diversification in birds. Am. Nat. 168 (2), 220–229. https://doi.org/10.1086/505763.

R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rambaut, A., Drummond, A.J., Xie, D., Baele, G., Suchard, M.A., 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. Syst. Biol. 67 (5), 901–904. https://doi.org/10.1093/sysbio/syy032.

Schliep, K.P., 2011. phangorn: phylogenetic analysis in R. Bioinformatics 27 (4), 592–593. https://doi.org/10.1093/bioinformatics/btq706.

Schodde, R., Van, T.G., Champion, C.R., Hope, G.S., 1975. Observations on birds at glacial altitudes on the Cartensz Massif, western New Guinea. Emu 75, 65–72. https://doi.org/10.1071/mu9750065.

Slatkin, Montgomery, 1987. Gene flow and the geographic structure of natural populations. Science 236 (4803), 787–792. https://doi.org/10.1126/science:3576198.

Smith, Brian Tilston, McCormack, John E., Cuervo, Andrés M., Hickerson, Michael. J., Aleixo, Alexandre, Cadena, Carlos Daniel, Pérez-Emán, Jorge, Burney, Curtis W., Xie, Xiaoou, Harvey, Michael G., Faircloth, Brant C., Glenn, Travis C., Derryberry, Elizabeth P., Prejean, Jesse, Fields, Samantha, Brumfield, Robb T., 2014. The drivers of tropical speciation. Nature 515 (7527), 406–409. https://doi.org/10.1038/nature13687.

Stephens, Matthew, Scheet, Paul, 2005. Accounting for decay of linkage disequilibrium in haplotype inference and missing-data imputation. Am. J. Hum. Genet. 76 (3), 449–462. https://doi.org/10.1086/428594.

Wickham, H., Chang, W., Henry, L., Pedersen, T.L., Takahashi, K., Wilke, C., Woo, K., Yutani, H., Dunnington, D., RStudio, 2020. ggplot2: create elegant data visualisations using the grammar of graphics.

Wright, Sewall, 1940. Breeding structure of populations in relation to speciation. Am. Nat. 74 (752), 232–248.

Wright, S., 1938. Size of population and breeding structure in relation to evolution. Science 87, 430–431.

Yu, G., Smith, D.K., Zhu, H., Guan, Y., Lam, T.T.-Y., 2017. ggtree: an r package for visualization and annotation of phylogenetic trees with their covariates and other associated data. Methods Ecol. Evol. 8 (1), 28–36. https://doi.org/10.1111/2041-210X.12628.