**Ian Bishop**

**BIO-594\_2014**

**Week 8 – Speciation and hybridization**

**Word Count: 995**

This week we read two articles, each focusing in their own way on rare forms of speciation, Kautt et al. (KE) on sympatric speciation and Lamichhaney et al. (LE) on homoploid hybrid speciation. The theoretical basis for both forms of speciation seems to be well understood, but each set of authors make the point that their topic of focus has little by way of empirical evidence and real world examples.

First, KE set out to confidently classify the speciation that took place in Nicaraguan crater lake cichlids thousands of years ago as a sympatric speciation event. Previous work by the group had determined that this speciation was sympatric, but critical responses, appealing to Coyne and Orr's criteria for this mode of evolution, made the case that KE had not ruled out the possibility that allopatry via a particular form of secondary contact took place. KE took a second pass and conducted a thorough phylogenetic and demographic modeling on RAD-seq data to settle the question, concluding that indeed, two separate sympatric speciation events happened in this region, each resulting from a single colonization event, followed by another wave of colonization from the source population, *then* finally by sympatric speciation. They note that their findings still do not pass Coyne and Orr's last criterion (“no historic phase of geographic isolation”), but that this is more a semantics argument than it is substantial. While it is true that some genetic variation developed between the first and second waves of cichlid immigrants, speciation took place *after* both waves of immigrants were genetically completely homogenized within each crater lake. This pre-speciation isolation between immigrant populations may have provided the raw materials for sympatric speciation to proceed, but the species diverged from one undifferentiated population in one specific place, which most would agree constitutes sympatric speciation.

There were several instances of analytical redundancy implemented in this study. Where this occurred it usually was when tools that were able to detect different levels of complexity  (e.g. phylogenetic trees provide topological relationships and even migration events, but don't allow you to estimate changes in population size and demographic models). Elsewhere, it seems they wanted to cover their bases, even if the second method came up short (e.g. f3 statistics vs treemix). This type of double checking seem particularly important in the context of these authors replying to previous critiques of their work.

Next, LE examined a very interesting case in which a single Darwin finch migrated from one Galapagos island to another, mated with a female Darwin finch from another species, and founded a heavily inbred (completely endogenous beyond f1 generation) yet very fit population of hybrid individuals spanning 6 generations to date. LE used both quantitative morphometrics and whole genome sequencing to sort out the pedigree of this population as well as the potential reasons for its ecological success/fitness. As expected, homozygosity increased with each generation, as did nucleotide diversity. The authors claimed, referencing only an entire book on the Daphne Island finches, that the success hybrid lineage’s success was likely due to its beak morphology, so they looked at that. The hybrid progeny exhibited transgressive segregation in beak phenotype, which was intermediate in size between the two parent species and, importantly, did not overlap in key features, such as depth and length, with other Daphne Island finches. The authors proposed that an available unused food source befitting this beak form led to their success, and highlighted the importance of chance events for unusual speciation events of this sort.

Because both types of speciation were considered rare (at least in empirical examples), I was curious about homoploid hybrid speciation (HHS) and looked into it a little bit more. After reading LE, I was also confused by the fact that the context for the study was HHS but I found it hard to follow how they argued this form of speciation over other types, if they did at all. Looking elsewhere, it seems that the only thing people can agree on is that HHS must develop out of hybridization and that the process must not result in whole genome duplication, i.e. the speciation event cannot change ploidy (Feliner et al. 2017). Schumer et al. (2014) has proposed three criteria that must be met to apply the term HHS. First, there must be a strong RI mechanism between the hybrids and parental species individuals. Although the stick it at the end, LE do point out that a strong barrier exists in the hybrid's singing behavior. Second, there must be genetic evidence of hybridization, which yes, LE did also show. And third, the isolation mechanisms must derive from the hybridization. I think they again could use the distinct hybrid bird song as evidence here. My point in bringing this up is that the paper seems more focused on examining the success of the hybrid lineage than intent on documenting an example of HHS that stands up to scrutiny. Even if you think the Schumer criteria are too narrow, as Feliner et al. do, LE did not even mention ploidy once (though I’m sure they would have if hybridization changed it). This is fine, but I think framing strategy of the paper doesn't quite fit the narrative structure they lay out.

Overall, major differences in the approaches each paper took had to do with both the genomic resources at hand and the temporal scale of the populations they wanted to examine. KE used reduced genomic data from modern cichlid populations to infer demographic processes of the geological past, whereas LE collected complete genomic data for nearly the entire 6 generation hybrid population they examined. Their genomic dataset was less a sample of the population than the population itself. They also took advantage of a massive genomic dataset of all of the non-hybrid finch species on the Galapagos, which helped them to sort out exactly which species the founding male was, as well as to test specific genes previously associated with beak phenotype.

**Works Cited:**

Nieto Feliner, G., Álvarez, I., Fuertes-Aguilar, J., Heuertz, M., Marques, I., Moharrek, F., … Villa-Machío, I. (2017). Is homoploid hybrid speciation that rare? An empiricist’s view. *Heredity*, *118*(6), 513–516. <https://doi.org/10.1038/hdy.2017.7>

Kautt, A. F., Machado-Schiaffino, G., & Meyer, A. (2016). Multispecies Outcomes of Sympatric Speciation after Admixture with the Source Population in Two Radiations of Nicaraguan Crater Lake Cichlids. *PLOS Genetics*, *12*(6), e1006157. <https://doi.org/10.1371/journal.pgen.1006157>

Lamichhaney, S., Han, F., Webster, M. T., Andersson, L., Grant, B. R., & Grant, P. R. (2018). Rapid hybrid speciation in Darwin’s finches. *Science*, *359*(6372), 224–228. <https://doi.org/10.1126/science.aao4593>

Schumer, M., Rosenthal, G. G., & Andolfatto, P. (2014). How common is homoploid hybrid speciation?. Evolution, 68(6), 1553-1560.