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On the brink of explosion? Identifying the source and potential spread of introduced *Zosterops white-eyes* in North America

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### Publication Date

2024

### DOI

10.1007/s10530-024-03268-8

### Supplemental Material

<https://escholarship.org/uc/item/8j83m50j#supplemental>

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1 On the brink of explosion? Identifying the source and potential spread of introduced *Zosterops*  
2 white-eyes in North America

3

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28

**29 Abstract**

30 Understanding the source of non-native introduced populations is crucial for forecasting  
31 geographic invasion potential and understanding the ecological consequences of potential  
32 establishment. Here we use genomics to identify the source populations and invasion dynamics  
33 of two non-native introduced populations from the iconic avian lineage of ‘great speciators’  
34 known as white-eyes (genus *Zosterops*). We established confidently for the first time that  
35 introduced *Zosterops* populations in Hawaii and southern California are completely unrelated  
36 and derived from independent introductions of the species *Z. japonicus* and *Z. simplex*,  
37 respectively. We used descriptive population genetic statistics to identify a reduction in genetic  
38 diversity and increase in private alleles in the southern California population, supporting a  
39 recent, potentially ongoing genetic bottleneck in this population. In contrast, the introduced  
40 population in Hawaii showed no such characteristics, likely due to a larger founding population  
41 size and repeated introductions in this intentionally introduced population. Ecological niche  
42 modeling indicated that there is little environmentally suitable habitat for *Z. simplex* across the  
43 continent of North America, suggesting limited invasion potential, assuming niche conservatism.  
44 Yet, portions of the introduced *Z. simplex* population have already surpassed areas projected as  
45 suitable, likely because the urbanized environment of southern California offers biotic resources  
46 and microhabitats that are not captured by our model. Because it appears to have overcome the  
47 ‘invasion paradox’ of low founding genetic diversity and established despite relatively  
48 unfamiliar environmental conditions in southern California, we suggest *Z. simplex* may continue  
49 expanding in beyond our environmental niche model projections in other temperate, urban  
50 regions.

51

## 52 **Introduction**

53 Dispersal and colonization have long been recognized as crucial aspects in the speciation  
54 process, and more broadly the accumulation of biodiversity in ecosystems across the globe  
55 (Diamond et al., 1976; Mayr, 1942). Within the past few millennia, human-aided population  
56 dispersal, facilitated by the advent of tool-aided human movement across the globe (Wilson et  
57 al., 2009), has become increasingly recognized as a force shaping the ecology and evolution of  
58 every corner of the world (Hulme, 2009). Some of these introductions were intentional, for  
59 example as food sources for European colonists for the last five centuries (Crosby, 2004;  
60 Osborne, 2000), for cultural reasons associated with European colonialism (e.g.,  
61 acclimatization), or more recently as attempted bio-control of native pest species (e.g., cane-  
62 toads; Mungomery, 1935). Other introductions were unintentional, when animals were moved  
63 unknowingly (e.g., rats on islands; Harper & Bunbury, 2015) or released accidentally (e.g.,  
64 naturalized parrots across the globe; Pruett-Jones, 2021). Regardless of the original intentions of  
65 these human-mediated introductions, once a non-native species is introduced, it may become  
66 established and gain access to novel resources (Belnap et al., 2012), and enemy release (i.e.,  
67 escape from predators and parasites limiting the species in its native range; Roy et al., 2011).  
68 These factors can facilitate rapid population expansion in the novel environment, with potential  
69 ecosystem-wide consequences for native species which may face increased competition (K. E.  
70 Barton & Fortunel, 2023), predation (Roemer et al., 2002), or toxicity (Okamiya et al., 2021),  
71 leading the introduced species to be dubbed as ‘invasive’ (Blackburn et al., 2014). Overall,  
72 invasive species have been implicated as one of the main factors threatening worldwide  
73 biodiversity (Clavero & García-Berthou, 2005; Roy et al., 2023).

74 In addition to these well-documented environmental consequences, there can also be  
75 economic costs associated with invasive species (Colautti et al., 2006; Linz et al., 2007).  
76 Therefore, both conservation and economic interests may align in efforts to identify introduced  
77 populations with invasion potential and mitigate their potential spread (Pimentel et al., 2005).  
78 Previous examples of this cooperation include efforts to eradicate: cane toads (*Rhinella marina*)  
79 in Australia (Greenlees et al., 2018), Burmese pythons (*Python bivittatus*) in Florida (Avery et  
80 al., 2014), and European Starlings (*Sturnus vulgaris*) at feed lots across the United States (Linz et  
81 al., 2018; Linz et al., 2007). This type of effort to mitigate the potential environmental and  
82 economic effects of an invasive population requires knowledge of the source of the introduction,  
83 in order to forecast the potential spread of the introduced population, and understand the  
84 potential ecological consequences of its establishment (Aagaard & Lockwood, 2016; Strayer et  
85 al., 2017). But, confidently identifying the source of an introduced population may be difficult in  
86 the absence of historical records, and these difficulties can be compounded if putative source  
87 populations have uncertain or confused taxonomic histories (Gotzek et al., 2012; Mazzamuto et  
88 al., 2016). In these cases, DNA sequencing can be used to confidently determine the genome-  
89 wide ancestry of individuals from the introduced population (Filipová et al., 2011; Mittan-  
90 Moreau et al., 2022; Sharaf et al., 2020). Only once the source of an introduced population is  
91 confidently identified can we begin to understand its genetic and ecological dynamics and the  
92 potential ecosystem-wide consequences of its establishment (Hudson et al., 2021; Kumar et al.,  
93 2015).

94 Abiotic and biotic factors limit the distributions of populations both in their native and  
95 introduced ranges. One particular approach, ecological niche modeling (ENM), has emerged as a  
96 useful tool in understanding distributional potential (Peterson et al., 2011). This approach works

97 via characterizing associations between species' occurrences and variation in environmental  
98 parameters. It assumes that the actual distribution of a population is a function of three  
99 interacting constraints: the fundamental ecological niche, interactions with other organisms, and  
100 dispersal capability (Soberón & Peterson, 2005). Early explorations (Peterson, 2003; Peterson &  
101 Vieglais, 2001) illuminated the possibility that model transfers (Yates et al., 2018) from native to  
102 introduced areas could anticipate the geographic invasion potential of a population. Indeed, once  
103 source populations have been identified rigorously (Lee, 2002), ENM approaches can be used to  
104 assess the ecological niche and geographic potential of introduced populations on any novel  
105 landscape, subject of course to the degree of analogy in environmental characteristics between  
106 the landscapes in question (Owens et al., 2013).

107         An introduced population that has received limited attention is a population of birds in  
108 the genus *Zosterops* (colloquially known as 'white eyes'), which have recently become  
109 established in coastal southern California (Garrett, 2018). This is in contrast with the well-  
110 studied introduced population of *Z. japonicus* on the Hawaiian archipelago (Venkatraman et al.,  
111 2021). While the putative *Z. japonicus* population in Hawaii was intentionally introduced from  
112 Japan by the Hawaii Board of Agriculture and Forestry in 1929 (Caum, 1933), there have been  
113 no documented intentional introductions of *Zosterops* in southern California. In fact, there was a  
114 successful effort to eradicate an established population of *Z. palpebrosus* that likely escaped from  
115 the San Diego Zoo and began breeding in the southern California area in the early 1980s (Unitt  
116 & Klovstad, 2004). This history, plus the fact that *Zosterops* white-eyes are routinely identified  
117 as some of the most common species sold in the cagebird trade globally (Chng et al., 2018;  
118 Eaton et al., 2017), strongly suggests the pet trade, via escape or intentional release, as the likely  
119 origin of the current day southern California population.

120           The genus *Zosterops* is known for harboring one of the highest speciation rates of all  
121 birds, containing over 100 species found in Africa, Asia, and Australia, and all estimated to have  
122 diverged within the past 2 million years (Moyle et al., 2009). These birds are also known as  
123 exceptional dispersers, with apparent long-distance dispersal and colonization events to far flung  
124 islands throughout the Pacific within their recent evolutionary history (Estandía et al., 2023;  
125 Vinciguerra et al., 2023). Because of this explosive speciation history, evidence for interspecies  
126 gene flow (Gwee et al., 2020; Oatley et al., 2017), and the overall conserved morphology of the  
127 genus (i.e., over 100 species that all look roughly like a small gray, green, and yellow songbird),  
128 the taxonomy of the *Zosterops* white-eyes has been plagued by ongoing uncertainty and  
129 phylogenetic recalcitrance (Lim et al., 2019). For this reason, the exact species identity of the  
130 introduced *Zosterops* population in southern California remains uncertain, and the genomic  
131 ancestry of the putative *Z. japonicus* population in Hawaii has never been confirmed with  
132 comprehensive sampling of potential source populations.

133           Here, we use a reduced representation (i.e., RADseq) approach to sequence thousands of  
134 genomic loci from samples across the native ranges of six putative source species (*Z. japonicus*,  
135 *Z. simplex*, *Z. palpebrosus*, *Z. erythropleurus*, *Z. everetti*, and *Z. nigrorum*) from the ‘asiatic  
136 *Zosterops*’ clade (Vinciguerra et al., 2023) and individuals from the introduced populations in  
137 Hawaii and southern California, to facilitate the first confident determination of the genomic  
138 ancestry of these populations. This information will be a crucial resource for future studies  
139 attempting to study the eco-evolutionary consequences of translocation and establishment of  
140 introduced species (e.g., Gleditsch & Sperry, 2019; Mathys & Lockwood, 2011; Sendell-Price et  
141 al., 2020). Further, these genomic sequence data will allow us to search for signatures of genetic  
142 bottlenecks (e.g., reduced genetic diversity) and founder effects associated with the establishment

143 of these introduced populations. Invasive populations regularly establish and spread despite  
144 limited genetic diversity (the ‘invasion paradox’; Estoup et al., 2016; Kolbe et al., 2004), and  
145 comparisons between two introduced populations of these ‘great speciators’ may help to  
146 understand whether and how the invasion paradox applies in rapidly evolving taxa (Diamond et  
147 al., 1976; Moyle et al., 2009). Finally, confident identification of the source of the introduced  
148 *Zosterops* population in southern California will allow us to use ecological niche modeling  
149 approaches to project the geographic invasion potential of this rapidly expanding population. The  
150 results of these investigations will have important implications for understanding both the  
151 invasion potential of *Zosterops* in North America and for understanding the eco-evolutionary  
152 consequences of the founding of novel populations more generally.

153

## 154 **Methods**

### 155 *Visualizing genetic sampling and species distributions*

156 We used the R (R Core Team, 2019) packages *sf* v1.0-12 (Yates et al., 2018) and *maps* v3.4.1  
157 (Brownrigg, 2013) to visualize the distributions of all six focal *Zosterops* species (*Z. japonicus*,  
158 *Z. simplex*, *Z. palpebrosus*, *Z. erythropleurus*, *Z. everetti*, and *Z. nigrorum*) and the two focal  
159 introduced populations. Here we treat *Z. japonicus* as encompassing the contentious taxa *Z.*  
160 *montanus* and *Z. meyeri* (Lim et al. 2019) for the sake of taxonomic simplicity. Although we  
161 identify phylogeographic structure that generally corresponds with the proposed limits of *Z.*  
162 *montanus* and *Z. meyeri* within this broadly defined *Z. japonicus* clade, because it is not the  
163 focus of this paper, we do not address the phylogeographic and taxonomic implications of these  
164 results. Instead we refer to clades within *Z. japonicus* strictly by geography, to minimize  
165 taxonomic confusion.



166 We plotted occurrence localities on these maps according to sample size and species  
167 identity using *ggplot2* v3.4.1 (Wickham et al., 2020), using a colorblind-friendly palette that is  
168 maintained throughout the manuscript. We manually outlined the breeding distribution for each  
169 species to contextualize the geographic extent of our genetic sampling. We also accessed annual  
170 distribution maps for the introduced *Zosterops* population in southern California over the past 20  
171 years using eBird (Sullivan et al., 2009; [www.ebird.org](http://www.ebird.org)). Code for mapping localities can be  
172 viewed here: <https://devonderaad.github.io/zosterops.rad/zosterops.mapping.html>.

173

#### 174 *DNA extraction, library preparation, and sequencing*

175 We extracted DNA from 155 tissue/blood samples, including samples from the two introduced  
176 *Zosterops* populations in Hawaii (collected in 2002) and southern California (collected 2016-  
177 2022), plus comprehensive geographic sampling of potential source populations from across East  
178 and Southeast Asia and the Philippines. The University of Kansas Genomic Sequencing Core  
179 performed RADseq library preparation according to protocols outlined in Manthey and Moyle  
180 (2015). Our protocol involves digesting each DNA extract with the enzyme *NdeI* and performing  
181 size selection for fragments in the range of 495-605 base-pairs. The entire library prep protocol,  
182 including detailed results for this set of samples, is available here:

183 [https://github.com/DevonDeRaad/zosterops.rad/blob/main/lab.protocols/MSG-NdeI\\_2plates-](https://github.com/DevonDeRaad/zosterops.rad/blob/main/lab.protocols/MSG-NdeI_2plates-)

184 [150samples\\_DAD-Moyle\\_230530.doc](#). These pooled, barcoded libraries were then sequenced on  
185 an Illumina NextSeq2000 machine, using a P2 flow cell to generate 414,215,817 single-end 100  
186 base-pair reads, i.e., ~41 giga-base-pairs of raw sequence data.

187

#### 188 *Read mapping, variant calling, and quality filtering*

189 In general, we followed the RADseq mapping and filtering pipeline detailed in DeRaad et al.,  
190 (2023). In specific, we demultiplexed the raw sequence data using the ‘process\_radtags’ function  
191 from *Stacks* v2.41 (Rochette et al., 2019), removing low quality reads (any bases with phred  
192 score <10), and reads with uncalled bases. We then mapped the raw reads from each individual  
193 sample to a publicly available *Z. japonicus* reference genome assembly (Venkatraman et al.,  
194 2021; available at [https://www.ncbi.nlm.nih.gov/assembly/GCA\\_017612475.1](https://www.ncbi.nlm.nih.gov/assembly/GCA_017612475.1)), using the  
195 command ‘mem’ from *BWA* v0.7.17 (Li & Durbin, 2009). We then converted each .sam file to a  
196 sorted .bam file using *SAMtools* v1.3.1 (Li et al., 2009). We used the *Stacks* module ‘gstacks’ to  
197 identify RAD loci using a sliding window algorithm and to call individual genotypes, and the  
198 *Stacks* module ‘populations’ to output an unfiltered set of sample genotypes as a variant call  
199 format (vcf) file. This generated an unfiltered SNP dataset containing 236,767 bi-allelic SNPs  
200 shared among 155 unique samples, with 65.5% missing genotypes.

201 We used the R packages *vcfR* v1.14.0 (Knaus & Grünwald, 2017) and *SNPfiltR* v1.0.1  
202 (DeRaad, 2022) to interactively visualize key parameter distributions and implement optimized  
203 quality filters on this SNP dataset. First, we implemented a hard filter, recoding genotypes with a  
204 sequencing depth of <3 reads or genotype quality <30 as missing data. We then recoded  
205 heterozygous genotypes where the ratio of read counts between the two alleles was <0.1 or >0.9  
206 as missing. We also removed SNPs with a mean genotype depth >250 from the dataset, as these  
207 SNPs likely have artificially inflated depth of coverage from the mapping of multiple, paralogous  
208 RAD loci to the same place in the reference genome. We then set a maximum threshold of 90%  
209 missing genotypes to allow a sample to be included in downstream analyses, resulting in removal  
210 of 25 samples from the dataset. Upon further investigation, we removed a further 6 samples that

211 consistently displayed a high proportion of missing genotypes even after implementing  
212 exploratory per-SNP missing data filters.

213 For the remaining 124 samples (Table S1; Fig. 1), we constructed a phylogenetic network  
214 to visualize sample relatedness at a 99% per-SNP completeness threshold (789 retained SNPs).  
215 We compared the same phylogenetic network constructed under a 90% per-SNP completeness  
216 threshold and found similar inference of sample relatedness with no noticeable variation  
217 attributable to the inclusion of missing genotypes. We implemented this 90% per-SNP  
218 completeness threshold, which appeared to optimize the trade-off between genotype  
219 completeness and total number of SNPs retained, resulting in a filtered SNP dataset of 15,704  
220 SNPs shared across 124 unique samples with 5.3% missing genotypes. Finally, we removed  
221 SNPs within a physical distance of <1,000 base-pairs, resulting in a filtered, unlinked SNP  
222 dataset comprising 1,554 SNPs shared across 124 unique samples with 5.5% missing genotypes.  
223 In both datasets, no individual sample retained for downstream analyses was missing >40% of  
224 genotype calls. The entire SNP filtering process along with exploratory data visualizations used  
225 to optimize these filtering thresholds can be followed in detail at  
226 <https://devonderaad.github.io/zosterops.rad/zost.radseq.filtering.html>.

227

### 228 *Population genetic analysis*

229 To visualize our SNP data as an unrooted phylogenetic network, we used our filtered SNP  
230 dataset (15,704 SNPs, 5.3% missing data) as input for the R package *StAMPP* v1.6.3 (Pembleton  
231 et al., 2013) and constructed a pairwise genetic distance (Nei's D; Nei, 1972) matrix among the  
232 124 samples. We used this distance matrix as input in *SplitsTree4* v4.15.1 (Huson & Bryant,  
233 2006), where we constructed a neighbor-net, with a single tip corresponding to each sample. This

234 approach allows the simultaneous inference of distance-based phylogenetic relationships among  
235 clades and informative placement of admixed individuals with ancestry strongly affected by non-  
236 tree-like processes. We color-coded all tips according to species assignment and highlighted  
237 putative hybrid individuals. Code and resulting phylogenetic networks can be viewed at  
238 <https://devonderaad.github.io/zosterops.rad/splitstree.html>.

239 We next used our filtered, unlinked SNP dataset (1,554 SNPs, 5.5% missing data) as  
240 input for *ADMIXTURE* v.1.3.0 (Alexander et al., 2009) to assign all samples to bins of genomic  
241 ancestry using a model-based framework without the need for *a priori* sample assignments. We  
242 performed 10 successive *ADMIXTURE* runs, iteratively increasing the number of genomic  
243 ancestry bins ( $K$ ) used to describe these 124 samples from 1-10. We specified the ‘--cv’ flag to  
244 perform fivefold cross-validation across these iterations. We identified the optimal value for  $K$  as  
245 the value that resulted in the lowest cross-validation error out of our 10 runs.

246 Because of signals of hierarchical structure (i.e., samples from the sister species *Z.*  
247 *everetti* and *Z. nigrorum* consistently assigned to a single genomic ancestry bin despite visually  
248 apparent genetic structure in the phylogenetic network), we downsampled our unlinked filtered  
249 SNP dataset to retain only the 7 samples from the species *Z. everetti* and *Z. nigrorum*. We then  
250 removed SNPs that had become invariant owing to sample removal, resulting in 402 putatively  
251 unlinked SNPs with 4.0% missing data across the 7 samples. We performed an identical set of  
252 *ADMIXTURE* runs, as described above, using this downsampled SNP dataset as input, and  
253 plotted the  $K = 2$  result to assess visually the degree of overlap in genomic ancestry between  
254 these species without the confounding effects of hierarchical structure present in the complete  
255 dataset. This entire *ADMIXTURE* procedure including all code necessary to reproduce these  
256 results is available at <https://devonderaad.github.io/zosterops.rad/zosterops.admixture.html>.

257 To quantify the degree of relative differentiation among our focal species, we calculated  
258 pairwise  $F_{ST}$  values for all possible among-species comparisons. We removed the two samples  
259 identified as putative hybrids in our *ADMIXTURE* investigation from our filtered SNP dataset  
260 (15,704 SNPs, 5.3% missing data), and then assigned the species identity of each of the  
261 remaining 122 samples based on ancestry assignments from *ADMIXTURE*. We used the *StAMPP*  
262 function ‘stampFst’ to calculate pairwise  $F_{ST}$  values between these six species, and *ggplot2* to  
263 visualize the results as a heatmap. We also assigned samples within *Z. japonicus* into three  
264 separate geographically delimited clades following the *ADMIXTURE* ancestry assignments at  $K$   
265 = 6 and calculated pairwise  $F_{ST}$  among these three groups using the same procedure. This entire  
266 process for calculating pairwise differentiation from an input vcf file can be viewed and  
267 reproduced at <https://devonderaad.github.io/zosterops.rad/zosterops.pairwise.fst.html>.

268 After confidently determining the species-level ancestry of these introduced populations  
269 (see Figures 1 and 2), we then performed detailed clustering analyses on subsets of the dataset to  
270 determine the exact sampling localities with the most genetic similarity to each introduced  
271 population using principal components analysis (PCA) via the R package *adeigenet* 2.1.10  
272 (Jombart, 2008). First, to investigate the source of the introduced population in Hawaii, we  
273 subset our unlinked filtered SNP dataset to only samples with >95% ancestry assigned to the  
274 northern *Z. japonicus* clade in the *ADMIXTURE* analysis. We then removed SNPs that became  
275 invariant and performed PCA retaining the first two axes of variation. We repeated this same  
276 procedure with individuals assigned >95% *simplex* ancestry to investigate the putative  
277 geographic source of the southern California introduction. For each of these subsets, we labeled  
278 each sample in the PCA based on sampling locality.

279 We then used each of these unique sampling localities described in the previous  
280 paragraph (22 for *Z. japonicus* and 13 for *Z. simplex*) to search for molecular signatures of  
281 ongoing population bottlenecks by comparing the genetic diversity of introduced populations to  
282 the diversity of conspecific populations sampled from the native range of each species. We used  
283 the *Stacks* ‘populations’ module to estimate per sample heterozygosity and per population  
284 nucleotide diversity ( $\Pi$ ) across all sites (including invariant sites) that mapped to the reference  
285 genome before applying any filtering criteria. We intentionally used this unfiltered dataset to  
286 calculate genetic diversity metrics to help to ameliorate the inherent biases introduced by the  
287 idiosyncratic process of filtering SNP datasets. Using an unfiltered dataset including all invariant  
288 sites is explicitly endorsed as resulting in more robust and comparable estimates of parameters  
289 describing the genetic diversity of natural populations (Shafer et al., 2017). We also visualized  
290 the number of unique (i.e., private) alleles present in each of the sampling localities, which is  
291 calculated as part of the standard suite of descriptive genetic diversity metrics by the *Stacks*  
292 ‘populations’ module. All of these analyses are available at  
293 <https://devonderaad.github.io/zosterops.rad/investigate.introductions.html>.

294

#### 295 *Data Preparation for Ecological Niche Modeling*

296 For occurrence data, we downloaded all data corresponding to *Z. simplex* in the GBIF  
297 biodiversity data portal (GBIF, 2023). Occurrence data were filtered to correspond only to the  
298 dates 15 May - 15 June in any year from 2000 to present, a conservative estimate of breeding  
299 occurrences. We removed one record under the name *Z. simplex salvadorii*, putative introduced  
300 records from the United States and Mexico, exact duplicate records, and records with no  
301 associated geographic coordinates or coordinate uncertainty  $>10,000$  m. We manually checked

302 the geographic distribution of occurrences against detailed descriptions in Avibase for each  
303 species (GBIF, 2023). We then assessed spatial clumping, as a way of reducing effects of spatial  
304 autocorrelation on model results, exploring records filtered to one per raster pixel, and records  
305 spatially filtered using distances of 10, 20, 50, and 100 km. We tested spatial autocorrelation via  
306 Moran's  $I$  for all sets of filtered records (Table S2). We kept the set of 119 records resulting from  
307 spatial thinning at 100 km considering that the effect of increasing distances did not change  
308 spatial autocorrelation substantially, but spatial clustering of points was not evident with this  
309 distance filter.

310 We summarized climatic landscapes via the MERRAClim dataset (Vega et al., 2017),  
311 downloading the most current version from  
312 <https://datadryad.org/stash/dataset/doi:10.5061/dryad.s2v81>. We used the 5' mean-value dataset  
313 for the 2000s (i.e., 2000-2010). Because MERRA data are not clipped to coasts, we used the  
314 China\_ADM coverages from DivaGIS (<https://www.diva-gis.org/>) to identify records that show  
315 up in the ocean because of minor disagreements about coastline shape between data sources. We  
316 used these variables for M simulation analyses (see below). We performed a principal  
317 component analysis (PCA) with these variables to reduce dimensionality and avoid  
318 multicollinearity. The first five principal components (accounting for ~99% of the total variance;  
319 Tables S3-S4) were used for ecological niche modeling (see below).

320

### 321 *Ecological Niche Model Development*

322 A crucial initial step in developing ecological niche modeling is that of establishing an  
323 appropriate area for model calibration (i.e., 'M', the area accessible to the species; Owens et al.,  
324 2013). We approximated M using the spatially thinned records, the variables from the

325 MERRAClim database and the *grinnell* R package v0.0.21 (Machado-Stredel et al., 2021). We  
326 used a simulation extent of 10°S to 80°N latitude, and 50°E to 135°E longitude, masked with the  
327 GADM world country layer at the highest resolution. We parameterized the simulations as  
328 “normal” distribution of the dispersal kernel, with standard deviations of 0.5, 1.0, 3.0, 5.0,  
329 numbers of dispersal events of 75, 150, and 300, and a barrier corresponding to Wallace’s Line.  
330 Our selected M area used a kernel SD of 3, 150 dispersal events, and the other features  
331 mentioned above. We created a buffer of 30 km around this final M and clipped it with the world  
332 country layer from GADM.

333         For model preparation, we masked each of the five PC variables to the extent of M. We  
334 assembled all possible combinations of  $\geq 2$  variables, for a total of 26 sets. We divided the 119  
335 filtered occurrence points into two subsets: 70% for model calibration and 30% for testing and  
336 comparing candidate models. We assessed regularization multiplier values of 0.1, 0.3, 0.5, 0.7,  
337 0.9, 1.0, 2.0, 3.0, 4.0, 5.0, and feature classes including “q,” “p,” “lq,” “lp,” “qp,” and “lqp”  
338 (where l = linear models, q = quadratic models, and p = product-based models). The total number  
339 of candidate models was 1560. We evaluated performance of candidate models on statistical  
340 significance of predictions (partial ROC; Peterson et al., 2008), omission rate (allowing a 5%  
341 omission error; Anderson et al., 2003), and model fit and complexity (based on the Akaike  
342 information criterion corrected for small sample sizes; Warren & Seifert, 2011). We produced  
343 final models using the parameter settings of candidate models that performed the best, with 10  
344 replicates, and cloglog outputs. We projected these models to both the native and introduced  
345 ranges of *Z. simplex*.

346         To understand where model outcome interpretations are risky due to the presence of  
347 conditions in transfer areas non-analogous to those in the calibration area, we used the MOP



348 metric (Owens et al., 2013). We downloaded spatial data using the R package *geodata* v.0.5.8  
349 (Hijmans et al., 2023) and all spatial analyses were done using the R package *terra* v1.7.29  
350 (Hijmans, 2023). Ecological niche modeling routines were run using the package *kuenm* 1.1.10  
351 (Cobos et al., 2019), using Maxent (Phillips et al., 2017) as the modeling algorithm. We  
352 performed the MOP analysis using the package *mop* 0.1.1 (Cobos et al., 2023). Commented code  
353 to perform data preparation and ecological niche modeling is available at:  
354 [https://devonderaad.github.io/zosterops.rad/zosterops\\_ENM.html](https://devonderaad.github.io/zosterops.rad/zosterops_ENM.html).

355

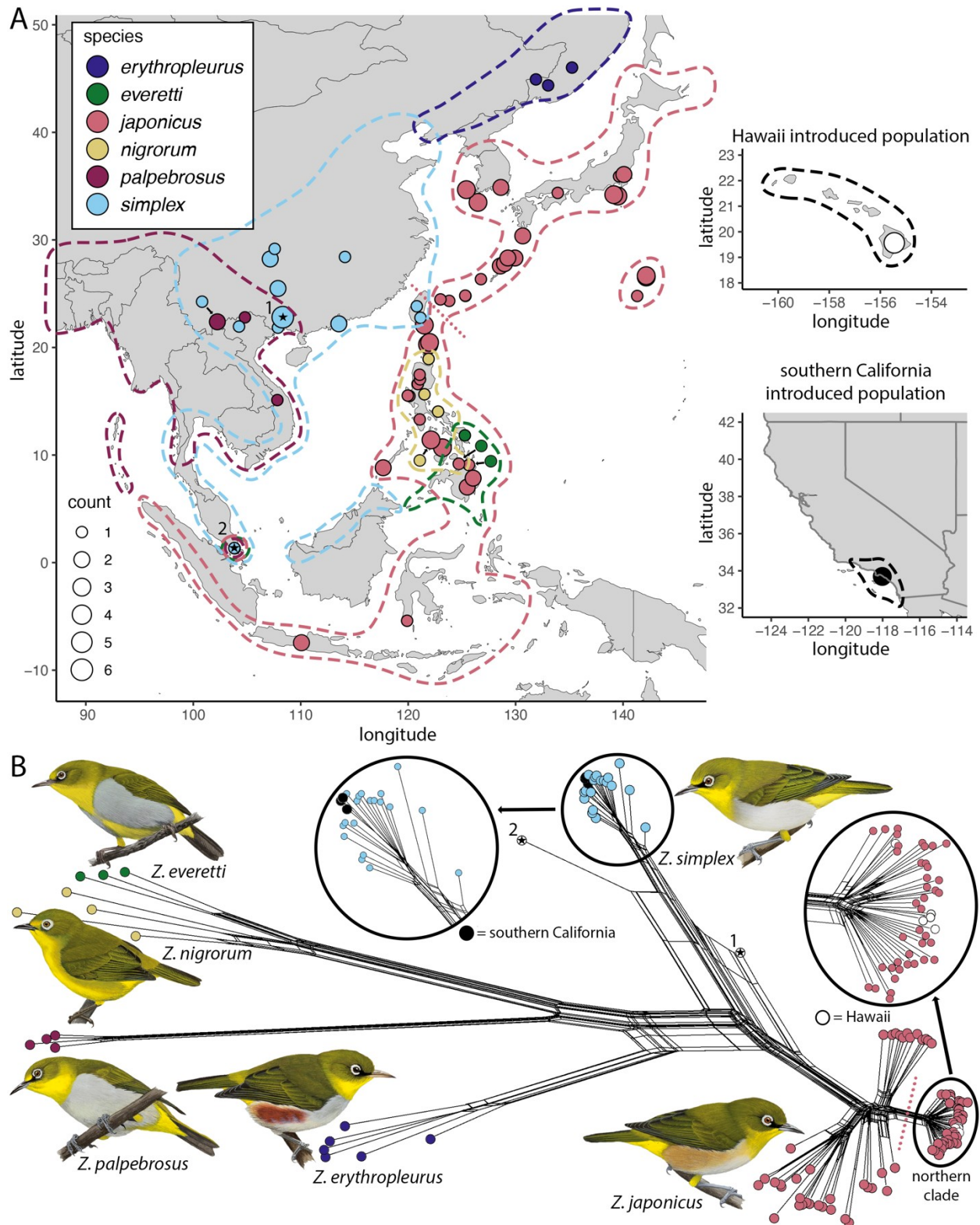
## 356 **Results**

### 357 *Population genetics*

358 A distance-based phylogenetic network describing relatedness among the 124 samples that  
359 passed filtering protocols revealed evidence for deep phylogenetic structure corresponding in  
360 largest part to the six focal species that we targeted with nearly comprehensive geographic  
361 sampling (Fig. 1A/B). The branching order in this network recapitulates known phylogenetic  
362 relationships (Gwee et al., 2020; Vinciguerra et al., 2023), including the sister relationship  
363 between *Z. everetti* and *Z. nigrorum*, and the sister relationship between *Z. simplex* and *Z.*  
364 *japonicus* (Fig. 1B). Within *Z. japonicus*, geographic substructuring was apparent, with a clear  
365 phylogeographic break separating populations in the Japanese archipelago and Korean peninsula  
366 from the rest of the clade.

367       Individuals sampled from the introduced southern California population formed a clade  
368 nested within a larger clade containing all *Z. simplex* samples. On the other hand, individuals  
369 sampled from the introduced population in Hawaii were scattered throughout the clade  
370 containing the Japanese and Korean *Z. japonicus* populations. Out of 124 samples, only two

371 could not be assigned confidently to a clade corresponding to one of the six focal species; these  
372 two samples were considered as putative hybrids and were clearly identified as such in  
373 downstream analyses (see below).



374

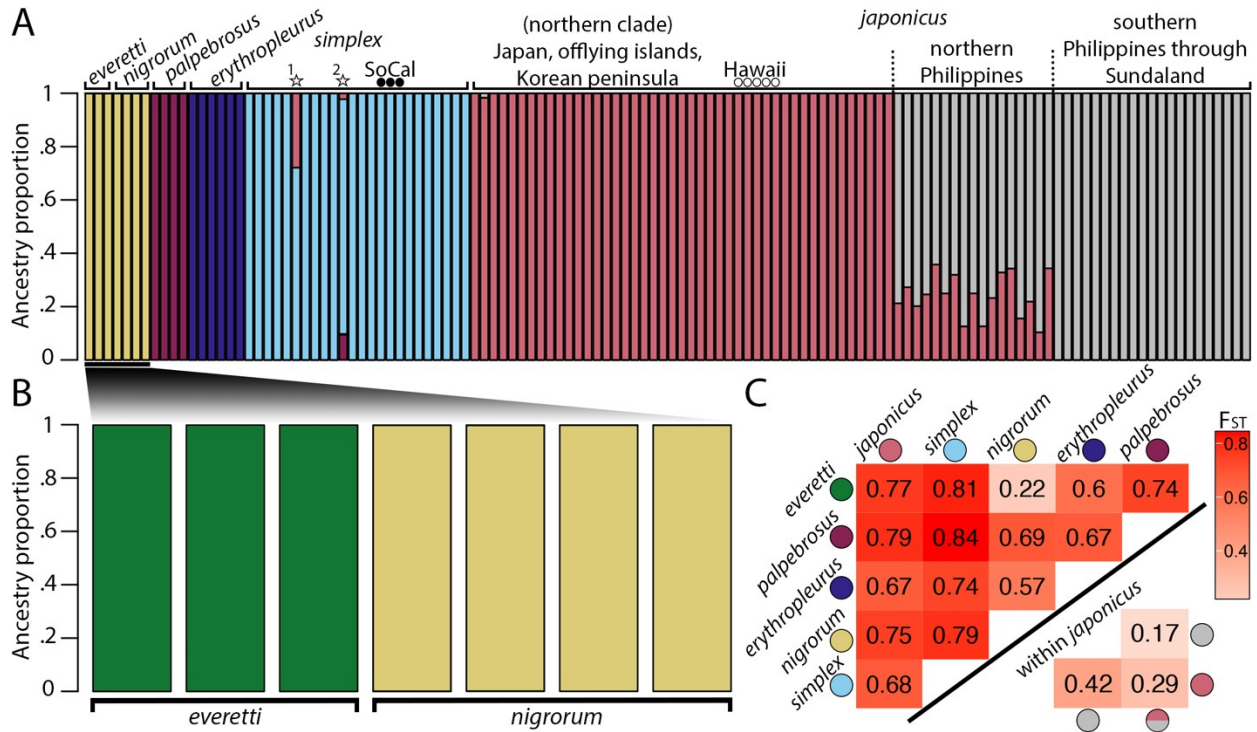
375 **Figure 1.** Connecting species distributions with genetic structure. (A) Map showing the sampling  
 376 scheme for our RADseq dataset, in which each dot denotes species identity by dot color and  
 377 sample size by dot size in the filtered SNP dataset (124 total samples). The breeding distribution

378 of each of the six focal species is enclosed by a color-coded dashed line. The breeding  
379 distribution of *Z. erythropleurus* continues slightly to the north, beyond the extent of this map,  
380 and the breeding distribution of *Z. palpebrosus* extends west across most of India. A single  
381 sampling locality for three *Z. erythropleurus* individuals collected from their wintering  
382 distribution in northern Vietnam is not shown for the sake of clarity. The introduced *Zosterops*  
383 populations of interest in Hawaii and southern California are each shown with distinct inset  
384 maps. The red dotted line between the southernmost islands of the Ryukyu archipelago and  
385 Taiwan indicates the location of the phylogeographic break identified within *Z. japonicus*. (B)  
386 Phylogenetic network showing relationships among all 124 individual samples passing filtering  
387 protocols. Individual tips are color-coded according to species identity. Two putative hybrid  
388 individuals that could not be confidently assigned to a specific clade are labeled with numbered  
389 stars corresponding to the sampling map.  
390

391 Assignment of genetic background into the optimal number ( $K = 6$ ) of predefined  
392 genomic ancestry bins using the program *ADMIXTURE* separated our six focal species, except  
393 that *Z. everetti* and *Z. nigrorum* were assigned to a single bin of genomic ancestry, while clades  
394 within *Z. japonicus* were assigned to two discrete bins of genomic ancestry. This result is  
395 corroborated by evidence that relative differentiation between clades within *Z. japonicus*  
396 (maximum pairwise  $F_{ST} = 0.42$ ) is greater than relative differentiation between recognized species  
397 *Z. everetti* and *Z. nigrorum* (pairwise  $F_{ST} = 0.22$ ; Fig. 2C). A subsequent *ADMIXTURE* analysis  
398 restricted to only *Z. everetti* and *Z. nigrorum* revealed no evidence for ancestry sharing among  
399 sampled individuals (Fig. 2B).

400 Of the 122 samples not identified as putative hybrids in the phylogenetic network, none  
401 were assigned >1% interspecies ancestry. This includes the samples from Hawaii and southern  
402 California, all of which were assigned >99% *Z. japonicus* and >99% *Z. simplex* ancestry,  
403 respectively (Fig. 2A). The putative hybrid sample from China was assigned 72.1% *simplex*  
404 ancestry and 27.9% *Z. japonicus* ancestry, whereas the putative hybrid sample from Singapore  
405 was assigned 88.0% *Z. simplex* ancestry, 9.4% *Z. palpebrosus* ancestry, and 2.2% *Z. japonicus*  
406 ancestry. All pairwise  $F_{ST}$  comparisons between recognized species (Fig. 2C), except the *Z.*

407 *nigrorum* / *Z. everetti* comparison, indicate high relative divergence (range 0.57 - 0.84). These  
 408 results are concurrent with the well-described propensity for rapid differentiation and speciation  
 409 among geographically isolated lineages of *Zosterops* white-eyes.



410

411 **Figure 2.** Population genetics of introduced and putative source Asiatic *Zosterops* populations.  
 412 (A) Ancestry assignments from *ADMIXTURE* for an optimal  $K = 6$ . Individual vertical bars (i.e.,  
 413 samples) are labeled according to species identity, with introduced populations and putative  
 414 hybrids labeled as in Figure 1. Southern California abbreviated as ‘SoCal’. (B) *ADMIXTURE*  
 415 ancestry assignments for only *Z. everetti* and *Z. nigrorum* samples reveal no ancestry sharing.  
 416 (C) The upper diagonal shows pairwise  $F_{ST}$  (a measure of relative genetic divergence ranging  
 417 from 0-1) comparisons among the six focal species (putative hybrid samples removed). Below  
 418 the diagonal are pairwise  $F_{ST}$  comparisons among the three geographically structured *Z.*  
 419 *japonicus* sub-populations identified in panel A. The red dot corresponds to the northern clade,  
 420 the gray and red dot to the northern Philippines clade, and the gray dot to the southern  
 421 Philippines through Sundaland clade.

422

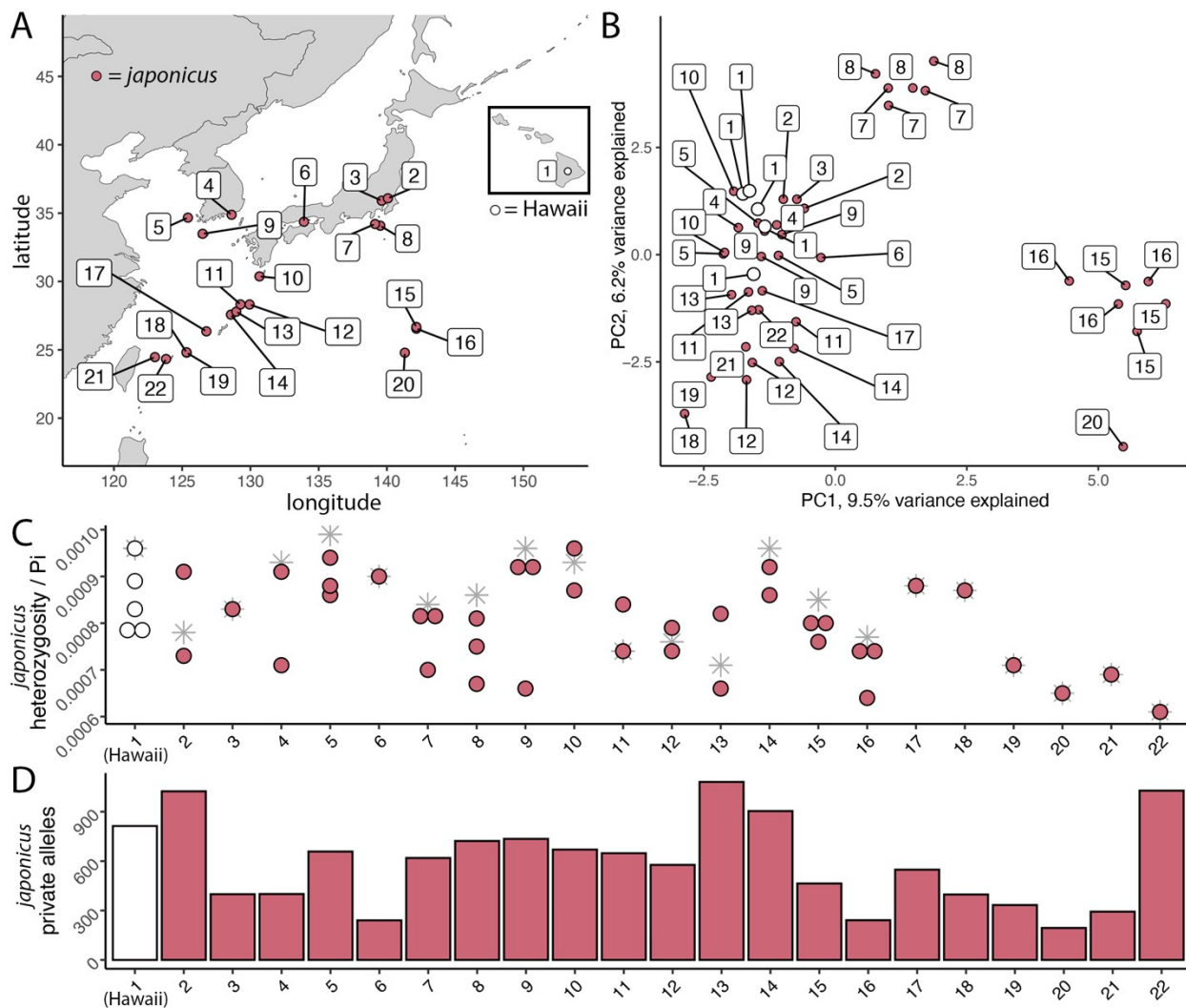
### 423 *Fine-scale structure and population dynamics*

424 Principal components analysis revealed that individual birds from the introduced

425 *Zosterops* population in Hawaii are genomically indistinguishable from *Z. japonicus* individuals

426 living on mainland Japan and the Korean Peninsula (sampling sites 2-6, 9, and 10; Fig. 3A/B),  
427 which is consistent with the reported intentional introduction of birds from mainland Japan to the  
428 Hawaiian Islands (Caum, 1933). Samples from offshore islands east of 135° longitude (sites 7, 8,  
429 15, 16, and 20) clustered discretely on PC1, while islands to the west of that line clustered  
430 separately on PC2 (except site 10). Meanwhile, measurements of heterozygosity and  $P_i$  indicated  
431 that the introduced Hawaii population contains comparable numbers of private (i.e., unique)  
432 alleles and levels of genetic diversity to populations from the native range of *Z. japonicus* (Fig.  
433 3C/D). In sum, these metrics indicate little evidence for meaningfully different population  
434 dynamics between the introduced Hawaiian population and conspecific populations from the  
435 native range of *Z. japonicus*.

436

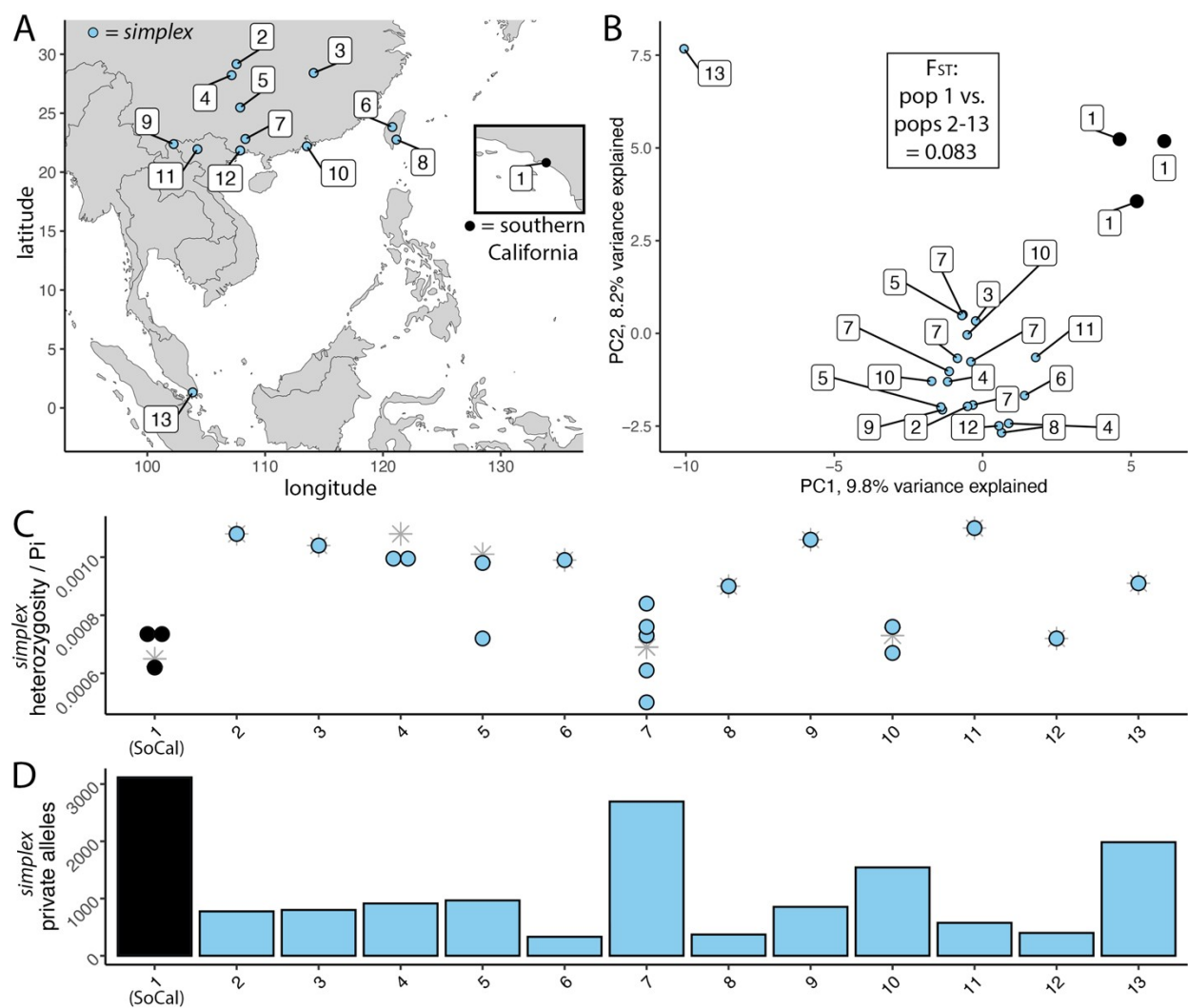


437

438 **Figure 3.** Comparing the genomes of introduced *Z. japonicus* in Hawaii with putative source  
 439 populations from the species' native range. (A) Map showing all sampling localities for the  
 440 northern *Z. japonicus* clade, with each sampling locality numbered arbitrarily but consistently  
 441 across panels. (B) Principal components analysis (PCA) reveals fine-scale genomic structure  
 442 within all sampled populations from the northern *Z. japonicus* clade. (C) Plots of heterozygosity  
 443 per sample (colored dots) and overall nucleotide diversity per sampling locality ( $P_i$ ; denoted with  
 444 a gray asterisk) for the northern *Z. japonicus* clade, including the introduced population in  
 445 Hawaii. (D) The number of private (i.e., unique) alleles identified in each sampling locality,  
 446 calculated from all successfully mapped genomic loci.  
 447

448 In contrast, samples from the introduced southern California population form a distinct  
 449 cluster in two-dimensional genomic space relative to all other sampled conspecific *Z. simplex*  
 450 individuals (Fig. 4A/B), supported by a modest pairwise  $F_{ST}$  value of 0.083. The single sample

451 from locality 13, located in the far southern extreme of the *Z. simplex* distribution, clustered  
 452 discretely on PC1 (Fig. 4B). Further, samples from the introduced population in southern  
 453 California rank among the lowest levels of genome-wide heterozygosity of all sampled *Z.*  
 454 *simplex* individuals (Fig. 4C). Additionally, this introduced population had lower overall  
 455 nucleotide diversity ( $P_i$ ) than any locality sampled from the native range of *Z. simplex*. This  
 456 introduced southern California population also possesses a greater number of private alleles than  
 457 any native population of *Z. simplex* that we sampled (Fig. 4D).



458

459 **Figure 4.** Comparing the genomes of introduced *Z. simplex* in southern California with putative  
 460 source populations from the species' native range. (A) Map showing all sampling localities for *Z.*

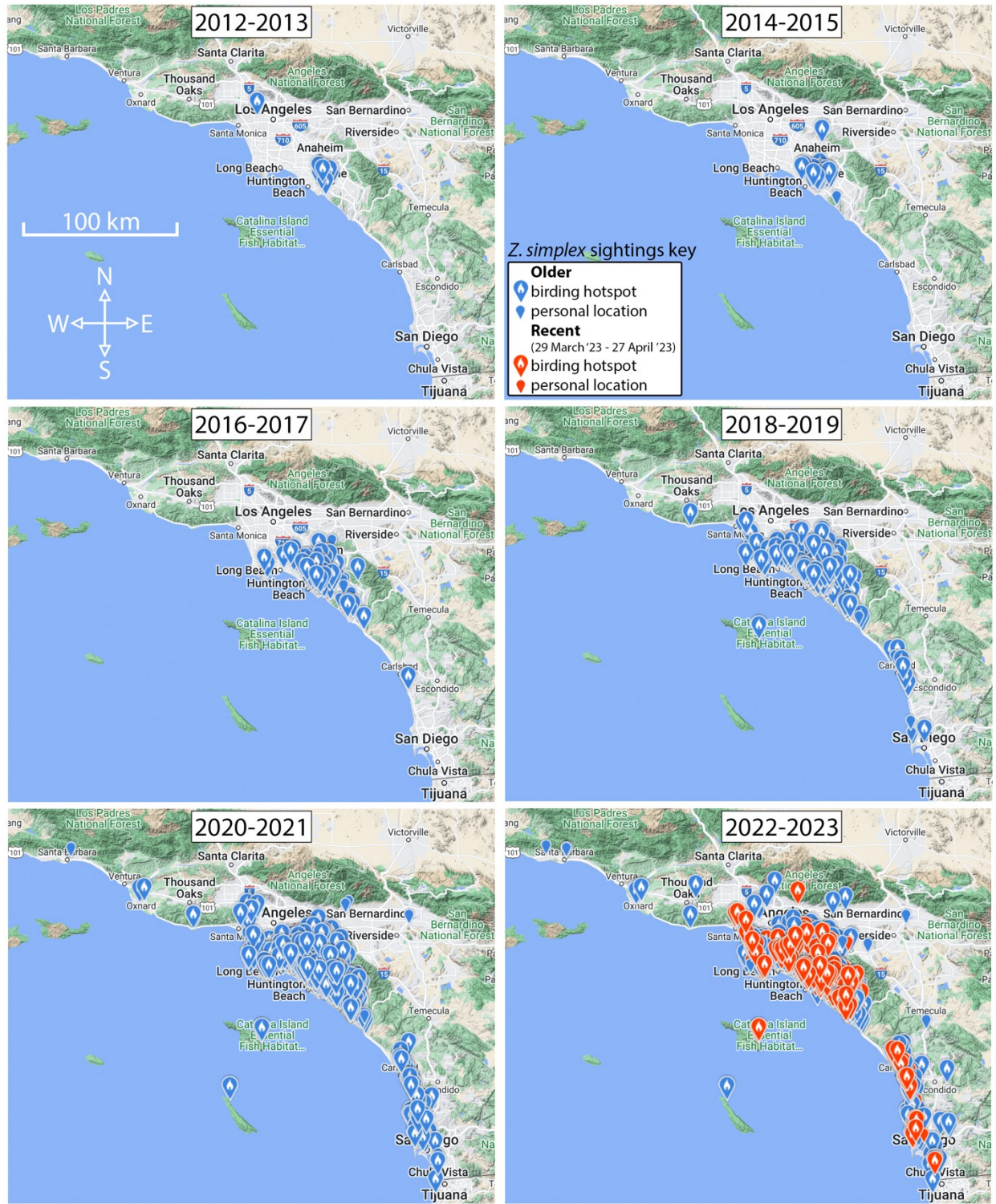


461 *simplex*, with each sampling locality numbered arbitrarily but consistently across panels. (B)  
462 Principal components analysis (PCA) shows sample clustering among all sampled *Z. simplex*  
463 populations. (C) Plots of heterozygosity per sample (colored dots) and overall nucleotide  
464 diversity per sampling locality ( $P_i$ ; denoted with a gray asterisk). The abbreviation ‘SoCal’ is  
465 used to denote the *Z. simplex* population established in southern California. (D) The number of  
466 private (i.e., unique) alleles identified in each sampling locality, calculated from all successfully  
467 mapped genomic loci.

468

469 *Ecological dynamics of Zosterops establishment in North America*

470 Observational data recorded by community scientists show the establishment and subsequent  
471 rapid geographic expansion of *Z. simplex* individuals across southern California over the past  
472 decade (Fig. 5). As recently as 2012-2013, this introduced population was restricted almost  
473 completely to a handful of locations along the Pacific coast in Orange County, California. Within  
474 a few years, however, the population expanded dramatically, reaching as far inland as San  
475 Bernardino, and radiating hundreds of kilometers north and south along the coastline. As of  
476 2023, *Z. simplex* has now been documented from Santa Barbara, California, to Tijuana, Mexico,  
477 a total range spanning >300 km from end to end. Additionally, *Z. simplex* is now apparently  
478 established on the offshore islands of Catalina and San Clemente, underscoring the proclivity for  
479 overwater dispersal and island colonization in the *Zosterops* white-eyes. This clear evidence for  
480 rapid and ongoing geographic expansion within southern California raises the obvious question,  
481 what is the invasion potential of *Z. simplex* across North America?



482

483 **Figure 5.** Maps showing the rapid expansion and establishment of introduced *Zosterops simplex*  
 484 in southern California over the last 12 years, as tracked by community scientists in the eBird  
 485 database. Images provided by eBird ([www.ebird.org](http://www.ebird.org)), created 27 April 2023. Each bubble

486 corresponds to a single geographic location where a sighting was reported. Refer to the inset key  
487 for detailed locality information.  
488

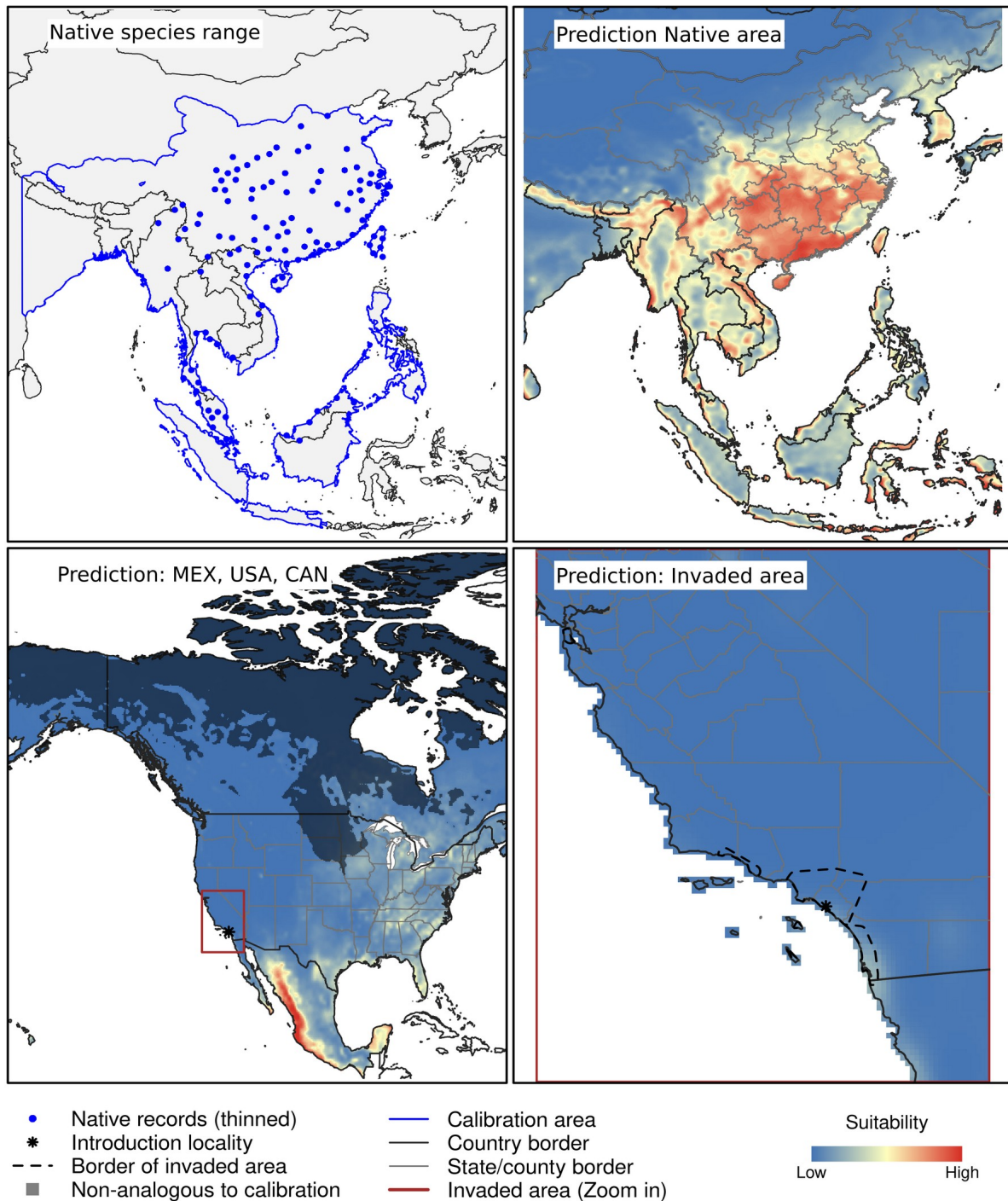
489         To address this question, we used ecological niche modeling to explore the distributional  
490 potential of the species under a variety of scenarios. We used breeding-season occurrence data  
491 from across the native range of *Z. simplex* to train correlative models of the fundamental niche of  
492 the species, which we then transferred onto North American climatic landscapes. 1,549 out of  
493 1,560 candidate models generated statistically significant predictions of independent subsets of  
494 the available occurrence data. Of those models, 487 also had sufficiently low omission rates, and  
495 AICc scores identified four individual models that had an optimal combination of good  
496 predictive ability while utilizing the fewest numbers of total input parameters. All selected  
497 models used four predictors, linear, quadratic, and product responses, and similar regularization  
498 multipliers (i.e., PC1, PC2, PC4, and PC5; see Table S5 for more details). On average, PC5  
499 contributed the most to our four models ~43%, followed by PC1 with ~22%; whereas, the  
500 average permutation importance was similar among the four predictors (i.e., 24.43-25.85; Table  
501 S6).

502         The consensus of these four best models is highly predictive of the overall distribution of  
503 *Z. simplex* across eastern China and Southeast Asia (Fig. 6). Suitability for the species is lower at  
504 the geographic extremes of the distribution in northeastern China, and on the Malay Peninsula  
505 and northern Borneo. Mean response curves for the species' distribution with respect to  
506 environmental dimensions were truncated only for PC5 (Fig. S1). For other predictors, response  
507 curves had a bell shape, which indicates relatively safe model extrapolations. Transferring this  
508 'best model consensus' to the species introduced range reveals a relatively low degree of  
509 environmental suitability across most of North America (Fig. 6), assuming a model of niche

510 conservatism from the native range of *Z. simplex*. However, the southern extremes of the United  
511 States and much of Mexico appear to closely match the abiotic environmental conditions of the  
512 species' breeding range, as indicated by high degrees of suitability. Zooming in on southern  
513 California, the current introduced *Z. simplex* population appears to inhabit a broad range of  
514 suitability values. The putative introduction site, near Huntington Beach (Fig. 5), is recovered as  
515 moderately suitable. Meanwhile individuals on the northern edge of the expansion front (Fig. 6)  
516 appear to inhabit areas of low environmental suitability, outside of the range experienced in the  
517 native distribution of *Z. simplex*.

518

519



520 **Figure 6.** Results from ecological niche modeling for *Zosterops simplex* across Mexico, United  
 521 States, and Canada. Top panels show all distance-thinned breeding season occurrence  
 522 observations used to build the ecological niche model, and the subsequent model projected onto  
 523 the native range of the species. The bottom panels show the model projected onto North  
 524 America, with a specific focus on the current introduced range in southern California. The border  
 525 of species range in southern California is represented as a convex hull produced from clusters of  
 526 invasive records, with a ~10 km buffer.

527

528 **Discussion**

529 Understanding the source of these introduced *Zosterops* populations is an important step toward  
530 understanding their invasion potential and more broadly, understanding the ability of these ‘great  
531 speciators’ (Moyle et al., 2009) to repeatedly overcome the genetic bottlenecks associated with  
532 founding new populations (i.e., the ‘invasion paradox’; Estoup et al., 2016; Kolbe et al., 2004).  
533 Here we confirm for the first time with genomic data that the recently introduced *Zosterops*  
534 white-eye population in southern California (~17 years; Cook, 2006) represents a distinct  
535 introduction of *Z. simplex* individuals with no apparent relation to the long established (~93  
536 years; Scott et al., 1986) introduced *Z. japonicus* population in Hawaii. We find no evidence for  
537 shared ancestry between these introduced populations and other closely related Asiatic *Zosterops*  
538 species. Further, we find limited evidence for hybridization (2/124 samples) across the native  
539 range of these Asiatic *Zosterops* species, which occur in various stages of secondary sympatry,  
540 suggesting the extraordinarily rapid evolution of reproductive isolating barriers among these  
541 natural populations (estimated *Zosterops* crown age = 1.6 – 2.5 MYA; Vinciguerra et al., 2023).  
542 These results are largely consistent with a recent detailed genomic investigation into the northern  
543 Melanesian *Zosterops* radiation, which found deep phylogenetic divergence between described  
544 taxa and no evidence of recent hybridization, despite statistical signatures of gene flow,  
545 suggesting incomplete reproductive isolation (Manthey et al., 2020). Our detailed genomic  
546 investigation revealed evidence for a population bottleneck associated with the founding of the  
547 introduced population in southern California, but not Hawaii, concordant with assumed  
548 differences in founding population size and ongoing propagule pressure between these  
549 populations. Finally, ecological niche models identified relatively limited geographic areas

550 across North America with suitable environmental conditions for *Z. simplex*. Intriguingly,  
551 community science observations from the northern edge of the expanding population front in  
552 southern California record *Z. simplex* individuals outside of suitable habitat identified by our  
553 model, suggesting that the geographic invasion potential of this population may prove to be  
554 broader than our ecological niche model suggests. Together, our parallel genomic and ecological  
555 investigations offer practical insights into the invasion potential of *Zosterops* across North  
556 America, and a window into the general ability of *Zosterops* lineages to rapidly overcome the  
557 invasion paradox (Estoup et al., 2016).

558

559 *The evolutionary history of native Zosterops populations*

560 Accurately resolving the ancestry of the introduced *Zosterops* populations studied here presents a  
561 unique challenge because the taxonomy and phylogenetic relationships of the genus have long  
562 been plagued by polytomies and a general lack of resolution (Guest, 1973; Moyle et al., 2009;  
563 Vinciguerra et al., 2023). The extraordinarily rapid radiation of the 111 (Gill et al., 2023)  
564 currently recognized *Zosterops* species within the last ~2.1 million years (estimated crown age  
565 1.6 – 2.5 MYA; Vinciguerra et al., 2023), has made the phylogenetic backbone of this clade  
566 extremely challenging to resolve, with startlingly short internode distances suggesting very little  
567 time for lineage sorting to occur (Maddison & Knowles, 2006). Among our small focal subclade,  
568 the ‘Asiatic *Zosterops*’ (Gwee et al., 2020; Vinciguerra et al., 2023), we did not attempt  
569 comprehensive phylogenetic sampling, instead focusing on just six geographically proximate and  
570 phenotypically similar species that could have plausibly been involved in founding the  
571 introduced *Zosterops* populations in Hawaii and southern California (Fig. 1).

572           Because the introduced *Zosterops* populations we investigate here likely contain some pet  
573 trade influence (Chng et al., 2018), we suspected that ongoing hybridization might be an  
574 important force in shaping patterns of relatedness among the samples we sequenced. Yet, we  
575 identified only two putatively admixed individuals using thousands of genomic loci (Fig. 1),  
576 neither of which were sampled from an introduced population. One of these admixed individuals  
577 came from Singapore, and was assigned > 2% ancestry from *Z. simplex*, *Z. palpebrosus*, and *Z.*  
578 *japonicus*, suggesting potential complex multispecies hybridization. Despite the rarity of  
579 documented tri-species hybridization events in birds (except see: Natola et al., 2022), this  
580 uncommonly complicated evolutionary history is especially plausible in Singapore, where the  
581 native *Zosterops* population was reported to have been locally extirpated by poaching for the pet  
582 trade in the 1970s, being subsequently replaced by a flock of feral white-eyes derived largely  
583 from captive escapees, including *Z. simplex*, *Z. palpebrosus*, and *Z. japonicus* individuals (Eaton  
584 et al., 2017; Ng & Wee, 1994). Lim et al. (2019) identified only *Z. simplex* haplotypes among the  
585 mitochondrial DNA of 17 birds from Singapore, but suggested that nuclear DNA sequence data  
586 would be needed to rule out hybridization. Despite our highly limited sample size (two samples  
587 from Singapore), our results suggest that the ancestry of Singapore's white eye population is  
588 derived from at least three *Zosterops* species commonly found in the pet trade. Future work with  
589 greater sample size will be essential for understanding the extent of hybridization, and the  
590 taxonomic status of the *Zosterops* population in Singapore.

591           Regarding the overall evolutionary history of the Asiatic *Zosterops*, we find support for  
592 rapid branching and strong yet imperfect (Manthey et al. 2020) reproductive isolation. Because  
593 of the lack of strong support for a single set of bifurcating phylogenetic relationships among taxa  
594 and statistical signatures of excess allele sharing between non-sister lineages, previous studies



595 have concluded that gene flow is rampant among naturally distributed *Zosterops* lineages (Gwee  
596 et al., 2020). In contrast, our genomic data suggests that ongoing hybridization among ‘Asiatic  
597 *Zosterops*’ species is quite rare (2/124 individuals with detectably admixed genomic  
598 backgrounds). We suggest that rampant significant ABBA/BABA tests between *Zosterops* taxa  
599 (Gwee et al., 2020) could be largely explained by rapid trifurcations and polytomies which make  
600 correct topology specification nearly impossible, and the well-documented ability of substitution  
601 rate variation to create false positive ABBA/BABA results (Frankel & Ané, 2023), rather than  
602 extensive ongoing hybridization. The exact nature of reproductive barriers (e.g., intrinsic versus  
603 extrinsic; Christie & Strauss, 2019) between *Zosterops* species deserves further study.  
604 Regardless, we suggest that the ‘great speciator’ status of the genus *Zosterops* (i.e., the ability to  
605 repeatedly colonize new locales and rapidly speciate; Moyle et al., 2009) is not only a result of  
606 exceptional dispersal capability, but also of this propensity for exceptionally rapid evolution of  
607 reproductive isolating barriers.

608

### 609 *The genomic signatures of Zosterops introductions*

610 Upon establishment, a novel population must overcome the genetic bottleneck and founder effect  
611 resulting from an inherently limited founding population size (i.e., invasion paradox; Estoup et  
612 al., 2016; Halliburton, 2004; Kolbe et al., 2004). Here we searched for signatures of population  
613 bottlenecks, which reduce genome-wide diversity, in the introduced *Zosterops* populations in  
614 Hawaii and southern California. We found reduced genetic diversity in the introduced *Z. simplex*  
615 population in southern California, but not in the introduced *Z. japonicus* population from Hawaii,  
616 indicating that the southern California population is experiencing an ongoing genetic bottleneck,  
617 while the Hawaii population is not. Further, we find evidence for both genetic divergence from

618 the putative source population and an increase in private alleles in the southern California  
619 population, but not in the Hawaiian population. These results indicate that unlike the Hawaiian  
620 population, the southern California population is genetically differentiated from any sampled  
621 source population. This could be explained by genomic adaptation to a novel environment in  
622 southern California (Lee, 2002, 2016), exacerbated by strong founder effects (Jamieson, 2011)  
623 and increased genetic drift during a genetic bottleneck (N. H. Barton, 1997; Sendell-Price et al.,  
624 2021), or a lack of genetic sampling from the closest source population. It is important to note  
625 that we did not sample any *Z. simplex* individuals directly from the pet trade, and it is possible  
626 that a series of genetic bottlenecks and novel selection pressures associated with a transition to  
627 captivity had already shaped the demographic history of the putative pet-trade escapees (see  
628 detailed discussion below) that founded the southern California population.

629         One obvious explanation for the difference in genomic diversity between these two  
630 introduced populations is a fundamental difference in their founding. Because the *Z. japonicus*  
631 population in Hawaii was initially founded by the Hawaii Board of Agriculture and Forestry on  
632 the island of Oahu in 1929 with the intention of establishing a viable population, the effort likely  
633 involved the release of dozens to hundreds of individuals (although no exact numbers of  
634 individuals are reported; Caum, 1933). Further, it was documented that in 1937, an additional  
635 252 *Z. japonicus* individuals were introduced to the big island of Hawaii with the goal of  
636 controlling insect populations (Guest, 1973). In contrast, as there is no record of *Z. simplex*  
637 introduction in southern California, and this population is likely the result of the release/escape  
638 of a small number of captive birds, meaning this population may have been founded by only a  
639 handful of individuals. In fact, only four birds were seen when the population was first  
640 documented in 2006 (Cook, 2006), and no one subsequently documented a group of white-eyes

641 containing more than four individuals in southern California for more than five years following  
642 this initial sighting (Daniels, 2011). Therefore, our genomic results indicating a reduction in  
643 genetic diversity and increase in private alleles in the southern California population, but not the  
644 Hawaii population, are concordant with expectations derived from population genetic theory  
645 given the number of individuals we think contributed to the founding of each population (Nei et  
646 al., 1975).

647         An important caveat to these interpretations is the availability of genetic samples. The  
648 genetic divergence between the southern California population and all putative source  
649 populations may indicate divergence between *Z. simplex* individuals found in the pet-trade  
650 versus the wild. It is notable that we find no evidence for genetic divergence between *Z.*  
651 *japonicus* from Hawaii and the native range, considering the documented evidence for significant  
652 morphological changes between these populations (Gleditsch & Sperry, 2019). This could  
653 indicate that morphological traits in *Z. simplex* have significant lability and are strongly affected  
654 by environmental conditions, or that we have simply missed the regions of the genome that  
655 encode these morphological differences in our RADseq dataset which covers <1% of the total  
656 genome. Additionally, in the Hawaiian archipelago, it is worth noting that all our samples from  
657 the Hawaii population come from the Big Island, Hawaii, the site of at least one intentional  
658 introduction effort. Based on this sampling, we cannot determine whether populations located on  
659 further outlying islands (e.g., Oahu or Kauai) may suffer detectable genetic bottlenecks or  
660 founder effects following repeated dispersal and colonization events across the Hawaiian island  
661 archipelago (Clegg et al., 2002; Shultz et al., 2016). Detailed genomic investigation of the  
662 varying strength of population bottlenecks across the Hawaiian archipelago offers yet another  
663 potentially fruitful avenue for future genomic research.

664 Another, potentially complementary, explanation for the genomic differences we observe  
665 between these populations is the difference in timing since introduction (~17 years in southern  
666 California, Cook, 2006; versus ~94 years in Hawaii, Scott et al., 1986). Population genetic theory  
667 has shown that even a severe reduction in genetic diversity from a population bottleneck can be  
668 quickly erased if it is followed by a rapid increase in population size (Nei et al., 1975). Based on  
669 the documented rapid expansion of the Hawaiian *Zosterops* population (estimated 245,000 *Z.*  
670 *japonicus* individuals in just the Ka‘ū Region of Hawaii, as of 2007; Gorresen et al., 2007), it is  
671 plausible that the Hawaii population has already overcome any initial reduction in genetic  
672 diversity associated with establishment and returned to stable levels of genetic diversity seen in  
673 putative source populations, with limited long term evolutionary cost (James et al., 2016). In  
674 comparison, the house finch (*Haemorhous mexicanus*) population on the Hawaiian islands was  
675 founded at a similar time and also grew rapidly, yet still shows a detectable reduction in genetic  
676 diversity, suggesting a more severe bottleneck, lower propagule pressure, a lower growth rate, or  
677 a combination of these factors (Shultz et al., 2016).

678 This ability to rapidly overcome relatively small founding population sizes via explosive  
679 population growth could be a key life history strategy that has facilitated the repeated  
680 colonization and speciation of *Zosterops* species throughout the Pacific (Gwee et al., 2020;  
681 Moyle et al., 2009; Sendell-Price et al., 2021; Sendell-Price, Ruegg, Anderson, et al., 2020). This  
682 would suggest that the continued, rapid expansion of the *Z. simplex* population in southern  
683 California may be erasing signatures of low genetic diversity in real time. It is worth noting that  
684 while effective population sizes can be tracked backwards through time using genomic  
685 information from even a single individual (Li & Durbin, 2011), these approaches are notoriously  
686 sensitive to population structure and gene flow (Heller et al., 2013; Shchur et al., 2022) and

687 unreliable on recent time scales (Liu & Hansen, 2017), which led us to forego this approach for  
688 the specific question of comparing recent genetic bottlenecks. Future investigations using whole  
689 genome sequencing, along with nuanced and careful approaches to demographic modeling, will  
690 be necessary to effectively reconstruct population dynamics through time in these introduced  
691 populations (e.g., Hewett et al., 2023).

692

### 693 *Forecasting the establishment of Zosterops in North America*

694 Forecasting the potential establishment and spread of introduced species is an important exercise  
695 because of the environmental (Clavero & García-Berthou, 2005) and economic (Linz et al.,  
696 2018) costs associated with ongoing biological invasions across the globe. Here, we use an  
697 ecological niche modeling approach to quantify the multidimensional environmental space  
698 inhabited by *Z. simplex* (Sóberon & Peterson, 2005) and project these environmental conditions  
699 across North America, effectively forecasting areas at the greatest risk for potential invasion and  
700 establishment (Peterson, 2003; Peterson & Vieglais, 2001). It is important to note that this  
701 exercise relies on the assumption of niche conservatism, or the idea that novel introduced  
702 populations will be limited by the abiotic conditions inhabited in the native range of the species  
703 (Losos, 2008; Peterson et al., 1999; Pyron et al., 2015). This assumption can be violated in cases  
704 where the inhabited niche is only a subset of the fundamental niche, meaning that the species is  
705 physiologically capable of inhabiting a broader suite of environmental conditions than it does in  
706 its native range (Sóberon & Peterson, 2005). For the rapidly expanding *Z. simplex* population in  
707 southern California, we discuss the implications of projected patterns of environmental  
708 suitability across North America, and highlight necessary caveats for interpreting forecasted  
709 habitat suitability.

710           Based on our forecast, the environmental conditions inhabited by *Z. simplex* across its  
711 native range cover only a small portion of North American geography, with the largest swath of  
712 contiguous habitat found on the Pacific coast of Mexico. If *Z. simplex* is limited to the projected  
713 suitable habitat, then we can expect the southern California population to continue expanding  
714 south in coastal Baja California, where the warm, temperate environment is similar to the  
715 subtropical conditions of the species' native range. If *Z. simplex* can disperse across barriers of  
716 unsuitable habitat, the species would find highly suitable conditions along the Pacific coast of  
717 Mexico, and moderately suitable conditions near the Atlantic gulf coast, throughout the  
718 southeastern United States. The main barrier to accessing these swaths of suitable habitat is their  
719 discontinuous nature, with the deserts of southwestern North America and the Sierra Madre  
720 Oriental mountain range presenting apparent barriers to the continuous establishment of *Z.*  
721 *simplex* across low latitude habitats in North America. It is worth noting that rapid warming of  
722 the global climate caused by massive anthropogenic release of greenhouse gases could bring the  
723 subtropical environmental conditions favored by *Z. simplex* in its native range further north,  
724 creating more continuous swaths of habitat (Anderson et al., 2012). Future work should explore  
725 the interaction between this rapidly adapting *Z. simplex* population and its rapidly changing  
726 climate.

727           Surprisingly, the main stronghold of this introduced population, coastal southern  
728 California, between San Diego and Los Angeles (Fig. 5), displayed low to moderate  
729 environmental suitability for *Z. simplex* according to our model. In fact, the northernmost front  
730 of the expanding population appears to be completely outside of the environmental conditions  
731 inhabited by *Z. simplex* in the species native range (Fig. 6). These results suggest that the model  
732 of niche conservatism assumed by this approach may be not be fully appropriate for projecting

733 the invasion potential of *Z. simplex* across North America. This could suggest that *Z. simplex* has  
734 a broader fundamental niche than is captured by occurrence points from the native range  
735 (Jiménez et al., 2019), due to interactions with other species (i.e., biotic conditions), or  
736 geographic barriers which prevent dispersal into other suitable habitats (Feeley & Silman, 2010;  
737 Fell et al., 2022). Under these circumstances, the geographic invasion potential of this population  
738 may prove to be broader than our ecological niche model suggests. Alternatively, populations on  
739 the leading expansion edge of the introduced population may prove ephemeral, leading to an  
740 eventual range contraction into a core distribution of suitable habitat in southern California.

741         Meanwhile, there are additional possibilities that could explain the observed colonization  
742 of areas predicted unsuitable by our model even if the fundamental niche of *Z. simplex* is  
743 perfectly captured by our native range occurrence points, such as the ability to exploit novel  
744 anthropogenic resources not included in our model variables, or rapid genetic adaptation to novel  
745 environmental conditions. For instance, *Z. simplex* has been documented using novel biotic  
746 resources such as ornamental flowers and fruit trees as food resources in the urban environment  
747 of southern California (e.g., Garrett, 1997). Additional resources facilitating establishment could  
748 include supplementary food sources such as hummingbird feeders (Battey, 2019), or warmer  
749 microhabitats offered by the urban built environment on cold nights (Wang & Chu, 2021). In  
750 addition, genetic adaptations could already be facilitating inter-generational adaptation to novel  
751 environmental conditions (Hofmeister et al., 2021; Lee, 2002, 2016; Stuart et al., 2023), although  
752 large evolutionary niche shifts have rarely been documented in vertebrate populations (Peterson,  
753 2011). Nonetheless, shifts in the frequencies of many alleles, each contributing weakly to highly  
754 polygenic traits such as body size, metabolism, or rate of shivering (e.g., Stager et al., 2021),  
755 may have already begun to expand the physiological tolerance range of this introduced

756 population. Ultimately, further study in the coming decades will be necessary to understand the  
757 nature of the mechanisms involved in adaptation to the novel environment of urban southern  
758 California, as well as the factors (i.e., biotic versus abiotic) that will eventually act to limit the  
759 geographic spread and establishment of this introduced population.

#### 760 *Conclusions*

761 This work contributes to a growing body of literature focused on projecting the invasion  
762 potential of introduced species in novel environments (Dong et al., 2020; Early et al., 2018;  
763 Mutamiswa et al., 2021; Nuñez-Penichet et al., 2021; Vega et al., 2021). Ours is one of the few  
764 investigations to date that has attempted to jointly assess the genetic effects of introduction and  
765 the suitability of environments across geographic space for a novel introduced population (e.g.,  
766 Banerjee et al., 2019; Estoup et al., 2010). While we identify a reduction in genetic diversity  
767 associated with the introduction of *Z. simplex* into southern California, the population is  
768 expanding rapidly in this novel environment. We suggest that this ability to overcome the  
769 invasion paradox (Estoup et al., 2016) via rapid population expansion could be a key factor in  
770 helping the *Zosterops* white-eyes earn their “great speciator” reputation (Diamond et al., 1976;  
771 Lee, 2002). Ecological niche modeling results suggest that broad-scale invasion of *Z. simplex*  
772 throughout the western United States is unlikely considering low suitability levels. Yet, the rapid  
773 expansion of *Z. simplex* throughout Los Angeles suggests that urban environments may offer  
774 biotic resources and suitable microhabitats that are not incorporated into our ecological niche  
775 model, and could aid in facilitating the expansion of this introduced population beyond the limits  
776 suggested by our forecast. If the introduced *Z. simplex* population is not limited by genetic  
777 bottlenecks or unfamiliar environmental conditions, only time will reveal what forces will  
778 eventually act to limit its geographic spread in North America.



779

**780 Acknowledgments**

781 Each *Zosterops* illustration shown in this manuscript is an original creation of H. Douglas Pratt  
782 and has been subsequently licensed and reproduced via the Cornell Lab of Ornithology Birds of  
783 the World, with permission from Lynx Ediciones. We thank the Urban Nature Research Center  
784 for helpful feedback on an in-progress draft of this manuscript. We would like to thank the  
785 Volcano Islands Research Team of Tokyo Metropolitan Government; the National Museum of  
786 Science and Nature, Tokyo; the South China Institute for Endangered Animals; the University of  
787 Washington Burke Museum; the Cincinnati Museum Center; the American Museum of Natural  
788 History; the Field Museum; Natural History Museum of Los Angeles County; the Smithsonian  
789 National Museum of Natural History; and the University of Kansas Natural History Museum for  
790 providing the sampling necessary to complete this project. This work was supported in part by  
791 National Science Foundation grant to RGM (DEB-1557053). This work was performed in part  
792 using the HPC facilities operated by the Center for Research Computing at the University of  
793 Kansas supported in part through the National Science Foundation MRI Award #2117449. DAD  
794 was supported by the Lila and Madison Self Graduate Fellowship during a portion of this project.  
795 HLM was supported through NSF Award #2322123.

796

**797 Data availability**

798 All code needed to reproduce the results of this study can be found by following the links on the  
799 homepage of the dedicated GitHub repository for this project at:

800 <https://github.com/DevonDeRaad/zosterops.rad>. Upon manuscript acceptance, this entire

801 repository will be archived permanently with a stable DOI via Zenodo, and all raw sequence data  
802 will be deposited on NCBI's Sequence Read Archive.

803

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1227

**1228 Statements and Declarations****1229 *Funding***

1230 This work was supported in part by National Science Foundation grant to RGM (DEB-1557053).

1231 This work was performed in part using the HPC facilities operated by the Center for Research

1232 Computing at the University of Kansas supported in part through the National Science

1233 Foundation MRI Award #2117449. DAD was supported by the Lila and Madison Self Graduate

1234 Fellowship during a portion of this project. HLM was supported through NSF Award #2322123.

**1235 *Competing interests***

1236 The authors have no competing interests to disclose at this time.

**1237 *Author contributions***

1238 DAD and AJS conceptualized and designed the study. DAD performed molecular lab work,

1239 genomic data analysis, and wrote the first draft of the manuscript. MEC and ATP performed

1240 ecological niche modeling analyses. RGM, AJS, KLG, IN, BM, FSZ, KK, CHK, RSY, CTY, and

1241 HLMJ all contributed crucial specimens and tissue samples to the project. RGM secured funding

1242 for genomic sequencing. All authors contributed substantial feedback on the analysis and

1243 interpretation of data across multiple drafts of this manuscript, and approved the final submitted

1244 version of the manuscript.