Island size shapes genomic diversity in a great speciator (Aves: *Zosterops*)

Ethan F. Gyllenhaal[1*], Michael J. Andersen[2], Robert G. Moyle[3], Joseph D. Manthey[1*]

[1]Department of Biological Sciences, Texas Tech University, Lubbock, TX, USA

[2] Department of Biology and Museum of Southwestern Biology, University of New Mexico, Albuquerque, NM 87111

[3]Department of Ecology and Evolutionary Biology and Biodiversity Institute, University of Kansas, Lawrence, KS 66045

*Corresponding author

Abstract.

Islands have long represented natural laboratories for studying many aspects of ecology and evolutionary biology, from speciation to community assembly. One aspect that has been well documented is the correlation between island size and taxonomic diversity, likely due to decreased complexity and population size on small islands. This same logic can apply to genetic diversity, which should predictably decrease with effective population size. The island size-diversity correlation has received support over the years, but often focuses on single metrics of genetic diversity. Here, we use *Zosterops* white-eyes in the Solomon Islands to study the correlation between island size and various metrics related to genetic diversity, including runs of homozygosity and fixation of transposable elements. We find that almost all these metrics strongly correlate with island size, and in turn with each other. We infer that island size is independently correlated with these different variables, demonstrating that population size

impacts genomic metrics of diversity in a variety of ways across temporal and hierarchical scales.

Introduction.

Genetic diversity is the fundamental component of adaptation and persistence, and understanding how variation is distributed among populations is essential for understanding how natural populations evolve (Wright 1982; Hughes et al. 2008). Islands serve as natural laboratories for exploring diverse topics in ecology and evolutionary biology, such as speciation and community assembly, because of their discrete geographic boundaries (Mayr 1942; MacArthur and Wilson 1967; Whittaker et al. 2017). Although archipelagos are characterized by dynamism, island size can be used as a proxy for population size, particularly in population genetic timescales in more stable archipelagos such as those produced by subduction zones (Neall and Trewick 2008). The fact that many species effectively occupy the whole island also allows robust modeling of species ranges over time with bathymetric data and data on sea level change (Tan et al. 2023). Thus, oceanic islands are useful as reliable proxies for estimating population size over time, which is a key factor influencing genetic diversity (Soulé 1976; Frankham 1996).

The species-area relationship (Preston 1962a, 1962b) and island biogeographic theory (MacArthur and Wilson 1963, 1967) suggest that larger islands host greater species richness, often due to increased habitat complexity and population sizes. Island biogeographic theory also postulates that distance between regions, a proxy for connectivity, correlates with species richness. The same stochastic processes that operate on taxonomic diversity should shape genetic diversity. This relationship between island size and genetic diversity has been observed in

numerous taxa and geographic contexts, such as lizards (Soulé and Yang 1973, Gorman et al. 1975), rodents (Patton 1984; Sato et al. 2017), frogs (Wang et al. 2014), and birds (Hoeck et al. 2010; Manthey et al. 2020). Such patterns have also been documented in continental contexts, including "sky islands" (Hill et al. 2017; Costanzi and Steifetten 2019) and habitat patches (Descimon and Napolitano 1993). Many of these studies focused on a single measures of genetic diversity and few included complex but important genomic metrics, such as those relevant to demographic history (e.g., effective population size over time) and conservation genetic health (e.g., runs of homozygosity; Szpiech et al. 2013; Ceballos et al. 2018) .

Zosterops white-eyes, a species-rich bird radiation across the Afro- and Australasian tropics, present an ideal system for studying these patterns. Distributed across many Indo-Pacific islands, they have long been central to speciation theory (e.g., Mayr 1942) and discussions of the 'great speciator' paradox (Diamond et al. 1976). Past work has also demonstrated high population densities, even in range-restricted endemics (Cowles et al. 2021). Rapid diversification within *Zosterops* has also made relationships within this clade difficult to resolve (Moyle et al. 2009; Cai et al. 2018; Oliveros et al. 2021, Vinciguerra et al. 2023). The *Zosterops griseotinctus* complex is largely composed of phenotypically distinct yet genetically similar endemics in the Solomon Islands and exhibits intricate patterns of gene flow (Manthey et al. 2020).

In this study, we used whole-genome resequencing of 15 species from the *Z. griseotinctus* complex to test the hypothesis that genomic diversity and other metrics of genetic variation correlate predictably with island size. We hypothesize a positive correlation between island size and (1) effective population size, (2) genome-wide genetic diversity, and (3) the variability of genetic diversity across the genome. Conversely, we predict a negative correlation

between island size and the length and number of runs of homozygosity. Finally, we expect to see fixation of derived polymorphic transposable elements (TEs) in smaller island populations, as these generally slightly deleterious elements are more readily selected against in large populations (Jurka et al. 2011, Leroy et al. 2021).

Methods.

Reference genome editing and TE annotation. We used the *Zosterops lateralis* genome (Cornetti et al. 2015) as a reference for this work. Because this genome was highly fragmented, we used Satsuma v2 (Grabherr et al. 2010) and the *Taeniopygia guttata* chromosome-scale genome assembly (Warren et al. 2010) to assign chromosomal coordinates to the *Z. lateralis* genome.

We annotated TEs and repetitive elements in the *Z. lateralis* genome using RepeatModeler v1.0.11 (Smit and Hubley 2008) followed by manual TE curation. RepeatModeler uses multiple programs to identify repeats: RECON (Bao and Eddy 2002), RepeatScout (Price et al. 2005), and Tandem Repeats Finder (Benson 1999). We filtered sequences previously curated (≥ 98% identity) in the RepBase vertebrate database v24.03 (Jurka et al. 2005) and created consensus sequences of novel elements with manual curation. We refined RepeatModeler consensus sequences as follows: (1) extract sequences matching *de novo* repetitive elements and flanking sequence with BLAST and bedtools (Camacho et al. 2009; Quinlan and Hall 2010), (2) alignment of extracted sequences using MAFFT (Katoh and Standley 2013), (3) trim ambiguous nucleotides on edges of newly created consensus sequences, and (4) repeating up to two times for any consensus sequences without recovered edges. We assessed any similarity of *de novo* elements to previously curated RepBase sequences with

BLAST, using matches for naming purposes. Lastly, we used the RepBase vertebrate database and newly curated repeats with RepeatMasker v4.08 (Smit et al. 2015) to mask and summarize repetitive and transposable elements in the *Z. lateralis* genome.

Resequencing and genotyping. We used a total of 17 *Zosterops* individuals in this study (Table S1), including 15 from the Solomon Islands (Fig. 1A), the closely related *Z. griseotinctus*, and outgroup *Z. simplex*. The Solomon Islands samples represented 9 species and 11 subspecies, with a single sample per island, excluding two sympatric species on Kolombangara (Table S1). Although the sample size per island was low, the metrics we chose were designed for single samples of similarly high depths of coverage (Fig. S1), as should be representative of the population. We used DNA extractions from previous work in these taxa (e.g., Manthey et al. 2020) to create Illumina sequencing libraries, and sequenced on a NovaSeq6000 at the Oklahoma Medical Research Foundation (OMRF) Clinical Genomics Center. We aimed to sequence each individual at 10–20x genomic coverage, and most samples reached this expectation (Fig. S1).

We used the bbmap (Bushnell 2014) script bbduk.sh to trim sequencing adapters and quality filter raw sequencing data. We aligned reads to the reference genome using the BWA-MEM function in BWA (Li and Durbin 2009) and samtools v1.4.1 (Li et al. 2009) to convert the output to BAM format and measure sequencing depth (Fig. S1). We cleaned, sorted, added read groups to, and removed duplicates from each BAM file using the Genome Analysis Toolkit (GATK) v4.1.0.0 (McKenna et al. 2010). We genotyped all individuals using three steps in GATK: (1) HaplotypeCaller function to call genotypes per individual, (2) CombineGVCFs function to concatenate output, and (3) GenotypeGVCFs to group genotype all individuals for variant and invariant sites. We used VCFtools v0.1.14 (Danecek et al. 2011) to filter output genotyped sites to: (1) minimum site quality of 20, (2) minimum genotype quality of 20, (3)

minimum depth of coverage of 5, and (4) maximum mean depth of coverage of 30. Some analyses used additional restrictions on data quality (see appropriate methods sections).

Phylogenomics. We estimated phylogenies for non-overlapping 25 kbp sliding windows using RAxML v8.2.12 (Stamatakis 2014) with the GTRGAMMA model of sequence evolution, the most flexible model available, which allows variable substitution rates and is time-reversible. Here, we filtered our data to include only biallelic and invariant sites and required a minimum of 10,000 genotyped sites to retain the window, resulting in 40,257 windows retained. From these 40,257 phylogenies, we estimated a species tree using two methods: (1) maximum clade credibility tree of all input trees using DendroPy to determine which input tree is best supported by the data (Sukumaran and Holder 2010), and (2) the coalescent-based species tree approach ASTRAL III (Zhang et al. 2018).

Genetic diversity estimates. We estimated per-individual genetic diversity as the observed heterozygosity across all genotyped sites (both variant and invariant). We estimated ROH (runs of homozygosity) per individual across 25 kbp windows with no heterozygosity and at least 80% of sites genotyped (i.e., 20+ kbp sites genotyped in 25 kbp windows).

Polymorphic TEs. We found ten endogenous retroviruses (ERVs) with more than 500 copies exhibiting low divergence from TE consensus sequences (Table S2). We used these ERVs as candidates to look for between sample TE insertion polymorphisms with the Mobile Element Locator Tool v2.1.2 (MELT; Gardner et al. 2017). MELT uses split and unaligned reads from the BWA alignments, the reference genome, and consensus ERV sequences to identify polymorphic ERVs. We used MELT in a multistep process: (1) discovery of potential ERVs per individual, (2) grouping together putative polymorphic ERVs based on reference genome location, (3) genotyping all individuals for the combined putative polymorphic ERV dataset, and (4) filtering

of all genotype calls. We ran these steps for each ERV separately, with a maximum 15% divergence from the ERV consensus sequence. Any genomic coordinates (± 100 bp) called for more than one ERV were filtered to the most similar ERV consensus sequence. We filtered the final ERV polymorphisms by removing: (1) those with imprecise breakpoints or limited evidence (MELT ASSESS flag ≥ 3), (2) polymorphisms not passing MELT's internal quality filters (MELT FILTER flag != PASS), and (3) polymorphic ERVs with > 25% missing data.

Demography. We estimated demographic history for each individual using MSMC2 v1.1.0 (Schiffels and Durbin 2014). For use in MSMC, we masked genomic regions that were not genotyped and sites with coverage of less than eight aligned reads (Nadachowska-Brzyska et al. 2016). MSMC estimates are particularly accurate in panmictic populations, but population structure or changes in gene flow between populations may mimic changes in population sizes (Mazet et al. 2016; Chikhi et al. 2018). Therefore, some caution should be used when interpreting raw demographic histories. However, we largely use the demographic histories to estimate recent and harmonic mean population sizes and not strict interpretation of the population trends. In MSMC, we allowed up to 20 iterations and up to 23 distinct time segments. We performed ten bootstrap replicates (1 Mbp genomic segments) to assess how demographic signal varied using different genomic regions. MSMC output is scaled relative to a species' generation time and mutation rate. Here, we used double the age of sexual maturity as a generation time proxy, as in previous studies (Nadachowska-Brzyska et al. 2015). Based on an estimate of six months to sexual maturity (Moyle et al. 2009), we used a one-year generation time. We used a mutation rate of 3.16×10^{-9} substitutions / site / year as reported from the *Z. lateralis* genome (Cornetti et al. 2015).

Island size estimation. We manually measured the area of each island for all species in the Solomon Islands using satellite imagery in Google Earth. For the one montane species, *Z. murphyi*, we calculated the area of the species' range by calculating the area of the highland region on the island of Kolombangara coincident with its estimated range.

Statistical analysis. We used R v4.4.1 (R Development Core Team 2023) to conduct an array of statistical analyses. First, we visualized correlations among variables using a correlogram made with corrplot v0.95 (Wei and Simko 2014). Second, we performed linear regressions to examine the relationship between island size and our genetic variables. Third, due to the high collinearity of the dataset, we performed LASSO regressions with GLMNET v4.1-8 (Friedman et al. 2010) to determine what variables were the most direct predictors of a given response variable. Although island size is an explanatory variable, to determine how it impacted different diversity metrics independently, we treated it as a response variable and all genomic variables as predictors for a LASSO regression. LASSO regressions were performed with an alpha value of 1 and lambda value selected by cross-validation.

Results.

We resequenced 17 *Zosterops* individuals from the Solomon Islands at 7–16x mean coverage (Fig. S1; Table S1). Using 40,257 phylogenies, we identified a species tree consistent with previous phylogenetic reconstructions using reduced-representation genomic methods (Fig. 1B; Manthey et al. 2020).

Demography. Demographic history varied widely across *Zosterops* taxa in the Solomon Islands (Fig. S2). Small island endemics generally have had small populations over the past 300,000 years (e.g., $N_E < 200{,}000$). Taxa with larger range sizes have experienced somewhat

fluctuating population sizes through time, and currently exhibit higher N_E than small island endemics (e.g., N_E ranging 200,000 to 800,000). The demographic history of *Z. metcalfii* varies widely by island and likely represents both changes in population sizes and population connectivity with other island populations during Pleistocene glacial cycles. All *Z. metcalfii* populations exhibited increases in population sizes prior to 100,000 years ago. Subsequently, the population histories differed: (1) populations on the large islands of Choiseul and Isabel experienced population declines 50,000 years ago followed by population size increases; (2) the Shortland population has drastically declined in size in the last 50,000 years; (3) the Ngella population has generally been smaller than on the larger islands, but more stable than Shortland. Recent population sizes and harmonic mean population sizes over the past 200,000 years both had a positive relationship with island size (Fig. 2A).

Genomic Diversity. Both genomic heterozygosity and variability in heterozygosity across the genome varied widely. Individuals from smaller islands generally exhibited lower genomic diversity and less variability (although not significantly, $p=0.056$) in diversity across the genome relative to individuals on larger islands (Fig. 2C, 2D; Fig. S3; Table S1). Most metrics of genetic diversity and effective population size covaried (Fig. S4). However, using a LASSO regression treating island size as a response and these genomic metrics as predictors, only non-reference ERVs, number of ROH, and recent population size were included in the final model (Table S3).

The number and total length of ROH were nearly perfectly correlated (Fig. S4, S5) and higher in individuals from smaller islands (Fig. 2F). Notably, the *Z. luteirostris* individual from Ghizo, the smallest island in our sample, showed the lowest genomic diversity and a highly elevated amount of ROH (Fig. 2F). However, only the number and size of ROH on Ghizo were

both notable outliers relative to the other islands (Fig 2). When considering the number and length of ROH segments, no islands strayed from a linear ratio of the two (Fig. S5).

TE Polymorphisms. We genotyped insertion presence/absence polymorphisms for ten recently active ERVs. We identified ~3000 polymorphisms with 100 to 300 homozygous ERVs absent in the reference genome per individual. Generally, individuals on smaller islands had more homozygous non-reference ERVs than individuals on larger islands (Fig. 2D). The number of homozygous non-reference ERVs was strongly, but not perfectly, correlated with heterozygosity (Fig. S4). In a LASSO regression with non-reference ERVs as the response variable, island size, heterozygosity, historic population size, and the total length of ROH segments were included as predictors in the model (Table S3).

Discussion.

We demonstrated that island size is correlated with effective population size, heterozygosity, and several other metrics related to genomic variability. Heterozygosity was not the strongest correlate of island size, and LASSO regression with island size did not retain it as a predictor, implying it did not explain sufficient unique variance relative to other variables (Table S3). Instead, the LASSO regression recovered that island size was most directly correlated with measures of recent population size, individual demography (i.e., ROH), and transposable element activity. This reflects the myriad effects that population size can have on genomes. It is also notable that these strong correlations arose from just modern island size, despite evidence of gene flow within and among species. However, the legacy of gene flow facilitated by glacial connectivity can still be seen in two medium-sized islands with high genetic diversity: Ngella and Shortland. Both belong to the Pleistocene Bukida group, which ranged from Guadalcanal to

Shortland islands and included Bougainville (not sampled in this study). This group showed elevated diversity compared to similarly sized islands (Fig. 2). However, they were not outliers for recent effective population size, ROH metrics, and transposon activity, which we also found as the most direct correlates of island size (Fig. 2, Table S3).

Runs of homozygosity (ROH) is one of the most important statistics in the modern conservation genetics toolkit (Szpiech et al. 2013; Ceballos et al. 2018). This statistic is a predictor of individual demography and inbreeding, and we found that island size is a predictor of ROH (Fig. 2F). The small island of Ghizo has extremely high ROH statistics, despite not being an outlier in any other metric (including overall genetic diversity). Additionally, its ratio between sum of ROH lengths and number of ROH was consistent with other populations (Fig. S5). Direct inbreeding (i.e., consanguineous individuals) is expected to produce fewer longer ROH segments, while the observed pattern is consistent with a bottleneck or persistent low population size (Ceballos et al. 2018). However, a bottleneck due to a founder effect is unlikely in the deeply diverged *Z. luteirostris*, and persistent low population size should manifest itself in other small New Georgia Group islands. Regardless, the high prevalence of ROH is a concern for this species' genetic health, demonstrating the need for continued conservation attention (Liligeto 2013). It is worth noting that the proportion of the genome contained within ROH is low compared to other mammalian (Kyriazis et al. 2023; Bertola et al. 2024; Khan et al. 2024) and avian (Martin et al. 2023) systems with small population sizes.

TEs are an important but not fully understood area of conservation genomics, as they are often weakly deleterious and may diversify in small populations, where selective forces are weaker (Jurka et al. 2011). Consistent with this hypothesis, we found that the number of homozygous non-reference ERVs was correlated with island size. This could occur due to drift

(where ERVs act like neutral SNPs) and stronger selective forces against ERVs in larger populations. Drift is likely a component of this phenomenon, but doesn't seem to be the only one, as the negative correlation between homozygous ERVs and SNP heterozygosity is strong but imperfect (r = -0.83), and both island size and genetic diversity were found to be predictors in a LASSO model relating ERV fixation to other measured variables. Future work could further explore whether ERV fixation is related to other metrics of natural selection, such as the population-level synonymous and non-synonymous diversity ratio (Leroy et al. 2021).

Gene flow can be a major correlate of genetic diversity (Epps et al. 2005; Botigué et al. 2013), but we were not able to assess it directly in this study. However, Manthey et al. (2020) recovered extensive gene flow among members of the Solomons *Zosterops* group, including two sympatric taxa that lack current gene flow (Cowles and Uy 2019). One case of gene flow that Manthey et al. (2020) recovered was between *Z. ugiensis* on Guadalcanal and *Z. metcalfi*. The impact of this gene flow can be seen in the relatively low genetic diversity of the Makira—but not Guadalacanal—population of this species. This finding is consistent with introgression from *Z. metcalfi* into *Z. ugiensis*, thereby bolstering its genetic diversity. Such gene flow may help explain why the correlation between genetic diversity and island size is not 1:1, as demonstrated by the need to use the logarithm of island size as a predictor. That relationship could be explained by Lewontin's paradox–the empirical finding that organisms show far lower genetic diversity than would be expected based on census size (Lewontin 1974; Buffalo 2021)–and density compensation–where smaller islands host fewer species at higher densities (MacArthur et al. 1972; Wright 1980).

In sum, our results emphasize the strength of island size as a predictor of a wide range of genomic variables. However, these variables are heavily correlated themselves, making it

difficult to untangle true relationships. Despite this shortcoming, we still recover unique signals from different aspects of genomic diversity. Most importantly, we show that measuring multiple metrics can reveal unique aspects of evolution, as we demonstrate here in this iconic geographic radiation of white-eyes.

Acknowledgements.

We thank the Solomon Islands Ministry of Environment, Climate Change, Disaster Management, and Meteorology for permits to conduct fieldwork (permit RP/2017/001) and the provincial governments in the Solomon Islands that gave permission to conduct research. We are especially indebted to the local communities that graciously invited us onto their lands and who provided assistance and logistical support with field work. We thank D. Boseto and staff at Ecological Solutions Solomon Islands for help with logistics, permitting, and fieldwork. We are grateful to the University of Kansas Biodiversity Institute, American Museum of Natural History, Smithsonian National Zoological Park, and University of Washington Burke Museum for loaning tissues used in this study. This work was supported by National Science Foundation grants (DEB-1557053 to RGM and DEB-1557051 to MJA) and startup from Texas Tech University to JDM. We would also like to thank Manuel Hoyos for discussion about transposable element evolution.

Data, code and materials.

All raw data is available on NCBI's sequence read archive (SRA) under BioProject ID: PRJNA686795. All code to analyze the data is available atgithub.com/jdmanthey/zosterops_genomes and archived on Dryad and Zenodo at https://doi.org/10.5061/dryad.z8w9ghxqf.

Figures and Tables.

Figure 1. Sampling and phylogenomic relationships of *Zosterops* taxa used in this study. (A) Sampling localities for this study. Dark gray indicates current island areas and lighter gray shows approximate land connectivity at low sea levels during Pleistocene glacial maxima. (B) Maximum clade credibility tree from 40,257 phylogenies and rooted with *Z. simplex*. Numbers above branches show the proportion of these phylogenies supporting specific relationships, and all nodes had 100% support in the species tree with the same topology estimated in ASTRAL III.

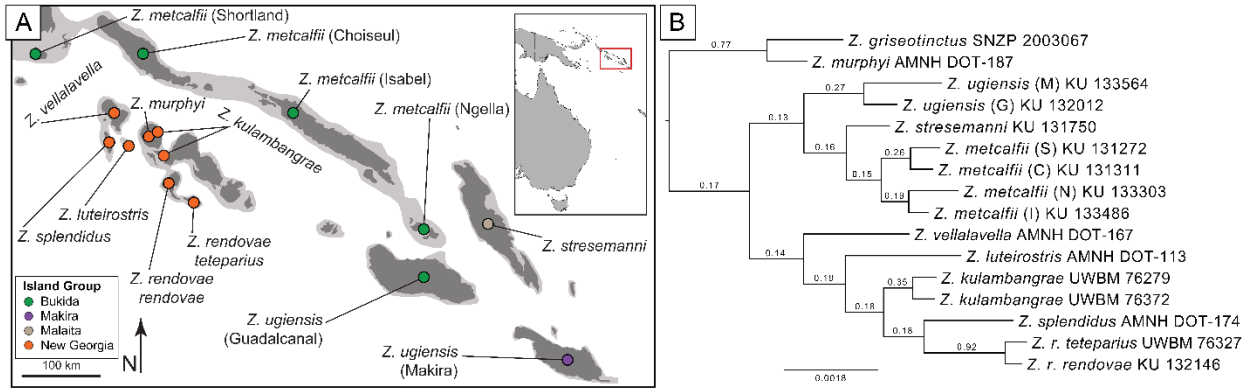
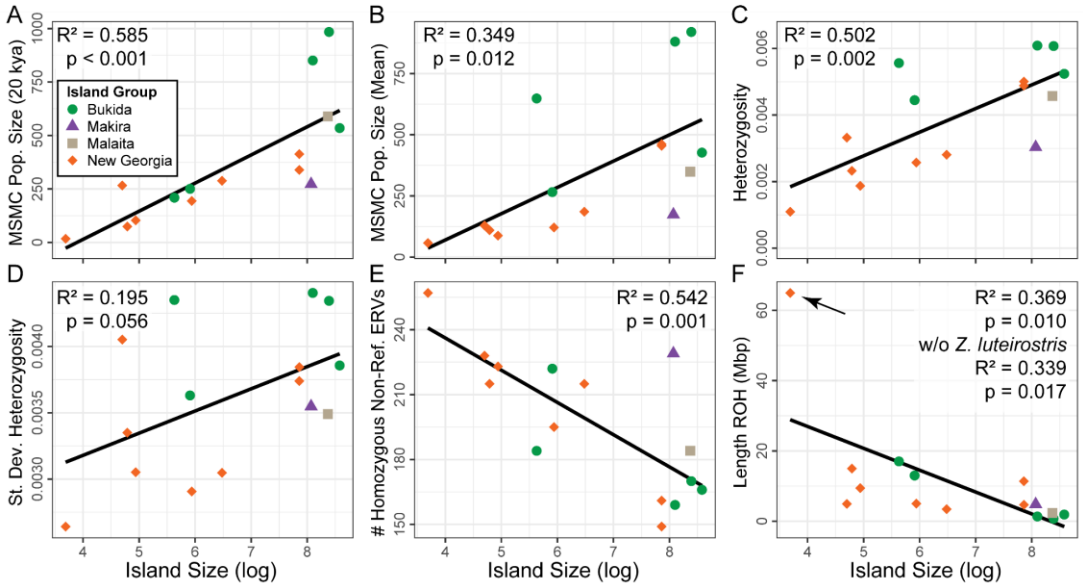


Figure 2. Relationships of island size and genomic parameters. Island size is strongly correlated with (A) recent and (B) harmonic mean of population size estimates in MSMC2, (C) genome-wide mean and (D) variability in heterozygosity, (E) homozygous non-reference endogenous retroviruses (ERVs) and (F) total length of runs of homozygosity (ROH). In (F), regression was performed with and without a putative outlier from the smallest island, but only the model with the outlier is shown (denoted with an arrow). Point shape and color correspond to the island group the population is from.



References

Bao Z., Eddy S.R. 2002. Automated de novo identification of repeat sequence families in sequenced genomes. Genome Res. 12:1269–1276.

Benson G. 1999. Tandem repeats finder: a program to analyze DNA sequences. Nucleic Acids Res. 27:573–580.

Bertola L.D., Quinn L., Hanghøj K., Garcia-Erill G., Rasmussen M.S., Balboa R.F., Meisner J., Bøggild T., Wang X., Lin L., Nursyifa C., Liu X., Li Z., Chege M., Moodley Y., Brüniche-Olsen A., Kuja J., Schubert M., Agaba M., Santander C.G., Sinding M.-H.S., Muwanika V., Masembe C., Siegismund H.R., Moltke I., Albrechtsen A., Heller R. 2024. Giraffe lineages are shaped by major ancient admixture events. Curr. Biol. 34:1576–1586.e5.

Botigué L.R., Henn B.M., Gravel S., Maples B.K., Gignoux C.R., Corona E., Atzmon G., Burns E., Ostrer H., Flores C., Bertranpetit J., Comas D., Bustamante C.D. 2013. Gene flow from

North Africa contributes to differential human genetic diversity in southern Europe. Proc. Natl. Acad. Sci. U. S. A. 110:11791–11796.

Buffalo V. 2021. Quantifying the relationship between genetic diversity and population size suggests natural selection cannot explain Lewontin's Paradox. Elife. 10.

Bushnell B. 2014. BBMap: A fast, accurate, splice-aware aligner. .

Cai T., Cibois A., Alström P., Moyle R.G., Kennedy J.D., Shao S., Zhang R., Irestedt M., Ericson P.G.P., Gelang M., Qu Y., Lei F., Fjeldså J. 2018. Near-complete phylogeny and taxonomic revision of the world's babbler (Aves: Passeriformes). Mol. Phylogenet. Evol.

Camacho C., Coulouris G., Avagyan V., Ma N., Papadopoulos J., Bealer K., Madden T.L. 2009. BLAST+: architecture and applications. BMC Bioinformatics. 10:421.

Ceballos F.C., Joshi P.K., Clark D.W., Ramsay M., Wilson J.F. 2018. Runs of homozygosity: windows into population history and trait architecture. Nat. Rev. Genet. 19:220–234.

Chikhi L., Rodríguez W., Grusea S., Santos P., Boitard S., Mazet O. 2018. The IICR (inverse instantaneous coalescence rate) as a summary of genomic diversity: insights into demographic inference and model choice. Heredity . 120:13–24.

Cornetti L., Valente L.M., Dunning L.T., Quan X., Black R.A., Hébert O., Savolainen V. 2015. The Genome of the "Great Speciator" Provides Insights into Bird Diversification. Genome Biol. Evol. 7:2680–2691.

Costanzi J.-M., Steifetten Ø. 2019. Island biogeography theory explains the genetic diversity of a fragmented rock ptarmigan (Lagopus muta) population. Ecol. Evol. 9:3837–3849.

Cowles S.A., Uy J.A.C. 2019. Rapid, complete reproductive isolation in two closely related Zosterops White-eye bird species despite broadly overlapping ranges*. Evolution. 73:1647–1662.

Cowles S.A., Weeks B.C., Perrin L., Chen N., Uy J.A.C. 2021. Comparison of adult census size and effective population size support the need for continued protection of two Solomon Island endemics. Emu. 121:45–54.

Danecek P., Auton A., Abecasis G., Albers C.A., Banks E., DePristo M.A., Handsaker R.E., Lunter G., Marth G.T., Sherry S.T., McVean G., Durbin R., 1000 Genomes Project Analysis Group. 2011. The variant call format and VCFtools. Bioinformatics. 27:2156–2158.

Descimon H., Napolitano M. 1993. Enzyme polymorphism, wing pattern variability, and geographical isolation in an endangered butterfly species. Biol. Conserv. 66:117–123.

Diamond J.M., Gilpin M.E., Mayr E. 1976. Species-distance relation for birds of the Solomon Archipelago, and the paradox of the great speciators. Proc. Natl. Acad. Sci. U. S. A. 73:2160–2164.

Epps C.W., Palsbøll P.J., Wehausen J.D., Roderick G.K., Ramey R.R. II, McCullough D.R. 2005. Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. Ecol. Lett. 8:1029–1038.

Frankham R. 1996. Relationship of genetic variation to population size in wildlife. Conserv. Biol. 10:1500–1508.

Friedman J., Hastie T., Tibshirani R. 2010. Regularization paths for generalized linear models via coordinate descent. J. Stat. Softw. 33:1–22.

368 Gardner E.J., Lam V.K., Harris D.N., Chuang N.T., Scott E.C., Pittard W.S., Mills R.E., 1000
369 Genomes Project Consortium, Devine S.E. 2017. The Mobile Element Locator Tool
370 (MELT): population-scale mobile element discovery and biology. Genome Res. 27:1916–
371 1929.

372 Gorman G.C., Soule M., Yang S.Y., Nevo E. 1975. Evolutionary Genetics of Insular Adriatic
373 Lizards. Evolution. 29:52.

374 Grabherr M.G., Russell P., Meyer M., Mauceli E., Alföldi J., Di Palma F., Lindblad-Toh K.
375 2010. Genome-wide synteny through highly sensitive sequence alignment: Satsuma.
376 Bioinformatics. 26:1145–1151.

377 Hill R., Loxterman J.L., Aho K. 2017. Insular biogeography and population genetics of dwarf
378 mistletoe (Arceuthobium americanum) in the Central Rocky Mountains. Ecosphere.
379 8:e01810.

380 Hoeck P.E.A., Bollmer J.L., Parker P.G., Keller L.F. 2010. Differentiation with drift: a spatio-
381 temporal genetic analysis of Galapagos mockingbird populations (Mimus spp.). Philos.
382 Trans. R. Soc. Lond. B Biol. Sci. 365:1127–1138.

383 Hughes A.R., Inouye B.D., Johnson M.T.J., Underwood N., Vellend M. 2008. Ecological
384 consequences of genetic diversity. Ecol. Lett. 11:609–623.

385 Jurka J., Bao W., Kojima K.K. 2011. Families of transposable elements, population structure and
386 the origin of species. Biol. Direct. 6:44.

387 Jurka J., Kapitonov V.V., Pavlicek A., Klonowski P., Kohany O., Walichiewicz J. 2005. Repbase
388 Update, a database of eukaryotic repetitive elements. Cytogenet. Genome Res. 110:462–

467.

Katoh K., Standley D.M. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Mol. Biol. Evol. 30:772–780.

Khan A., Sil M., Thekaekara T., Garg K.M., Sinha I., Khurana R., Sukumar R., Ramakrishnan U. 2024. Divergence and serial colonization shape genetic variation and define conservation units in Asian elephants. Curr. Biol. 34:4692–4703.e5.

Kyriazis C.C., Beichman A.C., Brzeski K.E., Hoy S.R., Peterson R.O., Vucetich J.A., Vucetich L.M., Lohmueller K.E., Wayne R.K. 2023. Genomic underpinnings of population persistence in Isle Royale moose. Mol. Biol. Evol. 40.

Leroy, T., Rousselle, M., Tilak, M.-K., Caizergues, A. E., Scornavacca, C., Recuerda, M., Fuchs, J., Illera, J. C., De Swardt, D. H., Blanco, G., Thébaud, C., Milá, B., Nabholz, B. 2021. Island songbirds as windows into evolution in small populations. Curr. Biol. 31:1303–1310.

Lewontin R.C. 1974. Genetic basis of evolutionary change. New York, NY: Columbia University Press.

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

Li H., Handsaker B., Wysoker A., Fennell T., Ruan J., Homer N., Marth G., Abecasis G., Durbin R., 1000 Genome Project Data Processing Subgroup. 2009. The Sequence Alignment/Map format and SAMtools. Bioinformatics. 25:2078–2079.

Liligeto W. 2013. Gizo Environment Livelihood Conservation Association (GELCA) Resource

Management Plan. .

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

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

MacArthur, R. H., Diamond, J. M., & Karr, J. R. (1972). Density compensation in island faunas. Ecology, 53(2), 330-342.

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

Martin C.A., Sheppard E.C., Illera J.C., Suh A., Nadachowska-Brzyska K., Spurgin L.G., Richardson D.S. 2023. Runs of homozygosity reveal past bottlenecks and contemporary inbreeding across diverging populations of an island-colonizing bird. Mol. Ecol. 32:1972–1989.

Maurer B.A., Rosenzweig M.L. 1996. Species diversity in space and time. Ecology. 77:1314.

Mayr E. 1942. Systematics and the Origin of Species. New York: Columbia University Press.

Mazet O., Rodríguez W., Grusea S., Boitard S., Chikhi L. 2016. On the importance of being structured: instantaneous coalescence rates and human evolution—lessons for ancestral population size inference? Heredity . 116:362–371.

McKenna A., Hanna M., Banks E., Sivachenko A., Cibulskis K., Kernytsky A., Garimella K., Altshuler D., Gabriel S., Daly M., DePristo M.A. 2010. The Genome Analysis Toolkit: a MapReduce framework for analyzing next-generation DNA sequencing data. Genome Res. 20:1297–1303.

Moyle R.G., Filardi C.E., Smith C.E., Diamond J.M. 2009. Explosive Pleistocene diversification and hemispheric expansion of a "great speciator." Proc. Natl. Acad. Sci. U. S. A. 106:1863–1868.

Nadachowska-Brzyska K., Burri R., Smeds L., Ellegren H. 2016. PSMC analysis of effective population sizes in molecular ecology and its application to black-and-white Ficedula flycatchers. Mol. Ecol. 25:1058–1072.

Nadachowska-Brzyska K., Li C., Smeds L., Zhang G., Ellegren H. 2015. Temporal Dynamics of Avian Populations during Pleistocene Revealed by Whole-Genome Sequences. Curr. Biol. 25:1375–1380.

Neall V.E., Trewick S.A. 2008. The age and origin of the Pacific islands: a geological overview. Philos. Trans. R. Soc. Lond. B Biol. Sci. 363:3293–3308.

Oliveros C.H., Andersen M.J., Moyle R.G. 2021. A phylogeny of white-eyes based on ultraconserved elements. Mol. Phylogenet. Evol. 164:107273.

Patton J.L. 1984. Genetical processes in the Galapagos. Biol. J. Linn. Soc. Lond. 21:97–111.

Preston F.W. 1962a. The Canonical Distribution of Commonness and Rarity: Part I. Ecology. 43:185.

449 Preston F.W. 1962b. The Canonical Distribution of Commonness and Rarity: Part II. Ecology.
450 43:410–432.

451 Price A.L., Jones N.C., Pevzner P.A. 2005. De novo identification of repeat families in large
452 genomes. Bioinformatics. 21 Suppl 1:i351–8.

453 Quinlan A.R., Hall I.M. 2010. BEDTools: a flexible suite of utilities for comparing genomic
454 features. Bioinformatics. 26:841–842.

455 R Development Core Team. 2023. R: A language and environment for statistical computing.
456 Vienna, Austria: R Foundation for Statistical Computing.

457 Sato J.J., Tasaka Y., Tasaka R., Gunji K., Yamamoto Y., Takada Y., Uematsu Y., Sakai E.,
458 Tateishi T., Yamaguchi Y. 2017. Effects of Isolation by Continental Islands in the Seto
459 Inland Sea, Japan, on Genetic Diversity of the Large Japanese Field Mouse, Apodemus
460 speciosus (Rodentia: Muridae), Inferred from the Mitochondrial Dloop Region. Zoolog. Sci.
461 34:112–121.

462 Schiffels S., Durbin R. 2014. Inferring human population size and separation history from
463 multiple genome sequences. Nat. Genet. 46:919–925.

464 Smit A.F.A., Hubley R. 2008. RepeatModeler Open-1.0. .

465 Smit A.F.A., Hubley R., Green P. 2015. RepeatMasker Open-4.0. 2013--2015. .

466 Soulé M.E. 1976. Allozyme variation, its determinats in space and time. In: Ayala F.J., editor.
467 Molecular Evolution. Sinauer Associates. p. 60–77.

468 Soulé M., Yang S.Y. 1973. GENETIC VARIATION IN SIDE-BLOTCHED LIZARDS ON

ISLANDS IN THE GULF OF CALIFORNIA. Evolution. 27:593–600.

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

Sukumaran J., Holder M.T. 2010. DendroPy: a Python library for phylogenetic computing. Bioinformatics. 26:1569–1571.

Szpiech Z.A., Xu J., Pemberton T.J., Peng W., Zöllner S., Rosenberg N.A., Li J.Z. 2013. Long runs of homozygosity are enriched for deleterious variation. Am. J. Hum. Genet. 93:90–102.

Tan D.J.X., Gyllenhaal E.F., Andersen M.J. 2023. PleistoDist: A toolbox for visualising and quantifying the effects of Pleistocene sea-level change on island archipelagos. Methods Ecol. Evol. 14:496–504.

Vinciguerra N.T., Oliveros C.H., Moyle R.G., Andersen M.J. 2023. Island life accelerates geographic radiation in the white-eyes (Zosteropidae). Ibis (Lond. 1859). 165:817–828.

Wang S., Zhu W., Gao X., Li X., Yan S., Liu X., Yang J., Gao Z., Li Y. 2014. Population size and time since island isolation determine genetic diversity loss in insular frog populations. Molecular Ecology. 23:637–648.

Warren W.C., Clayton D.F., Ellegren H., Arnold A.P., Hillier L.W., Künstner A., Searle S., White S., Vilella A.J., Fairley S., Heger A., Kong L., Ponting C.P., Jarvis E.D., Mello C.V., Minx P., Lovell P., Velho T.A.F., Ferris M., Balakrishnan C.N., Sinha S., Blatti C., London S.E., Li Y., Lin Y.-C., George J., Sweedler J., Southey B., Gunaratne P., Watson M., Nam K., Backström N., Smeds L., Nabholz B., Itoh Y., Whitney O., Pfenning A.R., Howard J., Völker M., Skinner B.M., Griffin D.K., Ye L., McLaren W.M., Flicek P., Quesada V.,

490 Velasco G., Lopez-Otin C., Puente X.S., Olender T., Lancet D., Smit A.F.A., Hubley R.,
491 Konkel M.K., Walker J.A., Batzer M.A., Gu W., Pollock D.D., Chen L., Cheng Z., Eichler
492 E.E., Stapley J., Slate J., Ekblom R., Birkhead T., Burke T., Burt D., Scharff C., Adam I.,
493 Richard H., Sultan M., Soldatov A., Lehrach H., Edwards S.V., Yang S.-P., Li X., Graves
494 T., Fulton L., Nelson J., Chinwalla A., Hou S., Mardis E.R., Wilson R.K. 2010. The genome
495 of a songbird. Nature. 464:757–762.

496 Wei T., Simko V. 2014. R package "corrplot": Visualization of a Correlation Matrix (Version
497 0.95). .

498 Whittaker R.J., Fernández-Palacios J.M., Matthews T.J., Borregaard M.K., Triantis K.A. 2017.
499 Island biogeography: Taking the long view of nature's laboratories. Science. 357:eaam8326.

500 Wright, S. J. (1980). Density compensation in island avifaunas. Oecologia, 45, 385-389.

501 Wright S. 1982. Character change, speciation, and the higher taxa. Evolution. 36:427–443.

502 Zhang C., Rabiee M., Sayyari E., Mirarab S. 2018. ASTRAL-III: polynomial time species tree
503 reconstruction from partially resolved gene trees. BMC Bioinformatics. 19.