IBIS
international journal of avian science

Ibis (2023), **165**, 817–828 doi: 10.1111/ibi.13177

Island life accelerates geographic radiation in the white-eyes (Zosteropidae)

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White-eyes are an iconic avian radiation of small passerines that are mainly distributed across the eastern hemisphere tropics and subtropics. Species diversity of white-eyes is particularly high on oceanic islands, and many species are restricted to single islands or island groups. The high rate of species diversification of white-eyes ranks them among the fastest radiations known in birds, but whether their accelerated diversification was the result of repeatedly colonizing islands remains unexplored. We used a newly estimated timetree for nearly all zosteropids and phylogenetic comparative methods to estimate and compare diversification rates between island and continental lineages. We show that island white-eyes have similar extinction rates, yet higher speciation rates compared with continental white-eyes. In addition, we find higher rates of transitions from islands to continents. Our results show the importance of islands, such as Wallacean and Melanesian archipelagos of the Indo-Pacific, in facilitating high rates of speciation within this remarkable clade.

Keywords: colonization, dispersal, great speciator, Indo-Pacific, speciation, *Zosterops*.

White-eyes (Zosteropidae) are an iconic avian radiation of small passerines known for their exceptional colonization abilities (Mayr & Diamond 2001). The distribution of white-eyes is mostly confined to the eastern hemisphere tropics and subtropics (van Balen 2008). Aside from some unusual island forms (Milá *et al.* 2010, Melo *et al.* 2011), relatively uniform appearance within the white-eyes has hindered efforts to circumscribe natural groups (Mees 1957, 1961, Mayr 1965a). Molecular systematic studies have resulted in several taxonomic revisions and helped clarify species composition of the family (Cibois 2003, Gelang *et al.* 2009, Moyle *et al.* 2009, 2012). The family now represents 141 species placed in 13 genera (Gill *et al.* 2020). However, the genus *Zosterops* represents more than 70% of species-level diversity, and with a crown age in accordance with the Plio-Pleistocene boundary, represents one of the highest rates of diversification among birds (Moyle *et al.* 2009).

Diamond *et al.* (1976) described the white-eyes as a classic example of a great speciator. These species are characterized by their ability to disperse widely and colonize large geographical areas, yet are prone to differentiate rapidly in allopatry. For example, some white-eyes in the Solomon Islands archipelago have differentiated into distinct species across water gaps as narrow as a couple of kilometres while other avian species disperse easily across these gaps (Diamond 1998, Mayr & Diamond 2001). Despite many examples of white-eye lineages diversifying within island archipelagos (Gwee *et al.* 2020, Manthey *et al.* 2020, Sendell-Price *et al.* 2020), taxonomic reassessments of *Zosterops* in Asia and Africa have also revealed unappreciated species diversity in continental regions (Lim *et al.* 2019, Martins *et al.* 2020).

Because of their rapid radiation, white-eyes have posed a significant challenge in understanding the drivers of their diversification. Phylogenetic

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[Correction added on 09 February 2023, after first online publication: a typo in article title has been corrected in this version].

relationships within the family have remained largely unresolved, especially within *Zosterops*, due to short intervals between speciation events in several parts of the tree. Recent studies have helped to resolve relationships in sections of the tree but have relied on either sparse geographical sampling or few loci (Warren *et al.* 2006, Moyle *et al.* 2009, Cox *et al.* 2014, Cai *et al.* 2019, Lim *et al.* 2019, Gwee *et al.* 2020, Martins *et al.* 2020). Studies that combine phylogenomic data and dense geographical sampling from across the range of white-eyes will allow for better assessment of broad-scale ecological, evolutionary and biogeographical hypotheses.

In this study, we investigate the tempo and mode of diversification in white-eyes by incorporating recently published topological information from a higher-level phylogenomic tree (Oliveros *et al.* 2021) and mitochondrial DNA of most zosteropid species from previous phylogenetic studies (Slikas *et al.* 2000, Cibois *et al.* 2002, Voelker & Spellman 2004, Warren *et al.* 2006, Zhang *et al.* 2007, Singh *et al.* 2008, Gelang *et al.* 2009, Moyle *et al.* 2009, 2012, Black 2010, Melo *et al.* 2011, Cox *et al.* 2014, Saitoh *et al.* 2015, Wickramasinghe *et al.* 2017, Cai *et al.* 2019, Lim *et al.* 2019, O'Connell *et al.* 2019b, Martins *et al.* 2020, Valente *et al.* 2020). We used these data to estimate a timetree for nearly all of the white-eye family. This timetree allowed us to test the hypothesis that the Zosteropidae experience fundamentally different diversification dynamics in different geographical contexts. We predict that the increased opportunity for allopatric speciation on islands resulted in higher diversification rates and hence a greater number of extant island taxa.

METHODS

Taxonomic sampling and DNA sequence data

We sampled three mitochondrial (mtDNA) genes (ND2, Cyt *b*, COI) from 126 of 145 white-eyes species (87% of the family) and two species from closely related families (Sylviidae and Timaliidae) as outgroups (Table S1; Moyle *et al.* 2012, Cai *et al.* 2019, Oliveros *et al.* 2019). Three species that we analysed are extinct: White-chested White-eye *Zosterops albogularis*, Marianne White-eye *Zosterops semiflavus* and Robust White-eye *Zosterops strenuus*. We sampled 12 of 13 zosteropid genera, only lacking the genus *Rukia*. Species sampling largely followed the taxonomy of the IOC World Bird List v10.2 (Gill *et al.* 2020) with four exceptions. We sampled four taxa that are recognized as subspecies by the IOC (Heuglin's White-eye *Zosterops poliogastrus kulalensis*, Ashy-bellied White-eye *Zosterops citrinella unicus*, Grey-throated White-eye *Zosterops rendovae oblitus*, Dark-eyed White-eye *Zosterops tetiparius paradoxus*), but are recognized as species by other authorities and so are treated as such here (Mayr & Diamond 2001, del Hoyo *et al.* 2016). Species that we did not sample, including their distribution and geographical context, are annotated in Table S2.

We obtained mtDNA from two sources: (1) off-target reads that we mined from Illumina raw reads, originally produced by sequence capture of ultraconserved elements (UCEs; Oliveros *et al.* 2021) and (2) Sanger sequences from NCBI GenBank (see Table S1). Off-target mtDNA reads are commonly recovered from sequence-capture protocols (Picardi & Pesole 2012, Raposo do Amaral *et al.* 2015, Zarza *et al.* 2016, Andersen *et al.* 2019), often resulting in recovery of complete mitogenomes. We opted to include mtDNA from the Oliveros *et al.* (2021) dataset because these sequences offered a more complete three-gene data matrix that was derived from vouchered specimen material compared with what was available on GenBank. To identify and assemble mtDNA data from Oliveros *et al.* (2021), we mapped trimmed Illumina reads to the Silvereye *Zosterops lateralis* mtDNA reference genome (GenBank accession NC_002069) in Geneious R9 (https://www.geneious.com). The Rufous-capped Babbler *Cyanoderma ruficeps* served as the reference mtDNA genome (GenBank accession KU362930) for one outgroup taxon, the Chestnut-capped Babbler *Timalia pileata*. Mean coverage for each mtDNA gene assembled from off-target UCE reads is reported in Table S1. The Oliveros *et al.* (2021) dataset comprised 46% of the mtDNA species sampling in this study. The remaining 54% came from existing mtDNA sequences on GenBank that we downloaded as singleton gene regions and combined into a supermatrix with the Oliveros data to improve taxonomic sampling and geographical coverage.

Phylogenetic inference

For each mtDNA gene, we aligned sequences with MAFFT v7 (Katoh & Standley 2013) and inspected alignments by eye for errors, spurious sequences and internal stop codons. Next, we performed maximum-likelihood (ML) inference on the concatenated matrix with RAxML-NG v1.1.0 (Kozlov *et al.* 2019) using the autoMRE bootstrapping function and the GTR + I + G nucleotide substitution model partitioned by gene, which was selected by ModelFinder (Kalyaanamoorthy *et al.* 2017). We used the topology from Oliveros *et al.* (2021) as a backbone constraint tree in our likelihood tree searches with the '--constraint-tree' command. The Oliveros tree sampled broadly across the zosteropid family and was inferred using thousands of UCEs. All but eight nodes in their ML tree had 100% bootstrap support; seven of the eight received at least 70% support. Our approach leveraged the robust support of the Oliveros tree across nearly all higher-level relationships that are otherwise largely equivocal in traditional multi-locus datasets (Moyle *et al.* 2009, Cai *et al.* 2019, Martins *et al.* 2020). The remaining tips for which we only had mtDNA from GenBank were allowed to float freely within this constraint framework – RAxML adds taxa in the alignment to the constraint tree using maximum parsimony and optimizes the comprehensive tree under ML while preserving the structure of the constraint tree (Stamatakis 2014, Kozlov *et al.* 2019). We constrained all nodes from the Oliveros tree except the one subtending *Zosterops emiliae* and *Zosterops atricapilla* because this topology received only 22% bootstrap support (Oliveros *et al.* 2021). We simply dropped these tips from the constraint tree so that they were allowed to float in our tree search. For comparison to the constraint tree (Fig. S1), we also generated an unconstrained ML phylogeny in RAxML-NG (Fig. S2).

Divergence time estimation

We estimated divergence times of white-eyes in BEAST v2.6.7 (Bouckaert *et al.* 2019) using the uncorrelated log-normal relaxed clock model, birth–death tree prior and an GTR + I + G model of rate substitution for each of the three gene partitions. To obtain a time-calibrated tree, we used two secondary node calibrations from a fossil-calibrated timetree of passerines (Oliveros *et al.* 2019) representing: (1) the split between *Sylvia atricapilla* and all other taxa, for which we assigned a normal distribution with mean 18.61 million years ago (Ma) and standard deviation (sd) ± 1.75, and (2) the split between *Timalia pileata* and all white-eyes for which we assigned a normal distribution with mean 16.87 Ma ± 1.6 sd. We chose these standard deviations so that 95% of their distributions matched the 95% highest posterior density (HPD) range from Oliveros *et al.* (2019). We ran two independent Markov chain Monte Carlo (MCMC) chains for 50 million generations, sampling every 100 000 generations, resulting in a posterior distribution of 1000 trees. We also ran these analyses by modifying the clock model (strict vs. relaxed) and tree prior (Yule vs. Birth-Death) to more fully explore tree space with respect to the appropriateness of these models. We evaluated convergence of MCMC chains and parameter estimates to ensure that effective sample size (ESS) values were greater than 200 by visualizing trace files in Tracer v1.7.1 (Rambaut *et al.* 2018). We rejected clock-like evolution by noting in Tracer that the mean ucld.stdv parameter estimate was greater than zero (ucld.stdv = 0.182; Drummond *et al.* 2007). We combined post burn-in (10%) chains from the two runs and generated a maximum clade credibility tree using LogCombiner v2.6 and TreeCombiner v2.6 (Bouckaert *et al.* 2019), respectively. This timetree was used in all downstream comparative analyses.

Diversification rates and rate shifts

We used the cladogenetic diversification rate shift model (ClaDS) to estimate diversification rates of Zosteropidae. ClaDS is a Bayesian method for estimating lineage-specific diversification rates and accounts for extinction by allowing lineages to vary in extinction rates but with a constant turnover (Maliet *et al.* 2019). To assess convergence, we ran three independent MCMC chains for 2×10^5 generations. We accounted for missing species in the phylogeny by incorporating a sampling fraction of 0.87 (126/145 white-eyes). After removing the first 25% of the posterior samples as burn-in, we calculated maximum a posteriori estimates. In addition, we estimated the number and location of diversification rate shifts using BAMM v2.5 (Rabosky 2014). We ran two independent MCMC chains for 10^7 generations each, sampling every 1000 generations, and removed the first 10% as burn-in. We checked for convergence by ensuring ESS values exceeded 200 and identified the maximum a posteriori shift configuration using BAMtools v2.1.7 (Rabosky *et al.* 2014).

Ancestral state estimation and lineage diversity through time

We estimated ancestral states at each node while accounting for possible state-dependent diversification using the BiSSE (Binary State Speciation and Extinction) model in the R package diversitree v0.9.1 (Maddison *et al.* 2007, FitzJohn 2012). Each species was coded as occurring on islands or continents based on distribution maps obtained from Birds of the World (Billerman *et al.* 2020). We focused on oceanic islands – those that have never been connected to continental land masses. For instance, we treated the Greater Sundas and New Guinea as continental because they were connected to mainland Asia and Australia, respectively, during recent glacial maxima (Voris 2000, Lambeck & Chappell 2001, Lambeck *et al.* 2002). In some cases, we considered islands of continental origin as oceanic (e.g. Madagascar, New Zealand, New Caledonia) if they separated from the mainland before the origins of Zosteropidae (i.e. more than 20 Ma), thus making the hypothesis of vicariance unlikely (see map in Fig. 1 for complete continental vs. island coding scheme). Three widespread species span continents and islands (Warbling White-eye *Zosterops japonicus*, *Z. lateralis* and Indian White-eye *Zosterops palpebrosus*); we coded these species as continental because the majority of their distribution is continental. Likewise, one species (Lemon-bellied White-eye *Zosterops chloris*) occurs on continental islands although it is largely distributed on oceanic islands; hence, we coded this species as occurring on islands. To explore the accumulation of lineages across islands and continents, we used the approach described by Mahler *et al.* (2010). The analysis involves estimating the geographical state (island or continent) at each node via ML ancestral state estimation; we used marginal ancestral state reconstructions from the BiSSE model. Ancestral states and lineage diversity at each node are then plotted against time to show how lineages accumulated through time in each geographical region.

Diversification on islands and continents

We used BiSSE to simultaneously model character change and its effect on speciation, extinction and transition rates. In particular, we tested whether diversification rates differ between island and continental lineages and whether transition rates from continent to island have the same likelihood as that from island to continent. We compared the relative fit of models where speciation, extinction and transition rates were free to vary to models in which these parameters were constrained to be equal. During the model-fitting step, we corrected for incomplete sampling by specifying the proportion of species included in the tree for each state. We assessed model fit using Akaike Information Criteria and Akaike weights. We calculated uncertainty in parameter estimates by sampling posterior probability distributions of each parameter from the best-fit model using MCMC. We ran the MCMC for 10 000 generations following FitzJohn (2012) and discarded the first 20% of the generations as burn-in. Because rate heterogeneity can confound state-dependent correlations (Maddison & FitzJohn 2015, Rabosky & Goldberg 2015) we also partitioned the tree to allow rates to vary according to where BAMM identified a diversification rate shift at the node subtending *Zosterops* (see Cai *et al.* 2020 and this study) and tested whether speciation rates are higher on islands within this clade relative to the background rate. We used 10 000 MCMC generations to sample the posterior probability distribution of parameters from the best-fit partitioned model. All analyses were performed in diversitree (FitzJohn 2012).

RESULTS

Our concatenated mtDNA alignment contained 278 sequences (3735 bp), of which 1328 sites were parsimony informative. The complete data matrix comprised three mtDNA loci: ND2 (*n* = 85 tips), Cyt *b* (*n* = 119) and COI (*n* = 74; Table S1). Of the 126 species of white-eyes, 77 species had both Cyt *b* and ND2 sequences (61%).

As we constrained our phylogenetic hypothesis to reflect the higher-level relationships from Oliveros *et al.* (2021), our results (Fig. S1) matched that tree. We therefore briefly outline the seven major clades defined by Oliveros *et al.* (2021). Clade I was sister to the rest of Zosteropidae and comprised the monotypic genus *Parayuhina*, which is distributed in mainland Southeast Asia. Clade II comprised the genus *Staphida*, which includes three species that are also distributed in mainland Southeast Asia. The genus *Yuhina* includes seven species across Southeast Asia and

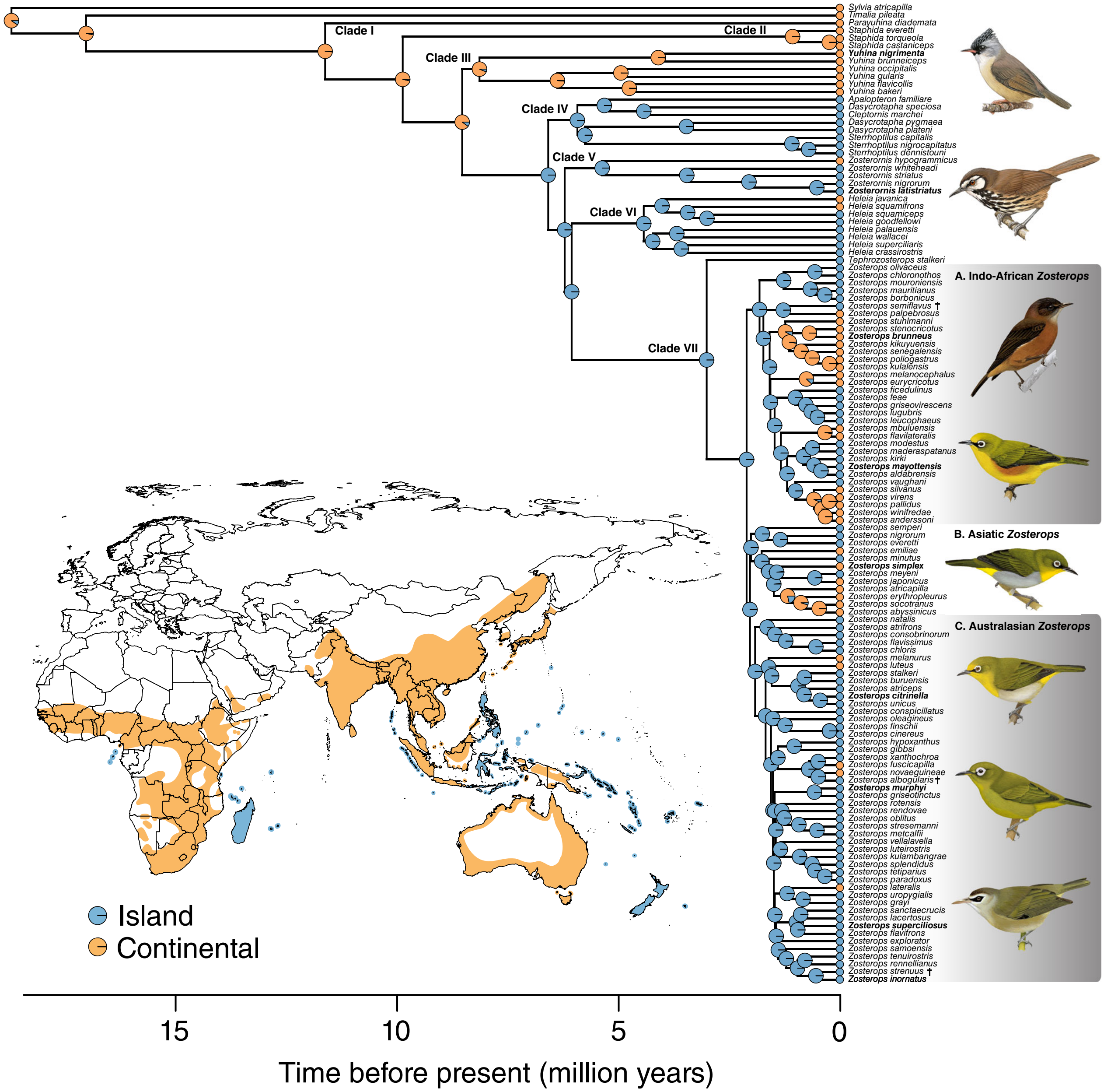

Figure 1. Timetree of white-eyes with maximum-likelihood ancestral state estimations of species occurring on continents or islands while accounting for potential state-dependent diversification (Maddison *et al.* 2007, FitzJohn 2012). The seven major clades follow Oliveros *et al.* (2021). Within *Zosterops*, the three major clades follow Gwee *et al.* (2020). Species in bold correspond to bird illustrations and extinct species are denoted with a dagger. Map shows the distribution of white-eyes on islands and continents. Bird illustrations reproduced with permission from Billerman *et al.* (2020).

comprised Clade III. Clade IV encompassed the monotypic genera *Apalopteron* (Bonin Island, Japan) and *Cleptornis* (Northern Mariana Islands), and the Philippine endemic genera *Dasycrotapha* and *Sterrhoptilus*. Clade V included the genus *Zosterornis* with five species also endemic to the Philippines. Clade VI comprised the genus *Heleia* and the Palau endemic taxon formerly treated as monotypic *Megazosterops*, which was recently recognized as Giant White-eye *Heleia palauensis*

(Oliveros *et al.* 2021). This clade is distributed across the Philippines, Wallacea, the Greater Sundas and Micronesia.

Consistent with Cai *et al.* (2019), we found strong support for the monotypic genus *Tephrozosterops*, endemic to Wallacea, as sister to the species-rich genus *Zosterops*, which together comprise Clade VII (*Tephrozosterops* was not sampled in Oliveros *et al.* 2021). Following Gwee *et al.* (2020), we recovered three well-supported clades within *Zosterops*: Indo-African, Asiatic and Australasian. Further details on the phylogenetic relationships and bootstrap support values are reported in Figure S1.

Divergence timing

Divergence times among white-eyes were consistent with previous estimates of white-eye diversification (Fig. 1; Moyle *et al.* 2012, Cai *et al.* 2019, Oliveros *et al.* 2019). The crown age of Zosteropidae was estimated to be c.11.4 Ma (95% HPD 9.0–13.5 Ma), placing the origins of white-eyes within the mid- to late Miocene. Following the crown divergence of *Parayuhina* (Clade I) from all white-eyes, the lineages leading to *Staphida* (Clade II) and *Yuhina* (Clade III) occurred at c.9.7 Ma (95% HPD 7.8–11.9 Ma) and 8.4 Ma (95% HPD 6.6–10.2 Ma), respectively. In quick succession thereafter, Clades IV, V and VI diversified in a period of c.6.0–6.5 Ma. It was not until c.3.0 Ma (95% HPD 2.1–3.9 Ma) that the split between *Tephrozosterops* and the remaining white-eyes (*Zosterops*) occurred. Shortly afterwards, the origins of the genus *Zosterops* occurred at c.2.1 Ma (95% HPD 1.6–2.5 Ma).

Ancestral state estimation and lineage accumulation among regions

ML estimation of ancestral states indicated that the most recent common ancestor of white-eyes and the clades representing *Staphida* and *Yuhina* were of continental origin (Fig. 1). The ancestral state transitioned from continental to island at the node uniting Clades IV–VII. Subsequent transitions from islands back to continents occurred in multiple independent lineages. Our regional lineage-through-time plot revealed different patterns of lineage accumulation on continents and islands (Fig. 2). Lineages on islands began to accumulate slowly followed by accelerated cladogenesis occurring around the time the *Zosterops* clade formed. The timing of this increase corroborated our BAMM analysis that showed a single rate shift associated with *Zosterops* (Fig. S3). In contrast, lineage accumulation on continents occurred at a slower rate relative to the accumulation of island lineages.

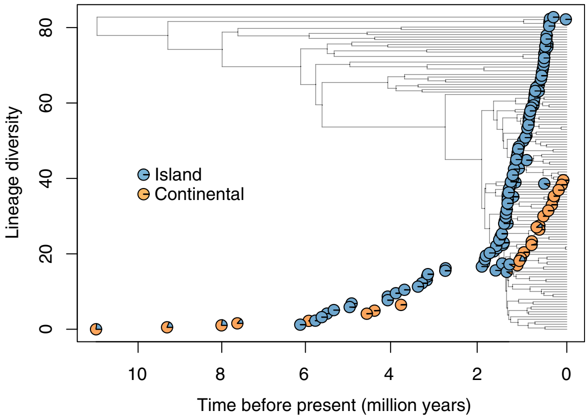

Figure 2. Ancestral state estimations and accumulation of white-eye species diversity through time according to the presence on islands or continents. Outgroups not included.

State-dependent diversification

The BiSSE analysis indicated significant differences in diversification rates between island and continental white-eyes (Table 1; Fig. 3). Our best-fit model was one in which speciation, extinction and transition rates were free to vary between continental and island white-eyes. The next best-fit model was one in which speciation and transition rates were significantly different between continental and island lineages, but with equal extinction rates. In both scenarios, island white-eyes showed elevated speciation rates and higher transition rates from islands to continents relative to continental white-eyes. These ML parameter estimates were reflected in distinct posterior probability distributions of speciation and transition rate parameters (Fig. 3). MCMC analysis inferred lower speciation rates for continental lineages ($\lambda_0 = 0.47$ species Myr^{-1} ± 0.15 sd). In contrast, island lineages were inferred to have higher speciation rates on average ($\lambda_1 = 0.76$ species Myr^{-1} ± 0.09 sd). Transition rates, on average, were inferred to be higher from islands to continents ($q_{10} = 0.17 \pm 0.05$ sd) and lower from continents to islands ($q_{01} = 0.04 \pm 0.04$ sd). When we permitted rates to vary according to

Table 1. BiSSE model comparison of speciation (λ), extinction (μ) and transition (q) rates of white-eyes occurring on continents versus islands (subscript 0 = continent, subscript 1 = island). Parameters estimated for each state (continent and island) are indicated with '$\neq$' whereas parameters constrained to be equal between states are denoted with '='. Best-fit model is in bold (note the second best-fit model [$\lambda_0 \neq \lambda_1$, $\mu_0 = \mu_1$, $q_{01} \neq q_{10}$] is nearly equivalent [ΔAIC score < 2]).

	Speciation rates		Extinction rates		Transition rates					
SSE Model	λ_0	λ_1	μ_0	μ_1	q_{01}	q_{10}	log*L*	df	ΔAIC	w
$\boldsymbol{\lambda_0 \neq \lambda_1, \mu_0 \neq \mu_1, q_{01} \neq q_{10}}$	0.46	0.70	0.32	0.00	0.01	0.14	−258.64	6	**0.00**	**0.58**
$\lambda_0 \neq \lambda_1, \mu_0 = \mu_1, q_{01} \neq q_{10}$	0.32	0.74	0.09	0.09	0.02	0.12	−260.16	5	1.04	0.35
$\lambda_0 \neq \lambda_1, \mu_0 = \mu_1, q_{01} = q_{10}$	0.30	0.69	0.01	0.01	0.10	0.10	−262.73	4	4.18	0.07
$\lambda_0 = \lambda_1, \mu_0 = \mu_1, q_{01} \neq q_{10}$	0.62	0.62	0.18	0.18	0.03	0.12	−267.98	4	14.69	0.00
$\lambda_0 = \lambda_1, \mu_0 = \mu_1, q_{01} = q_{10}$	0.62	0.62	0.18	0.18	0.11	0.11	−268.76	3	14.25	0.00

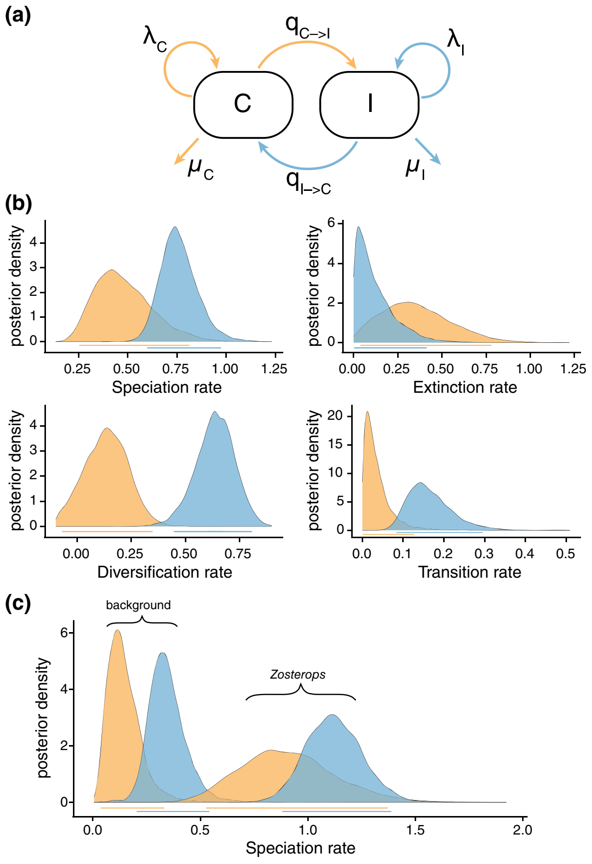

Figure 3. (a) Best-fitted BiSSE model, (b) posterior densities of rate estimates from the best-fitted model and (c) posterior density estimates of speciation rates from the best-fitted partitioned model ('background' refers to Zosteropidae excluding *Zosterops*).

where BAMM identified a rate shift at the node subtending *Zosterops*, we still found that islands influenced speciation in the direction we predicted (Fig. 3c). This result was also favoured by ML model selection (Table S3).

DISCUSSION

We used phylogenetic comparative methods to clarify the role of islands as sources of species generation across the broad distribution of white-eyes. Using a newly estimated timetree for nearly all white-eyes, our results indicated that dispersal to islands aided in higher speciation rates within the family, specifically for *Zosterops*. Although extinction rates are challenging to estimate from molecular phylogenies alone, we attempted to do so on a moderately sized tree (>100 taxa) while accounting for rate heterogeneity and incomplete sampling (Beaulieu & O'Meara 2015). We found that extinction rates varied little between island and continental lineages, suggesting that the high rate of diversification in this group can be attributed to differential rates of speciation, not extinction. Furthermore, we found higher transition rates from islands to continents, demonstrating that islands are not only sinks but also sources of species diversity. Compared with continental white-eyes, island white-eyes have evolved a substantial number of species within the last c.1.5–2.5 million years. This result is in large part due to their exceptional colonization abilities, which have allowed white-eyes to disperse to new geographical areas, in particular oceanic islands, where allopatric speciation could proceed with relatively little gene flow.

White-eyes are embedded within the babbler radiation, a large clade with over 400 species (Cai *et al.* 2019). Babblers have their origins and centres of diversity in continental Southeast Asia (Cai *et al.* 2020). However, white-eyes are notable for having colonized many geographical areas outside Southeast Asia, including more islands than any other passerine group in the world (Moreau 1964). We show with comparative analyses that the rapid diversification of white-eyes is based on their exceptional ability to successfully colonize oceanic islands. Ringing studies have shown that some white-eyes are capable of dispersal distances greater than 1500 km (van Balen 2008); likewise, some clades contain species with highly disjunct distributions compared with close relatives (e.g. *Zosterops minutus*, *Zosterops semperi*), demonstrating the strong dispersal propensity of this lineage. Our findings add to a growing body of studies that have documented cases of elevated rates of avian diversification on oceanic islands at different spatial and taxonomic scales, especially in the Indo-Pacific region (Irestedt *et al.* 2013, Andersen *et al.* 2015, 2018, Pedersen *et al.* 2018, O'Connell *et al.* 2019a, Lapiedra *et al.* 2021).

In contrast to speciation rates, we found low rates of extinction for island white-eyes (Fig. 3b). The natural history of white-eyes, including their generalist ecology, fast generation times and canopy-dwelling habits, are consistent with the idea that they may be less prone to extinction (van Balen 2008, Cornetti *et al.* 2008, Fjeldså *et al.* 2020). This pattern contrasts with other avian lineages on islands, such as habitat-specialist and ground-dwelling rails (Rallidae) that have experienced high rates of extinction (Steadman 1995, 2006). However, the difficulty in accurately estimating extinction rates from empirical phylogenies should be acknowledged (Quental & Marshall 2010, Rabosky 2010, Davis *et al.* 2013).

According to the theory of island biogeography (MacArthur & Wilson 1967), species diversity on islands develops as a dynamic equilibrium between immigration and extinction. Islands are often regarded as evolutionary sinks, thus contributing little to species diversity on continents, with 'downstream colonization' from continents to islands being the major pattern (MacArthur & Wilson 1963, Mayr 1965b, Diamond 1977). However, molecular phylogenies have provided increasing evidence for a higher frequency of recolonization of mainlands by island lineages than previously thought (reviewed in Bellemain & Ricklefs 2008). Our inference of higher transition rates of white-eyes from islands to continents calls into question the idea of colonization from continents to islands as a one-way journey. This result adds to several examples documenting 'upstream colonization' (Filardi & Moyle 2005, Jønsson *et al.* 2010, Lapiedra *et al.* 2021, Brady *et al.* 2022, McCullough *et al.* 2022), suggesting the need to reassess the role of islands not as evolutionary sinks but as potential sources of species diversity.

Islands have undoubtedly acted as a driver of diversification in white-eyes through the process of allopatric speciation. However, the high rate of species formation in this lineage is probably determined not only by extrinsic factors (islands) but the combination of extrinsic and intrinsic (taxon-specific characteristics) factors. The exceptional dispersal ability or propensity of white-eyes allows them to colonize many islands, but in theory this ability should oppose diversification because of the countering effects of gene flow and range expansions (Price 2008). Intrinsic life history traits in combination with geographical context may help to explain the cause of rapid speciation in white-eyes. Traits hypothesized to influence speciation rate in white-eyes include sociality, generalist ecology and fast generation times when compared with other lineages (Moyle *et al.* 2009). In addition, Diamond *et al.* (1976) and Moyle *et al.* (2009) suggested that evolutionary changes in dispersal ability provide a possible underlying mechanism of diversification in this group. Once established on islands, reluctance to cross open water gaps may have led to reductions in dispersal ability. This reluctance to cross water is perhaps best exemplified in the New Georgia Group, Solomon Islands, where seven species occur on islands that are separated by only a few kilometres of open water (Manthey *et al.* 2020).

Our study used new topological information from a higher-level UCE tree and dense species-level mtDNA sampling to analyse the tempo and mode of diversification in a classic great speciator. Using phylogenetic comparative methods, we find support for the hypothesis that occurrence on islands triggered the rapid diversification of white-eyes. However, it is likely that islands alone are not the single cause of their rapid diversification and that a combination of islands and taxon-specific characteristics better fits the patterns we observed. Nevertheless, our results highlight islands, such as the island archipelagos of the Indo-Pacific region, as important components in explaining the colonization history and diversification dynamics within this iconic avian radiation.

We thank the natural history museums, researchers and collectors whose specimen data made this study possible. We thank the reviewers, Associate Editor and Editor Rauri Bowie for comments that improved earlier versions of the manuscript.

AUTHOR CONTRIBUTIONS

Nicholas T. Vinciguerra: Conceptualization (lead); Formal analysis (lead); Methodology (lead); Writing – original draft (lead); Writing – review & editing (lead). **Carl H. Oliveros:** Conceptualization (supporting); Formal analysis (supporting); Methodology (supporting); Writing – original draft (supporting); Writing – review & editing (supporting). **Robert G. Moyle:** Conceptualization (supporting); Formal analysis (supporting); Methodology (supporting); Writing – original draft (supporting); Writing – review & editing (equal). **Michael J. Andersen:** Conceptualization (equal); Formal analysis (supporting); Methodology (supporting); Writing – original draft (supporting); Writing – review & editing (equal). [Correction added on 09 February 2023, after first online publication: the degree of contribution of each author has been included in this version].

CONFLICT OF INTEREST

None.

FUNDING

This work was supported by the National Science Foundation (DEB 1311513 to C.H.O. and R.G.M., DEB 1146345 and 1557053 to R.G.M., and DEB 1557051 and 2112467 to M.J.A.).

ETHICAL NOTE

None.

Data Availability Statement

Sequence alignment in NEXUS format, BEAST Maximum Clade Credibility trees in Newick format, posterior distribution of trees in NEXUS format, character state data and code for comparative analyses are available as Appendix S1.

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Received 2 December 2021;
Revision 16 May 2022;
revision accepted 11 December 2022.
Associate Editor: Martin Stervander.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. README file, sequence alignment, code for comparative analyses, character state data and timetrees (maximum clade credibility and posterior distribution of trees).

Figure S1. RAxML constraint tree with bootstrap support.

Figure S2. RAxML unconstrained tree with bootstrap support.

Figure S3. ClaDS estimate of heterogeneity in white-eye diversification rates.

Table S1. Taxon sampling, DNA sequences used in this study and mean coverage for each mtDNA gene mined from UCE off-target reads.

Table S2. Species that we did not sample, including their distribution and geographical context (island vs. continental).

Table S3. BiSSE model comparison of speciation (λ), extinction (μ) and transition (q) rates of white-eyes occurring on continents (subscript 0) vs. islands (subscript 1).