

The dynamics of hybridisation between an avian island endemic and a recent coloniser.

Professor Sonya Clegg, University of Oxford.



Research objective:

To determine whether there has been hybridisation between the coloniser, *Zosterops lateralis*, from New Zealand and *Zosterops tenuirostris*, the endemic species of Norfolk Island, and whether this hybridisation has led to introgression between the species.

Sample collection:

Birds were captured in the field using mistnets. The sample included 15 silvereyes and 7 slender-billed whiteeyes from Norfolk Island and 12 silvereyes from the North Island of New Zealand.

Sequencing strategy:

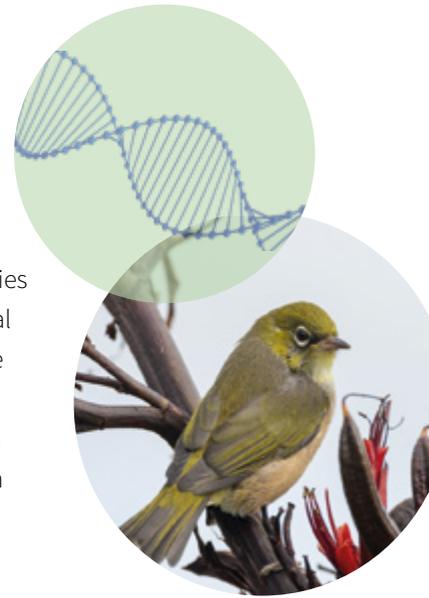
Paired-end 150bp reads on the Illumina NovaSeq 6000 platform at 5X sequencing depth.

Data amount:

>15M SNPs for downstream analysis.

Background:

Hybridisation between species was once thought of as an inconvenience to the biological species concept and an evolutionary dead-end. One good example would be a mule, a hybrid between a female horse and a male donkey, or a liger, a hybrid of a lion and a tiger sometimes formed in a zoo environment. Neither of these hybrids can produce offspring. But in many cases hybridisation produces fertile hybrids, and over the last few decades we have come to appreciate that hybridisation is common but variable in frequency across taxa. Hybridisation may produce new species very quickly when hybrids reproduce with each other while isolated from both parental species. This type of speciation is not terribly common in animals, more so in plants, but we do find cases such as with Darwin's finches where a new lineage called 'Big Bird' – a hybrid of a Cactus Finch and a Medium Ground Finch has been described.



Introgressive hybridisation occurs when there is repetitive backcrossing from the hybrid species to at least one of the parental species, such that alleles are transferred between the parental species via the hybrids. One outcome of extensive introgression is reverse speciation where two forms that may not even be sister taxa merge together. Another outcome is adaptive introgression, where alleles may persist in the recipient parental species because they offer a selective advantage. Examples of this have even been shown in humans, with introgression of alleles from ancient hominids, Neanderthals and Denisovans into modern humans.

The *Zosteropidae* Family:

The *Zosteropidae* family of birds contains 13 genera and 142 species, largely made up of the white-eyes. Members of the family are not well-known for hybridising, - there is some evidence that some southern African species hybridise but in other places, such as east Africa and the Solomon Islands, there is currently no evidence of hybridisation.

“One of the situations where hybridisation might be more common is during the early stages of secondary contact, at the beginning of population expansion. In this kind of situation, you get a large imbalance in population sizes and usually the rare colonisers may not have as many mating opportunities with members of its own species so there may be some choosing of mates from the more common endemic population”, said Sonya during her presentation at Novogene’s 2021 NGS Forum. One of the white-eyes, called the silvereye, *Z. lateralis*, is extremely widespread species and an excellent coloniser of islands of the Indian and Pacific Oceans. It has undergone a recent population expansion, from Tasmania to New Zealand and then to Norfolk Island off the coast of Australia, arriving in 1904. The endemic species of *Zosteropidae* on Norfolk Island, *Z. tenuirostris*, is separated by over 2 million years of divergence from the silvereye.

Results:

Whole genome sequencing uncovered a signal of hybridisation between the two species on Norfolk Island. Using paired-end 150bp sequencing with 5X depth, Sonya and her team ended up with 15 million SNPs for downstream analysis to determine if introgression had occurred after the contact of these two species. Using imputation methods to identify SNPs, and D statistics and analysis of ABBA/BABA patterns, they asked the question “have the hybrids back crossed with parental populations resulting in introgression?”. The answer was yes. A positive D value, indicating an elevation of ABBA allele patterns rather than BABA patterns supports introgression. The next question was “where in the genome is introgression evident?”. Using a sliding window approach with 50kb windows and a 10kb sliding step, they showed that introgressed windows occurred widely across the genome, with interesting candidate genes for features such as plumage colouration and bill size and shape being highlighted in these windows. This genetic evidence aligned with phenotypic features of some museum specimens that are thought to be hybrid individuals.

The D statistic results tell us little about the direction of introgression, the timeframe over which it occurred or whether the species are currently hybridising. To elucidate some of this information Sonya's team compared the likelihood of alternative demographic models. The best supported of these models was one that described ongoing geneflow but at a changing rate over time.

Future work:

Sonya and her team are currently working to characterise the changes in directionality of gene flow over time, and to ask if introgression could be adaptive. In the future, WGS of putative museum specimen hybrids will add to the hybridisation story by comparing their genomes to that of the Norfolk Island endemic species before and after the silverevee colonisation. Further modelling will attempt to incorporate population size changes of both species over time with an aim to understand how directionality of introgression changes with time and population sizes. Sonya and her team are confident that this will develop into some very interesting work with important ecological and conservation implications, particularly for island endemics like *Z. tenuirostris*, that could be impacted by hybridisation after long periods of isolation.



Sonya Clegg is an evolutionary ecologist who received her PhD from the University of Queensland, Australia in 2000, and held postdoctoral and fellowship positions at the University of San Francisco and Imperial College London, and a lectureship at Griffith University Australia, before moving to the University of Oxford where she is an Associate Professor of Evolutionary Ecology.

Her research group studies biodiversity at a range of scales, from macroecological perspectives to genomic variation within populations. She has a long-running interest in the direction and rate of evolutionary responses to novel environments, and in the relative importance of biotic and abiotic drivers of these changes.

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