NEWS AND VIEWS

PERSPECTIVE

Magadi tilapia ecological specialization: filling the early gap in the speciation continuum

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Cichlid fish are well known for their high speciation rates, which are usually accompanied by spectacular and rapid diversification in eco-morphological and secondary sexual traits. This is best illustrated by the famous repeated explosive radiations in the African Great Lakes Tanganyika, Malawi and Victoria, each lake harbouring several hundreds of mostly endemic species. Correspondingly, cichlids diversified very rapidly in many other lakes across their range. Although the larger radiations, unparalleled in vertebrates, are certainly the most intriguing, they are also the most intricate and difficult to address because of their complex nature. This is where smaller, simpler systems may prove to be the most useful. In this issue of Molecular Ecology, Kavembe *et al.* (2016) report very recent genetic diversification accompanied by ecological specialization in cichlids of the small and ecologically extreme Lake Magadi, in Kenya. Combining geometric morphometrics, stable isotope analysis, population genomics using RADSeq data and coalescent-based modelling techniques, the authors characterize the eco-morphological differences between genetically distinct populations of Magadi tilapia (*Alcolapia grahami*), which are consistent with the different environmental conditions they experience, and infer their history of divergence. The simplicity of the focal system and the use of a multidisciplinary approach make this work particularly important for our understanding of the early stages of speciation, in both cichlids and other organisms.

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### Cichlid diversification within small soda lakes: the Magadi tilapia

Soda lakes are extreme ecosystems characterized by alkaline waters. Lake Magadi, in Kenya, is one such lake which is inhabited by a single cichlid species, the Magadi tilapia. Using diverse approaches, Kavembe *et al.* (2016) provide relevant insights about ecological specialization and genetic differentiation in this species (Fig. 1). First, they corroborate a previous study (Kavembe *et al.* 2014) suggesting the existence of three genetic clusters: one confined to Little Magadi (LM), a smaller satellite of Lake Magadi, and two other to different lagoons within the main lake; LM shows higher genetic differentiation relative to the other two clusters. Second, and in agreement with these patterns, they reveal measurable body shape differences between representatives of each genetic cluster, probably reflecting specialized feeding behaviour, which is supported by isotope analysis. Third, powerful simulation tools (Excoffier *et al.* 2013) suggest (i) a simultaneous split of the three populations ~1100 generations ago, possibly after a major flood, (ii) absent to very low gene flow between LM and Lake Magadi populations, contrasting with the higher levels between populations within the latter, conceivably associated with heavy rains allowing migration between lagoons and (iii) an increase in the effective population size of LM, perhaps reflecting adaptation to a new niche. Finally, a genome scan suggests that genome-wide differentiation is more homogeneous between Lake Magadi populations than between these and LM, presumably because of higher levels of gene flow and more stable demography in the former. Kavembe *et al.* (2016) conclude that this rapid trophic diversification accompanied by morphological and genetic divergence is compatible with early stages of ecological speciation.

Below, we highlight aspects of this study that are especially useful for gaining insights about the processes shaping diversification.

Speciation is easier to study in simple systems

Paradoxically, as Kavembe *et al.* (2016) point out, the most spectacular of the cichlid adaptive radiations are precisely the most difficult to study. Choosing reduced, tractable units is not straightforward because all species in a lake radiation are potentially interconnected by a recent common history of divergence and admixture. Such complexity makes it hard to evaluate the relative contributions of geographical isolation, ecological and trophic specialization, sexual selection and hybridization as drivers of speciation. This is certainly why the best documented cases of sympatric ecological speciation in cichlids come from smaller and not so speciose lakes (Schliewen *et al.* 1994; Barluenga *et al.* 2006).
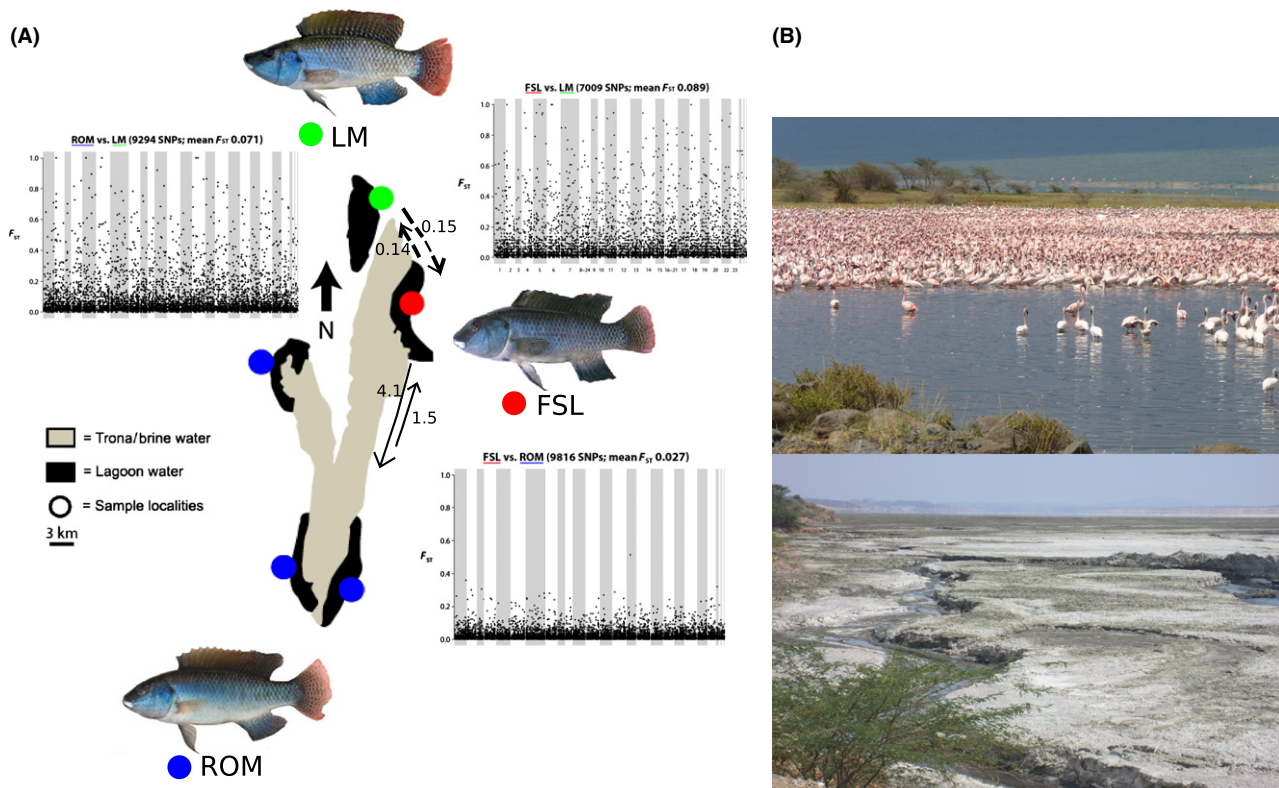
Fig. 1 (A). Map of Lake Magadi, sampled locations and patterns of genomic differentiation and gene flow among Magadi tilapia populations inferred by Kavembe *et al.* (2016). Each dot represents a sampled location. Dots are coloured according to their population of origin (as inferred from genetic analyses): LM, Lake Little Magadi; FSL, Fish Springs Lagoon; ROM, rest of Lake Magadi. Photographs of representative fish of the population sampled are shown, as well as plots depicting genome-wide F_{st} between populations pairs of Magadi tilapia using RADseq loci and the Nile Tilapia linkage groups as reference. Arrows represent the inferred number of migrants per generation according to the model receiving the highest support among 63 tested scenarios. No migration between LM and ROM was inferred. (B). Photographs of Lake Magadi. Top: An example of a lagoon (shown in black in A). Bottom: Trona (deposits of sodium sesquicarbonate dihydrate) which act as barriers for fish migration among lagoons (shown in grey in A). All images in A were adapted, with permission, from Kavembe *et al.* 2016. (B) Photograph credits: Prof. Michael Schagerl (top); Prof. Gudrun De Boeck (bottom).

Likewise, the study by Kavembe *et al.* (2016) draws upon a simple geographical setting, a relatively well-known geological record and a single but phenotypically diverse species, reducing the complexity usually associated with large radiations to a manageable number of parameters, while keeping in sight the big picture of cichlid speciation.

Model-based inference is essential for evaluating speciation modes

In recent years, statistical modelling in divergence population genetics has experienced tremendous advances, tracking the growing availability of more comprehensive and informative data sets (Sousa & Hey 2013; and refs. therein). For the most part, cichlid speciation research has not yet taken full advantage of this progress (but see, e.g. Won *et al.* 2005; Elmer *et al.* 2013). Kavembe *et al.* (2016) on the other hand apply sophisticated modelling techniques based on the site frequency spectrum calculated over thousands of single nucleotide polymorphisms (SNPs). Such

frequency data are sensitive to demography and divergence history, and simulation methods can be used to evaluate the fit of complex evolutionary models and estimate parameters of interest. Using these methods, Kavembe *et al.* (2016) make statistically supported inferences regarding splitting events, population size changes and gene flow between Magadi tilapia populations which would not be possible using conventional summary statistics or other traditional methods. Therefore, this study clearly demonstrates the power of combining genomic data with statistical modelling in speciation research, even in less simple contexts provided enough data are used.

Interdisciplinary approaches for a multifactorial problem

The ecological causes of speciation cannot be investigated by looking only at genetic information; integrating genetics with complementary approaches is required so that the link between genotypes, phenotypes and the environment

is uncovered (Faria *et al.* 2014). Kavembe *et al.* (2016) combine genetic data with a characterization of the phenotypes, the target of natural selection, and with a stable isotope analysis to investigate dietary differences between populations. Furthermore, they try to identify outlier loci associated with the eco-morphological differences and, using simulations, they test complex scenarios of divergence that could explain the genome-wide patterns of differentiation between populations, setting ground for future evaluation of more specific hypotheses.

Filling the gap in the ecological divergence continuum

Ecological speciation studies tend to focus on systems with established phenotypic differentiation, typically maintained by some degree of reproductive isolation. This focus can create a bias towards studying 'older' systems (Faria *et al.* 2014). Kavembe *et al.* (2016) make a rare report of remarkably incipient differentiation that fills an important gap in our knowledge on the early stages of ecological speciation. From this point of view, it becomes even more important to gather additional evidence from this system: (i) Can phenotypic plasticity be ruled out? (ii) What is the level of reproductive isolation between populations? (iii) Is the apparent lack of gene flow between the two lakes the result of geographical barriers or the product of selection against immigrants and/or potential hybrids? (iv) What is the genetic basis of eco-morphological adaptations? Addressing these questions will allow a more comprehensive view of the chain of events and processes driving the development of reproductive barriers across the different stages of the speciation continuum.

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References

Barluenga M, Stolting KN, Salzburger W, Muschick M, Meyer A (2006) Sympatric speciation in Nicaraguan crater lake cichlid fish. *Nature*, **439**, 719–723.

Elmer KR, Lehtonen TK, Fan S, Meyer A (2013) Crater lake colonization by neotropical cichlid fishes. *Evolution*, **67**, 281–288.

Excoffier L, Dupanloup I, Huerta-Sanchez E, Sousa VC, Foll M (2013) Robust demographic inference from genomic and SNP data. *PLoS Genetics*, **9**, e1003905.

Faria R, Renaut S, Galindo J *et al.* (2014) Advances in ecological speciation: an integrative approach. *Molecular Ecology*, **23**, 513–521.

Kavembe GD, Machado-Schiaffino G, Meyer A (2014) Pronounced genetic differentiation of small, isolated and fragmented tilapia populations inhabiting the Magadi Soda Lake in Kenya. *Hydrobiologia*, **739**, 55–71.

Kavembe GD, Kautt AF, Machado-Schiaffino G, Meyer A (2016) Eco-morphological differentiation in Lake Magadi tilapia, an extremophile cichlid fish living in hot, alkaline and hypersaline lakes in East Africa. *Molecular Ecology*, **25**, 1610–1625.

Schliewen UK, Tautz D, Pääbo S (1994) Sympatric speciation suggested by monophyly of crater lake cichlids. *Nature*, **368**, 629–632.

Sousa V, Hey J (2013) Understanding the origin of species with genome-scale data: modelling gene flow. *Nature Review Genetics*, **14**, 404–414.

Won Y-J, Sivasundar A, Wang Y, Hey J (2005) On the origin of Lake Malawi cichlid species: a population genetic analysis of divergence. *Proceedings of the National Academy of Sciences USA*, **102**, 6581–6586.

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