

Uncovering endemism in a lake of invasive species introgression

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Species distributions are rapidly being altered by human globalisation and movement. As species are moved across biogeographic boundaries, human-mediated secondary contacts between historically allopatric taxa may promote hybridisation between closely related native and introduced species. The outcomes of hybridisation are diverse from strong reproductive barriers to gene flow to genome-wide admixture that may enhance (Fitzpatrick et al., 2010; Mesgaran et al., 2016; Valencia-Montoya et al., 2020) or impede (Kovach et al., 2016) invasive spread. For native species, introgressive hybridisation may disassemble locally adapted genomes, and in extreme cases, extensive asymmetric introgression may lead to the “genomic extinction” of endemic diversity (Rhymer & Simberloff, 1996; Todesco et al., 2016). Undoubtedly, introgressive hybridisation can rapidly alter the evolution of introduced and endemic populations and is a major conservation issue (Leitwein et al., 2020), with the greatest potential consequences on small, range-restricted native populations where introduced species may reach higher relative densities (Currat et al., 2008). In this issue of *Molecular Ecology*, Blackwell et al. (2020) explore the history of divergence and admixture between the highly invasive Nile tilapia, *Oreochromis niloticus*, and a recently discovered *Oreochromis* lineage that is endemic to the coastal lakes of southern Tanzania. *Oreochromis* tilapias belong to the African cichlids and the most diverse family of vertebrates (Cichlidae), with almost 2000 species inhabiting the Great Lakes and river environments of Eastern Africa (Kocher, 2004; McGee et al., 2020). By analysing previously unrecognised cichlid diversity from southern lakes, Blackwell et al. (2020) provide novel evidence for how introgressive hybridisation with introduced species can alter native genetic makeup, illustrating the potential susceptibility of Tanzania's endemic biodiversity to genetic threats from introduced taxa.

Combining microsatellite genotyping and whole genome resequencing with morphological analyses, Blackwell et al. (2020) show that southern populations of *Oreochromis korogwe* within lakes Rutamba, Nambawala and Mitupa are genetically distinct from allopatric *O. korogwe* populations in northern Tanzania, as well as other *Oreochromis* congeners studied within the region. Furthermore, substantial divergence in morphological traits (e.g., body depth, fin dimensions and eye size) between genetically pure-bred southern and northern *O. korogwe* populations implies possible ecological divergence and local adaptation to southern regions. Altogether, these results make

a strong case to recognise newly discovered southern *O. korogwe* populations as a distinct evolutionarily significant unit that should be managed independently from northern ones.

Unfortunately, however, Blackwell et al. (2020) provide evidence that recent introductions of invasive Nile tilapia, *O. niloticus*, into isolated southern watersheds have resulted in repeated hybridisation with endemic *O. korogwe* populations at various degrees among sampled lakes. *O. niloticus* is a globally cultivated aquaculture species and is of prime importance for food security in Africa. Although native to Tanzania within the Lake Tanganyika catchment, deliberate

translocations for inland aquaculture and accidental escapes have promoted *O. niloticus* establishment outside of its natural distribution (Shechonge et al., 2018). Today, the Nile tilapia has been introduced throughout Africa with potential negative effects on receiving communities, including habitat alternation and competitive displacement of native taxa (Canonico et al., 2005). *O. niloticus* also hybridises with multiple *Oreochromis* species where congeners are sympatric (Deines et al., 2014; Shechonge et al., 2018). Blackwell et al. (2020) infer that 6–29% of individuals sampled in southern lakes comprise hybrids, with levels of individual admixture from *O. niloticus* varying between 12 and 85% (genomic mean). These results suggest the presence of early-generation hybrids or backcrossed individuals probably resulting from recent admixture. Moreover, whole genome sequencing on a subset of 12 individuals revealed that the impact of *O. niloticus* introgression is variable across the genome, whereby morphologically “pure” southern *O. korogwe* genomes are a mosaic

of ancestry originating from introduced *O. niloticus*, further confirming that hybrids are fertile and reproductively viable.

The growing availability of genomic data for invasive species and closely related lineages (Bay et al., 2019; Valencia-Montoya et al., 2020) suggests that the consequences of introgressive hybridisation are highly variable across the genome and thus difficult to predict (Abbott et al., 2013). For closely related native and introduced taxa, such as *Oreochromis* congeners, understanding hybridisation outcomes is further complicated by recent divergence histories and genome-wide ancestral polymorphisms that may obscure signatures of contemporary introgression (Popovic et al., 2020). Applying a phylogenomic approach, Blackwell et al. (2020) partly disentangle these processes. They quantified admixture history between *Oreochromis* species using a tree weighting approach that counts alternative species topologies estimated from consecutive genomic intervals, where discordant phylogenies can result from ongoing lineage sorting or

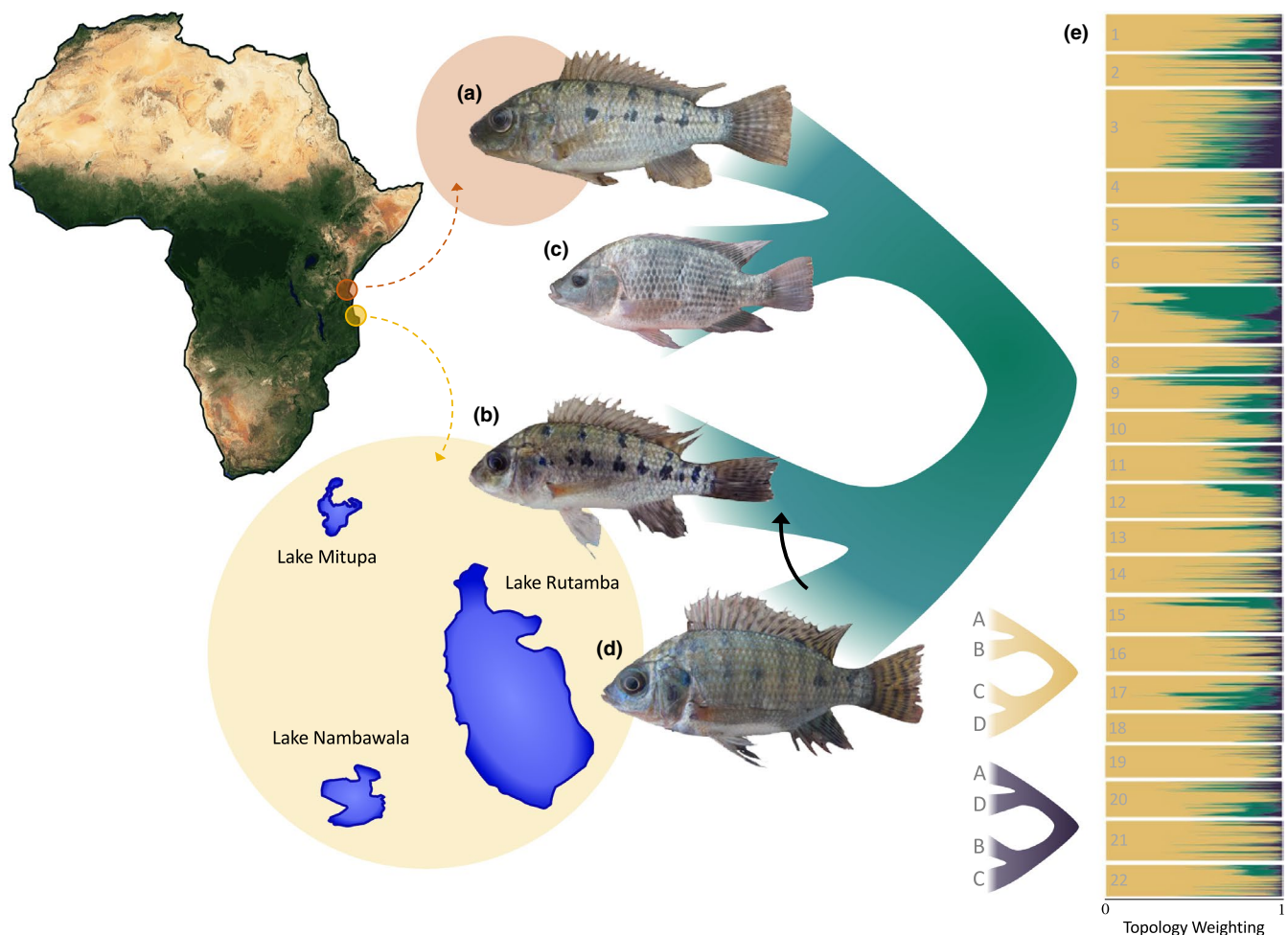


FIGURE 1 Females of *Oreochromis* species sampled in Tanzania and genome-wide species relationships inferred with TWISST. (a) Northern lineage *Oreochromis korogwe* from the Pangani region; (b) southern lineage *O. korogwe* sampled from lakes Rutamba, Nambawala and Mitupa; (c) parapatric congener *O. urolepis*; and (d) invasive Nile tilapia, *O. niloticus*. (e) Phylogenomic species relationships across 23 linkage groups, where colours corresponding to relative weightings for three alternative species topologies; modified figure 5g from Blackwell et al. (2020). Genomic regions (e.g., LG7, LG8, LG17) showing high relative weightings for the green discordant topology grouping native southern *O. korogwe* with invasive *O. niloticus* (ACBD) are consistent with *O. niloticus* introgression into the southern *O. korogwe* native genetic background. The consensus species phylogeny (ABCD) and the alternative discordant topology (ADBC) for the four taxa are shown in yellow and purple

introgressive hybridisation (Martin & Van Belleghem, 2017). While the consensus species topology grouping northern and southern *O. korogwe* as sister taxa was the dominant genomic relationship, discordant topologies showed multiple frequency peaks and localised clustering, especially within three linkage groups (Figure 1). Although gene tree discordance can occur through incomplete lineage sorting, a substantial excess in the topology grouping invasive *O. niloticus* together with native southern *O. korogwe* suggests their recent admixture. In contrast, similar patterns were not apparent when *O. korogwe* from a northern waterbody, where *O. niloticus* is not introduced, were compared with *O. niloticus*. Thus, by leveraging knowledge of species distributions and utilising multispecies comparisons, Blackwell et al. (2020) show that *O. niloticus* introgression is heterogeneous across the southern *O. korogwe* genome and that admixture probably occurred after their split from northern *O. korogwe* (Figure 1). Another intriguing outcome of the genome scans was that southern *O. korogwe* shared similar regions of low differentiation with a parapatric congener, *Oreochromis urolepis*, highlighting the possibility of historical hybridisation and the complex nature of endemic demographic histories within the southern lakes.

It is now accepted that hybridisation is a prominent feature of the evolutionary process, with many species experiencing periodic contact and gene flow throughout their evolutionary histories (Roux et al., 2016). Indeed, and somewhat in sharp contrast with the reported negative effects of contemporary hybridisation during species invasions, it is clear that historical introgressive hybridisation and admixture have played a crucial role in the explosive adaptive radiations that characterise the evolution of cichlid diversity in Africa (Kagawa & Seehausen, 2020; McGee et al., 2020; Meier et al., 2017). Such complex speciation histories are already difficult to resolve and recent admixture between introduced and native taxa may exacerbate the problem. Blackwell et al. (2020) overcome this challenge by focusing on the least admixed regions of the southern *O. korogwe* genome to characterise their divergence from northern populations. The authors estimate that northern and southern *O. korogwe* lineages have been diverging for ~140,000 years as isolated populations, suggesting that their present day disjunct distributions (~500 km apart) probably resulted from natural long-distance colonisations or historical range contractions. Importantly, the genetic and morphological distinctiveness of southern *O. korogwe* from northern populations supports the recognition of this lineage as an evolutionarily significant unit of conservation. With clear signatures of genome-wide introgression and no apparent signs of hybridisation at the morphological level for sequenced southern individuals, Blackwell et al. (2020) present an example of how invasive introgression can quickly alter native genetic backgrounds, with potential impacts on their local adaptation.

Invasive species hybridisation with native taxa has long been recognised as a major conservation issue (Rhymer & Simberloff, 1996). Yet, genome-enabled studies of aquatic invasive species and especially anthropogenic hybrid zones are still rare relative to the scope of the problem. While a number of cichlid genomes have recently been sequenced (McGee et al., 2020; Ronco et al., 2020), *O. niloticus* is among the few invasive species for which a

linkage-informed genome assembly has been developed (Conte et al., 2019; Tao et al., 2021). Enabled by high-quality genomic resources, the study by Blackwell et al. (2020) provides clear evidence for the evolutionary distinctiveness between southern and northern *O. korogwe* populations, as well as the occurrence of recent introgressive hybridisation from invasive *O. niloticus*. The use of 13 microsatellites, however, does not offer genome-wide resolution needed to rigorously evaluate the proportion of various hybrid classes among admixed individuals. Additionally, few resequenced individuals ($n = 3$ per group) and low genomic coverage (5×) limits the accuracy of differentiation estimates. More comprehensive genomic investigations would provide deeper understanding of both the evolutionary history of *O. korogwe* as well as the dynamics of hybridisation. Modelling approaches that allow inferences of historical demography would improve estimates of divergence times and the role of possible past hybridisation events in shaping *O. korogwe* diversity (Fraïsse et al., 2021; Rougemont et al., 2020). Similarly, new methods that take advantage of haplotype information could be used to examine recent histories of gene flow, selection, and the evolutionary outcomes of hybridisation (either positive or negative) at local genomic scales that may inform the timing of anthropogenic admixture that is relevant for addressing conservation issues (Leitwein et al., 2020).

As new genomic studies of introduced species elucidate the frequency and consequences of anthropogenic hybridisation (Blackwell et al., 2020), they also raise ethical and practical considerations for endemic species conservation. The management of hybridising taxa is a contentious topic (Allendorf et al., 2001; Hamilton & Miller, 2016; Jackiw et al., 2015), with some authors advocating for a gene-level framework for managing introgressed populations and tracking the dispersal of invasive genes through novel habitats (Crispo et al., 2011; Petit, 2004). Indeed, incorporating genomic tools into invasive species management will be essential for quantifying the risks of introgressive swamping in small and isolated endemic populations. For the case of tilapia species, restocking of *O. niloticus* and other commercially significant taxa for aquaculture could facilitate introductions into new waterways, and the widespread genetic impact of *O. niloticus* introductions is evident in the finding of a *O. placidus* × *O. niloticus* hybrid in the relatively poorly studied Ruvuma catchment (Blackwell et al., 2020). With the possibility that northern *O. korogwe* populations are also genetically distinct from each other, the evolution of more unrecognised diversity in Tanzanian watersheds could be influenced by hybridisation with introduced lineages. While understanding admixture timing and the processes modulating genomic introgression rates will require more in-depth analyses of hybrid genomes, the study by Blackwell et al. (2020) illustrates how genomic data from few sampled individuals can uncover endemic lineages at risk of losing diversity and provides a first glimpse of how anthropogenic hybridisation has shaped their evolution.

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