



# Genomic data reveal shift in geographic source of an illegally traded songbird

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## Abstract

Wildlife trade is one of the major contributors to biodiversity loss in Southeast Asia, especially in songbirds. Wildlife forensics using genomic data can be instrumental in informing conservation action by identifying trade routes and animals' provenance to help law enforcement. We obtained ~10,000 genome-wide markers spanning a panel of 87 wild, captive, and confiscated individuals of one of the most widely traded songbirds in Southeast Asia, Swinhoe's white-eye (*Zosterops simplex*), to examine shifts in trade routes. Our population-genomic analyses reveal that a well-studied population of this white-eye on Singapore Island exhibits a major genomic contribution from the geographically distant subspecies *simplex*, reflecting historic trade into Singapore from China. In contrast, modern confiscated samples as well as a minority of wild Singapore samples carry the genomic signature of the Southeast Asian subspecies *erwini*, suggesting that modern trade sources in Singapore have shifted from China towards adjacent Malaysia. Our study highlights how accurate identification of trade routes can help conservationists' efforts in tackling the growing songbird crisis in the region.

**Keywords** Wildlife trade · Poaching · Sundaland · Wildlife forensics

## Introduction

The Greater Sundaic region in Southeast Asia is rich in biodiversity, being home to over 850 bird species, including many endemics (Eaton et al. 2021; Lee et al. 2016). It is also a hotspot for the global trade of wildlife and their products, with birds constituting a major component (Krishnasamy and Zavagli 2020; Nijman 2010; Scheffers et al. 2019). A strong demand for caged birds has led to the unsustainable poaching of birds from the wild (Butchart 2008). With a burgeoning middle class in countries where caged birds are regarded as status symbols and owning birds is a deeply entrenched social practice, consumer demand for these birds is expected to grow even further (Marshall et al. 2020). High levels of trapping to meet increasingly insatiable market demand have already caused extinction or near-extinction in some Sundaic species, leading to the current 'Asian Songbird Crisis' (Baveja et al. 2021; Lee et al. 2016; Nijman 2010; Sadanandan et al. 2020; Shepherd and Cassey 2017). Monitoring trade routes of caged birds is critical for effective management and regulations to be implemented. However, the monitoring process is challenging, as it is still not formally recognized as a key conservation priority by

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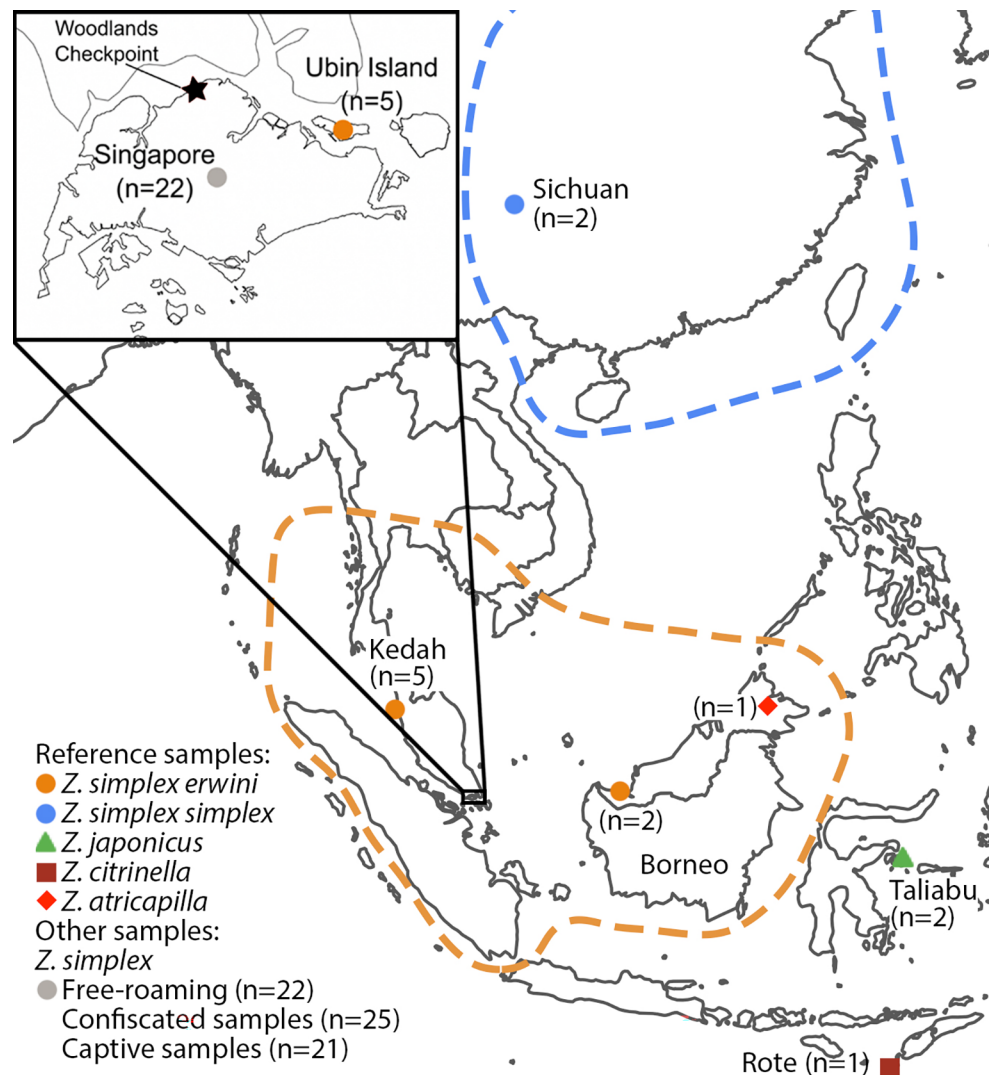
authorities, which causes transactions made through public and private channels to be often underreported.

White-eyes (genus *Zosterops*) are a popular group of caged bird, prized for their beautiful songs (Nash 1993). Intense trapping pressure to supply the wildlife trade and habitat destruction in their native range have compounded their potential risk for local extinction in the wild (Eaton et al. 2015; Lee et al. 2016). However, most Southeast Asian white-eyes are listed as ‘Least Concern’ by the IUCN Red List and omitted by the appendices of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) because of their extensive distribution ranges (International Union for Conservation of Nature and Natural Resources 2022). Given the lack of known large-scale breeding programs for these taxa, the massive volumes of white-eyes in the trade are most likely extracted from the wild – a practice that is unlikely to be sustainable in the long term.

One of the more widespread white-eye species that is affected by some of the highest trade volumes is Swinhoe’s white-eye (*Zosterops simplex*) (Chiok and Chng 2021; Chng et al. 2015; Chng and Eaton 2016; Eaton et al. 2017a; Lim et al. 2019). This species occurs across East and Southeast Asia (Fig. 1) but is not thought to be native to the main island of Singapore despite its occurrence on the adjacent Malaysian mainland and nearby smaller islands (Hume 1879). Their historical absence notwithstanding, Swinhoe’s white-eyes are nowadays common on Singapore Island, likely as a result of accidental releases from the trade that have been ongoing for decades against a backdrop of a thriving local culture of bird-keeping (Eaton et al. 2017b). A four-day survey across 39 licensed pet shops in Singapore found that Swinhoe’s white-eye was the most commonly proffered bird species, with 6,473 individuals recorded, accounting for 46% of birds tallied (Eaton et al. 2017b).

Amid all this trade activity, multiple instances of illegal trade have been laid bare over the years. An attempt

**Fig. 1** Distribution map of select white-eyes (genus *Zosterops*) sampled across Asia following the taxonomic treatment of Gwee et al. (2020). The native ranges of *Z. simplex erwini* (orange) and *Z. simplex simplex* (blue) are demarcated by stippled lines. *Z. simplex* samples from Jurong Bird Park, Singapore, are labelled as ‘Captive’. *Z. simplex* samples obtained from the seizure of illegally traded birds are labelled as ‘Confiscated’. Free-roaming individuals of *Z. simplex* from Singapore island with an admixed genomic profile are labelled as ‘Free-roaming’. Number of individuals sampled per locality is indicated in brackets. A single *Z. japonicus* individual introduced into Hawaii was included in the analyses but is not shown on the map



to smuggle 815 live birds into Singapore was intercepted at Woodlands Checkpoint on the Malaysia-Singapore border (Fig. 1) in 2019 by the Singapore Immigration and Checkpoints Authority (ICA 2019), constituting the most sizable confiscation of birds in Singapore in recent years. The source of the birds was unknown, making it challenging to determine the identities of the confiscated birds. The batch included 141 white-eyes of unconfirmed taxonomic identity. The identification challenge was exacerbated by the close morphological resemblance within and between white-eye taxa (Mayr 1965; Mees 1957; Eaton et al. 2021).

A growing body of research recommends the usage of genetic tools to combat illegal wildlife trade, termed wildlife forensics (Alacs et al. 2010; Dawnay et al. 2007; Ogden 2011). Genome-wide single nucleotide polymorphisms (SNPs) have been classed as informative genetic markers that can provide more resolution than traditional markers such as mtDNA or microsatellites (Alacs et al. 2010). In this study we used genome-wide SNPs to resolve the population identities and source origins of a confiscated consignment of illegally transported white-eyes. We found that the white-eyes most likely originated from Peninsular Malaysia, and we provide inferences of a possible shift in trade routes and recommendations for law enforcement and conservation management in Southeast Asia.

## Materials and methods

### Sample collection and sample treatment

We follow the taxonomic treatment of Gwee et al. (2020) with a focus on Swinhoe's white-eye (*Zosterops simplex*), which has long been imported into Singapore from China (Chasen 1935). A total of 25 confiscated white-eyes that died in transit were obtained from the National Parks Board Singapore following the seizure of an illegal import from Malaysia into Singapore. Based on the morphology and point of entry of the confiscated birds, they were believed to be *Z. simplex* but of unknown subspecific identity and provenance.

To verify the origin of the confiscated individuals, 14 wild-caught samples of *Z. simplex* of known identity and locality were added as reference points. They include samples of the nominate subspecies (*Z. simplex simplex*) from Sichuan, China ( $n=2$ ), and samples of the Southeast Asian subspecies *Z. simplex erwini* from Peninsular Malaysia (Kedah;  $n=5$ ), Borneo (Sarawak;  $n=2$ ) and Singapore (Ubin island;  $n=5$ ) (Fig. 1). Wild samples of *Z. simplex* from across Singapore Island ( $n=22$ ) were also included, with the caveat that they should not automatically be attributed to the Southeast Asian subspecies *Z. s. erwini* because

the Chinese subspecies *Z. s. simplex* is known to have been historically imported into Singapore in large numbers (Chasen 1935; Lim et al. 2019). We supplemented the dataset with 21 captive samples of *Z. simplex* from Jurong Bird Park, Singapore, most of which are derived from donations to the bird park and potentially share the same population-genetic identity as the current wild population on Singapore Island (Lim et al. 2019). We also included morphologically similar species from the region as outgroups, including the Warbling white-eye (*Z. japonicus*) (Hawaii, USA; Taliabu, Indonesia;  $n=3$ ), Ashy-bellied white-eye (*Z. citrinella*) (Rote, Indonesia;  $n=1$ ) and Black-capped white-eye (*Z. atricapilla*) (Sabah, Borneo;  $n=1$ ) (Fig. 1). A total of 87 samples were sequenced for this study (Supplementary Table S1).

### DNA extraction and ddRADseq library preparation

DNA extraction was performed using the DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany) following the manufacturer's protocol with an additional incubation step with RNase A. We prepared reduced representation libraries following a modified double digest restriction-site associated DNA sequencing (ddRADseq) protocol from Peterson et al. (2012) using enzymes EcoRI and MspI (New England BioLabs Inc., MA, USA). The DNA concentration of each pooled library was estimated using a Qubit® dsDNA High Sensitivity DNA Assay Kit (Thermo Fisher Scientific, Massachusetts, USA) and fragment size range was quantified with an Advanced Analytical (AATI) Fragment Analyser. The prepared ddRADseq library was sequenced at NovogeneAIT Singapore on Illumina HiSeq 4000 lanes, producing 150 bp paired-end reads.

### Bioinformatic analyses

The sequencing quality was first assessed using FastQC version 0.11.2 (Babraham Bioinformatics). To filter out low quality bases at the terminal ends, all reads were truncated to 145 bp to obtain a mean phred score  $> 30$  (for  $\geq 99.9\%$  base call accuracy). Raw sequences were demultiplexed and filtered using process\_radtags in Stacks version 2.41 (Catchen et al. 2013). Reads with uncalled bases (-c) or low-quality scores (-q) were discarded. The reads were then aligned against a reference genome of the Silvereye *Z. lateralis melanops* (GenBank assembly accession: GCA\_001281735.1) (Cornetti et al. 2015) in Burrows-Wheeler Alignment tool (BWA) version 0.7.15 within BWA-MEM (Li and Durbin 2010). The aligned sequences were converted and sorted to coordinate order using samtools version 1.9 (Li et al. 2009) for further analyses.

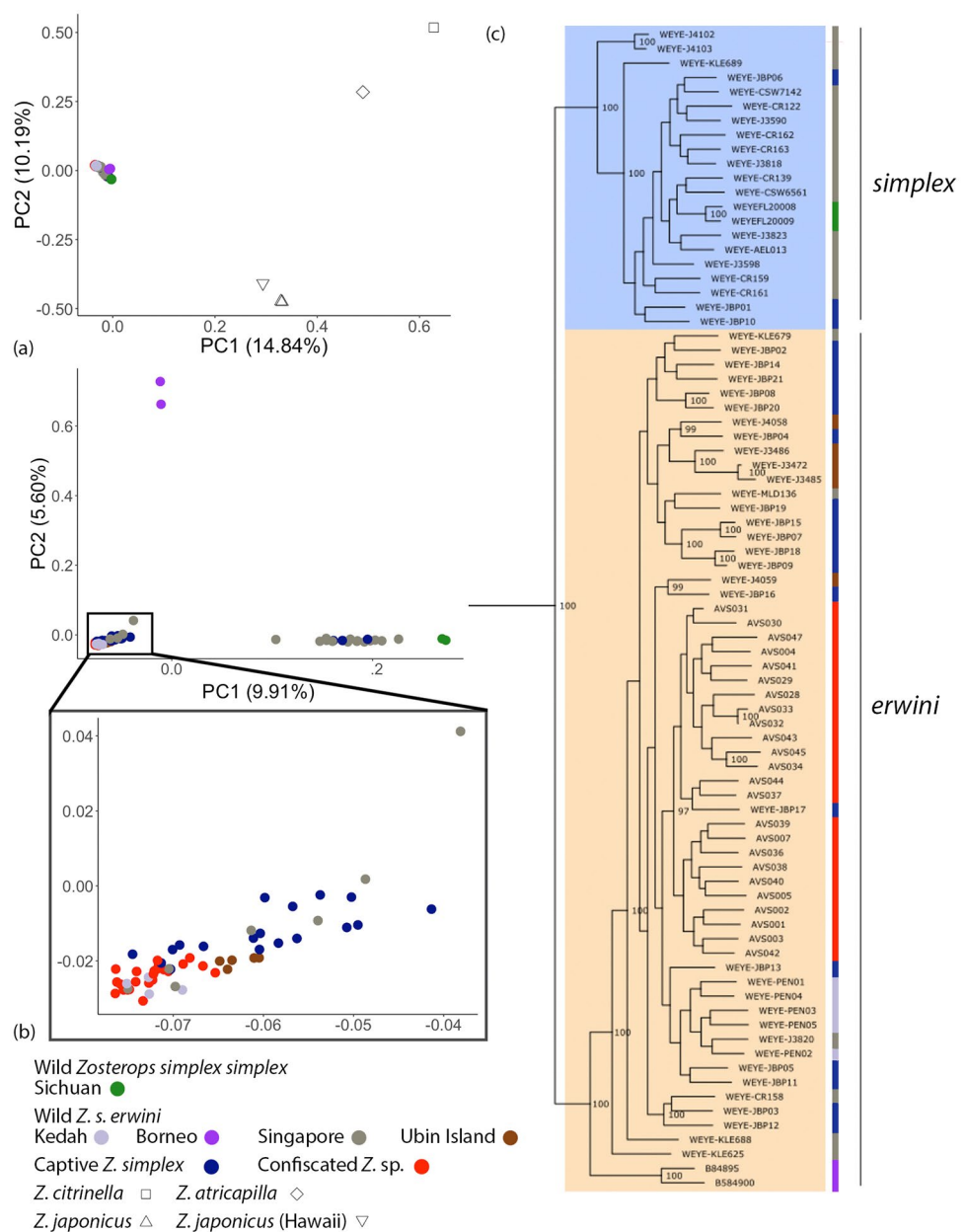
SNPs were called using the pipeline `ref_map.pl` in Stacks version 2.41 and filtered (`-r 0.9 -write-single-snp`) using populations (Catchen et al. 2013). Plink 1.9 was subsequently used to remove SNPs in linkage disequilibrium which were strongly correlated using a simple pairwise threshold of 0.5 with a window size of 25 SNPs in steps of 10 SNPs (Chang et al. 2015). The amount of missing data was also checked for each sample (`--missing`). One *Z. simplex* sample (AVS006) was removed due to its high proportion of missing data.

Principal component analysis (PCA) was conducted on all retained samples in R version 3.5.1 with SNPRelate (Zheng et al. 2012). An initial PCA included all white-eyes in our sampling regime including outgroups to preclude any

misidentification of confiscated samples (Fig. 2a). A separate SNP set was called excluding the outgroup samples (*Z. japonicus*, *Z. atricapilla*, *Z. citrinella*). PCA was performed again for a closer examination of the relationships among the confiscated samples and the confirmed *Z. simplex* samples (Fig. 2b, Supplementary Fig. S1). As the PCA suggested possible admixture between *Z. s. simplex* and *Z. s. erwini* in the introduced population on Singapore Island (see results, Fig. 2), we conducted a population inference analysis using STRUCTURE (Pritchard et al. 2000) at  $K=2$  to characterize potential admixture patterns between *erwini* and *simplex*. We also ran STRUCTURE for  $K=3$  to 6 to investigate potential population substructure. This analysis included the 22 wild samples from Singapore Island as well

**Fig. 2** Genomic population structure of Swinhoe's white-eyes.

**a** Principal component analysis (PCA) plot of all white-eyes including outgroups (7,623 SNPs,  $n=86$ ). **b** PCA plot of all Swinhoe's white-eyes (subspecies *simplex* and *erwini*) including confiscated samples (9,451 SNPs,  $n=81$ ), with the samples within the black box magnified. The percentage of total variation explained by each principal component is shown in brackets. **c** Maximum likelihood tree topology based on 8,979 sequence loci each spanning 100 bp for all 87 samples using RAxML with 100 bootstraps. Outgroups not shown. Bootstrap values lower than 95 are not displayed. Samples are color-coded according to the PCA legend





as the five Ubin Island samples as a reference for subspecies *erwini* and the two samples from Sichuan as a reference for subspecies *simplex*. We applied a burn-in period of 100,000 iterations and 500,000 MCMC simulations. The output was run through CLUMPAK (Kopelman et al. 2015) and summarised.

To generate a phylogeny, a concatenated sequence alignment was assembled using ipyrad version 0.9.65 using the demultiplexed sequences on the same Silvereye reference genome (Eaton and Overcast 2020). The maximum depth was set at 500 (maxdepth 500), the required level of similarity for two sequences to be identified as homologous was raised to 0.90 (clust\_threshold 0.90), the maximum number of mismatches allowed between the barcodes and the sequences was increased to 1 base (max\_barcode\_mismatch 1), the maximum fraction of heterozygous bases allowed in sequences was set at 8% (max\_Hs\_consens 8, 8), and the minimum number of samples that must have data at a given locus for the locus to be retained was adjusted to 80% of the total number of samples (min\_samples\_locus 68). All other parameters were left at default. A total of 8979 loci each spanning 100 bp were harvested for tree building. A maximum likelihood tree was generated using RAXML version 8.2.12 with the model GTGAMMAI and 100 bootstraps (Stamatakis 2014).

## Results

### Sequencing results

A total of 557,921,778 demultiplexed paired-end 150 bp Illumina sequence reads were obtained for 87 individuals, with an average of 6,412,894 reads per sample, including the *Z. simplex* sample (AVS006) with a high proportion of missing data. A total of four SNP sets were called with the Stacks pipeline: (1) all sequenced samples (7,623 SNPs,  $n=86$ ); (2) all confiscated and confirmed *Z. simplex* samples (9,451 SNPs,  $n=81$ ); (3) samples within the *erwini* cluster only (9,370 SNPs,  $n=60$ ); (4) samples from Singapore in combination with select reference samples for *erwini* and *simplex* (7,818 SNPs,  $n=29$ ) (Supplementary Table S2). A total of 8,979 loci each spanning 100 bp were obtained in ipyrad for phylogenomic analyses shared by at least 68 out of 86 individuals (80%).

### Population-genomic structure of Swinhoe's white-eyes

A PCA using 7,623 SNPs and all 87 samples, including outgroups, corroborated that the confiscated samples cluster closely with the Swinhoe's white-eye complex and are

genomically distant from the outgroup white-eye species (Fig. 2a). A closer inspection of a PCA including only the Swinhoe's white-eyes – to the exclusion of outgroups – revealed deep genomic differentiation between the nominate subspecies *simplex* from mainland China (Sichuan) and subspecies *erwini* from Southeast Asia (PC1 in Fig. 2b). Within Southeast Asia, there was a secondary population-genetic division between samples from Borneo and the Malay Peninsula (Kedah and Ubin Island) (PC2 in Fig. 2b), with the confiscated samples clustering most closely with the latter group. PCA results were generally supported by the maximum likelihood tree, which placed the two Bornean samples sister to a large grouping of *erwini* samples consisting of the confiscated birds and the wild samples sourced from around the Malay Peninsula (including Kedah and Ubin Island off Singapore) (Fig. 2c). Within the confines of our sampling regime, the confiscated samples were shown to be genetically most similar to the samples from Kedah, Malaysia (Fig. 2b, c; Supplementary Fig. S1).

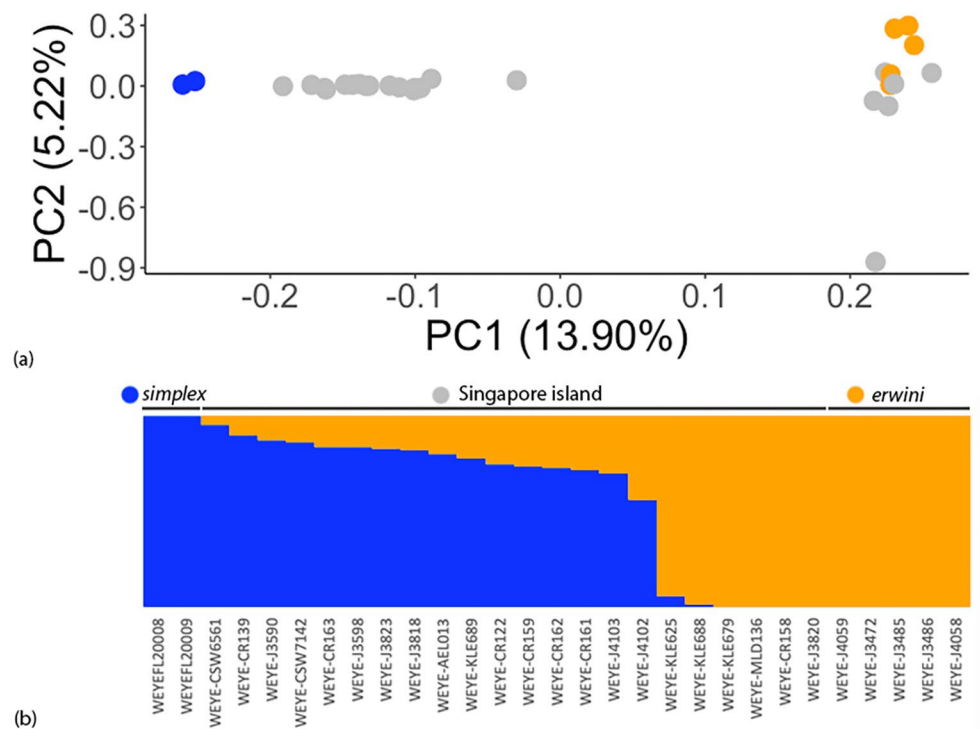
### Genomic structure of the Singapore Island population

The wild individuals sampled from Singapore Island, which are thought to be descended from escaped captive individuals, exhibited a signature of clinal genomic differentiation along the *erwini-simplex* continuum, indicative of possible admixture between the two taxa in Singapore (Figs. 2b and 3). Using STRUCTURE based on 7,818 SNPs ( $n=29$ ), we found 81.8% (18 out of 22) of wild samples from Singapore Island to be admixed with genomic contributions from *simplex* (Fig. 3). The admixture proportion from *simplex* is not equal across individuals, but ranges from 0 to 95.3% (Fig. 3). The captive individuals from Jurong Bird Park (JBP) primarily emerged within the *erwini* cluster, with some also scattered along the *erwini-simplex* cline (Fig. 2b), in congruence with the phylogenetic tree in which 85.7% of captive JBP samples were nested within the *erwini* clade (Fig. 2c). No additional population structure was found in STRUCTURE analyses (Supplementary Fig. S2).

## Discussion

There is limited knowledge currently available about trade routes of illegally traded songbird species in Southeast Asia. Identifying such illegal trade routes assists authorities and conservationists in tackling one of the most important causes of avian biodiversity loss in Southeast Asia. In this study, we identify a likely shift in trade routes in the region and discuss its conservation implications.

**Fig. 3** Genomic population structure of Swinhoe’s white-eyes on Singapore Island. **a** Principal component analysis plot of all wild samples from Singapore Island (shown in grey), with select individuals from Sichuan and Ubin Island (off Singapore) serving as reference points for the genomic profiles of *simplex* (blue) and *erwini* (orange), respectively (7,818 SNPs,  $n=29$ ). The percentage of total variation explained by each principal component is shown in brackets. **b** Consensus plot of  $K=2$  from STRUCTURE based on 7,818 SNPs ( $n=29$ ) illustrating genomic contributions from *simplex* and/or *erwini* into each Singapore Island individual



### Sources of white-eyes for the cage bird trade in Singapore may have changed over time

Singapore Island is not thought to have harboured native populations of Swinhoe’s white-eye in pre-industrial times despite being broadly located within the distribution range of the Southeast Asian subspecies *erwini* (Hume 1879). It was not until the 1930s when Swinhoe’s white-eyes were first seen in Singapore, likely escapees from the bird trade (Chasen 1935). These first white-eyes on Singapore Island were almost certainly of the nominate Chinese subspecies *simplex*, given that the DNA of so many wild modern individuals of Swinhoe’s white-eye on Singapore Island is dominated by a *simplex* genomic signature (i.e., blue in Fig. 3). These white-eyes managed to establish wild populations up until the 1970s, before further intensification of urbanisation across the island led to a dramatic population decline owing to the loss of most forest and mangrove habitats (Wang and Hails 2007). Throughout the 1980s, there were few sightings of Swinhoe’s white-eyes on Singapore Island, but they have slowly become more abundant again with the modern transformation of Singapore into a ‘City in Nature’, with more green spaces that are suitable habitats for these birds (Lim et al. 2020). The rapid increase in population size of Swinhoe’s white-eyes on Singapore Island in the 1980s attests to their origin as escapees from the trade.

Based on the natural distribution of Swinhoe’s white-eye subspecies, the population found on Singapore Island should be expected to belong to the Southeast Asian subspecies

*erwini* (Fig. 1). Being a shelf island that is separated from Peninsular Malaysia by only 800 m of open water across the Johor Straits, with land connections as recent as a few thousand years ago when modern humans were already present, the fauna of Singapore exhibits no known terrestrial endemism and shares all its fauna with adjacent Malaysia. Yet, more than 70% of individuals sampled across Singapore Island possess genomic contributions from the Chinese subspecies *simplex*, most of them with relatively minor contributions from *erwini* (Figs. 2b and 3). Based on our data, the population on Singapore Island is mostly composed of allelic contributions from birds from China, which escaped and spread throughout the island.

In contrast, samples from the adjacent offshore island of Ubin all emerged within the native *erwini* cluster, grouping closely with samples from Kedah, Malaysia, about 940 km to the north, rather than with the majority of samples from Singapore Island, despite being separated by a waterway of only less than 1 km width (Figs. 1 and 2). Although politically part of Singapore, Ubin Island is closer to the Malay Peninsula (Johor) than to Singapore Island, only separated by a few hundred meters of water along the Johor Straits. The population here most likely constitutes a natural remnant of the native population of *erwini* that still exists along Malaysia’s mangrove belt. These results mirror a study on another popular cage bird in Singapore affected by the wild-life trade, the white-rumped shama (*Copsychus malabaricus*), in which the population on Singapore Island was found to be composed of escapees from non-native populations,

while the indigenous subspecies persisted on Ubin Island (Ng et al. 2017). A similar pattern has been demonstrated in the red junglefowl (*Gallus gallus*), whose Ubin population has preserved a genomic profile characterized by less admixture from domestic chickens as compared to the one on Singapore Island (Wu et al. 2020).

All samples recently confiscated from the illegal trade at the Singapore-Malaysia border emerged with a genomic signature consistent with a pure *erwini* origin, most closely resembling our reference samples from Kedah, Malaysia (Fig. 2). This result stands in stark contrast with the identity of most wild birds from Singapore Island. While we cannot completely rule out the possibility of continuing importation of Chinese *simplex*, our results suggest there has been a shift in the origin of trade of Swinhoe's white-eyes in Singapore from China to Malaysia over the last 90 years.

### Genomic provenance of *erwini* in Singapore

If Singapore Island's population of Swinhoe's white-eyes primarily reflects genomic contributions from historically traded individuals from China, the low genomic contribution of Southeast Asian *erwini* alleles to the wild population on Singapore Island may indicate that *erwini* has only recently arrived (Fig. 3; Lim et al. 2019). Two potential sources may account for the *erwini* contribution on Singapore Island: (1) a natural expansion of adjacent *erwini* populations from the Malaysian mainland or Ubin Island, (2) recent escapees from the trade sourced from neighbouring Malaysia.

Our data do not allow inferences on whether some of the *erwini* contributions to wild Singapore Island samples may be due to a recent natural expansion from Malaysia. However, regardless of whether such a natural expansion has occurred or not, our results highlight that Malaysia has become a source for the modern Swinhoe's white-eye trade in Singapore (Nash 1993):

- (1) The individuals confiscated at Woodlands Checkpoint along the Singapore-Malaysia border tightly clustered with *erwini* from Kedah, Malaysia. Their import route via the causeway from Malaysia suggests that Malaysia is a source of the modern trade of white-eyes into Singapore.
- (2) The genetic profile of 85.7% of Swinhoe's white-eyes donated to Singapore's Jurong Bird Park, mostly in the form of abandoned pets, clustered with *erwini* (Fig. 2). These donated birds are likely recent purchases from licensed or unlicensed vendors, thereby indicative of present trade routes. Most of this *erwini* ancestry is likely to have been imported into Singapore along one of its two bridges/causeways to the Asian continent, both from Malaysia. It is possible that some of these donated

birds had been trapped locally, as local Singaporean bird keepers have been caught posting their trapping methods on social media sites. However, given intense anti-trapping law enforcement and high deterrent penalties for poaching in the Republic of Singapore, it is riskier to trap birds in Singapore than to import them illegally, such that local captures most likely represent only a small proportion of the entire white-eye trade in Singapore.

All in all, our results suggest that the white-eyes in Singapore exhibit contributions from *simplex* from China and *erwini* from Malaysia, suggesting that there might have been a shift in the source of Singapore's white-eye trade from China to Malaysia in the course of the last few decades.

### Conservation implications for Swinhoe's white-eye subspecies *erwini*

It is likely that the introduced population on Singapore Island was initially composed predominantly of Chinese birds belonging to subspecies *simplex* (Chasen 1935). As illustrated by our results, recent shifts in trade routes seem to have accounted for modern imports primarily originating from adjacent Malaysia, leading to genomic admixture between newly-arriving *erwini* individuals with the longer-established *simplex* population (Figs. 2 and 3). While modern individuals from Singapore Island remain – on average – genomically closer to *simplex*, levels of genomic admixture vary greatly among individuals. A steady increase of *erwini* alleles can be expected in the main island population for the coming decades, most likely through further accidental or deliberate pet releases, but possibly reinforced by self-colonization from *erwini* populations in adjacent Malaysia or Ubin Island.

On a national level, this renders the native *erwini* population on Ubin Island of some importance in maintaining the genomic integrity of the local subspecies of Swinhoe's white-eye within the Republic of Singapore. The introduced and admixed population on Singapore Island would be considered irrelevant in a conservation context under IUCN criteria. However, the likely future continuation of genomic contributions from Malaysian *erwini* into Singapore Island's population may soon convert it into one whose gene pool increasingly resembles that of native populations from nearby coastal Malaysia.

### Use of genomic methods to aid in tackling illegal wildlife trade

Wildlife forensics is a field that combines the application of scientific techniques and forensic investigations in order to

address crimes or violations related to wildlife. The ability to obtain DNA data from smuggled wildlife samples correspondingly facilitates law enforcement (Wasser et al. 2007; Alacs et al. 2010). Our study adds to a slowly increasing body of literature outlining genomic methods used to trace and uncover illegal trade routes, not only in birds but across the animal kingdom (Nash et al. 2018; Wasser et al. 2007; LaCasella et al. 2021). These methodologies can be useful for other species threatened by the wildlife trade. The ability to identify a source population plays a vital role and is likely to become a game changer in combating illegal wildlife trade, which is a major threat to biodiversity and conservation efforts worldwide.

## Conclusions

With similarities in plumage and song, the subspecies *simplex* and *erwini* of Swinhoe's white-eye are difficult to differentiate in the field. An additional complication arises when introgression occurs, leading to individuals with intermediate biological traits. Our use of a genomic approach allowed us to achieve a level of resolution that would be impossible to gain through phenotypic traits. Our study suggests a potential shift in the source of the white-eye trade in Singapore from China to Malaysia in the course of several decades. This shift has begun to change the genomic composition of the well-studied invasive population of Swinhoe's white-eye on Singapore Island, which originally descended from escaped cage birds from China. Our study highlights the utility of genomic approaches for wildlife forensics to aid in conservation efforts, which will be useful for many agencies.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10592-023-01564-9>.

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**Author contributions** FER and EYXN conceptualised the project. Material collection and funding acquisition was performed by JGHL, RRYO, BTML, AMSW, FER. Data collection was carried out by EYXN and HWC with supervision from MYW and YYT. Formal analyses were performed by HWC and MYW. An initial draft was written by HWC and MYW, with major input from FER, and all authors reviewed and contributed to editing and revising the final manu-

script. MYW and HWC contributed equally and should be considered co-first authors. All authors read and approved the final manuscript.

**Data availability** All sequence data are deposited on Sequence Read Archive (accession number PRJNA1002129).

## Declarations

**Competing interests** The authors declare no competing interests.

**Conflict of interest** The authors have declared that no competing interests exist.

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