Midas cichlids are a Central American species flock of the genus *Amphioptus* that inhabit a series of freshwater lakes and rivers in western Nicaragua (Figure 1). This system centres around two large lakes of tectonic origin (Lake Nicaragua and Lake Managua) that formed a single lake ~500,000 years ago, but since have been only intermittently connected by the Tipitapa River. More recent volcanic activity along the Central American Volcanic Arc has created several young and hydrologically isolated crater lakes in the region (Kutterolf, Freundt, Perez, Wehrmann, & Schmincke, 2007). The oldest of these crater lakes is the 24,000-year-old Lake Apoyo, which serves as the study site in Raffini, Schneider, Franchini, Kautt, and Meyer (2020). It is estimated that ancestral cichlids arrived in the Nicaragua Lake system around 100,000 years ago, with the two larger and older lakes subsequently serving as the source of founding populations for the crater lakes as they formed (Barlenga & Meyer, 2010). Mitochondrial data derived from individuals from Lake Apoyo point to a single colonization event of a small number (~260; Kautt, Machado-Schiaffino, & Meyer, 2016) of benthic individuals (Barlenga & Meyer, 2004). Similar to the African cichlids, cichlids in the Nicaragua Lake system rapidly speciated in parallel
within each crater lake after colonization. With an average depth of only 15 m, Lake Nicaragua does not host a limnetic morphotype. On the other hand, Lake Apoyo reaches at least 125 m and hosts six described endemic species of Midas cichlid, including five benthic and a single limnetic species. Similar divergences along benthic/limnetic morphotypes have been observed in several freshwater taxa, including three-spined sticklebacks (Schluter & McPhail, 1992), African cichlids (Hulsey, Roberts, Loh, Rupp, & Streelman, 2013), salmonids (Langeland, L'Abée-Lund, Jonsson, & Jonsson, 1991) and whitefish (Bernatchez, Chouinard, & Lu, 1999). Research shows that niche divergence along the benthic/limnetic axis alleviates competition for food resources and that a more streamlined (elongated) morphology typifies the limnetic morphotype, including Amphiophus zaliosus in Lake Apoyo.

Comparing individuals of a limnetic/benthic species pair from Lake Apoyo (A. zaliosus/A. astorquii; Figure 1) Raffini et al. (2020) investigate differences in physiology and gene expression profiles. Recently diverged (<2,000 generations; Kautt et al., 2016), these two species demonstrate significant ecological (Table 1; Kautt, Machado-Schiaffino, & Meyer, 2018) but very limited genetic differentiation with low but significant pairwise $F_{ST}$ values recorded ($F_{ST} = 0.089$ based on mitochondrial DNA, Barlengua & Meyer, 2010). A more recent data set based on single nucleotide polymorphisms indicates five genetic clusters among the six recognized species in Lake Apoyo, with both A. zaliosus and A. astorquii unambiguously assigned to distinct clusters (Kautt et al., 2016). Using body shape analysis, the authors confirm the distinct morphological traits of each species. They then examined how swimming ability and $O_2$ consumption differed between the species during swimming trials (critical/sustained swimming speed and sprinting [burst swimming]), and generated transcriptomic

<table>
<thead>
<tr>
<th>Interspecific differences</th>
<th>Deep-bodied vs. streamlined</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat</td>
<td>Benthic vs. limnetic</td>
</tr>
<tr>
<td>Diet</td>
<td>Algae/molluscs vs. insects/fish; distinct stable isotope signatures</td>
</tr>
<tr>
<td>Microbiome</td>
<td>Distinct gut microbiomes</td>
</tr>
<tr>
<td>Mating</td>
<td>Assortative mating</td>
</tr>
<tr>
<td>Genetics</td>
<td>Shallow divergences but form distinct genetic clusters</td>
</tr>
</tbody>
</table>

FIGURE 1 Species and area of study in Raffini et al. (2020)
profiles for individuals after sustained swimming speed and at rest. They determined that while the two species did not differ in sprinting ability or O$_2$ consumption at rest, the limnetic $A$. zaliosus, with its more streamlined shape, demonstrated greater ability for sustained swimming with higher O$_2$ demand compared to the benthic $A$. astorquii. Swimming ability and O$_2$ intake were correlated with differences in gene expression patterns in gills, and to a lesser extent in white muscle tissue. Together, the data indicate that the streamlined morphology of $A$. zaliosus was probably the result of selection for increased cruising performance in the open water habitat. Importantly, the streamlining greatly diminished its nuchal hump, a secondary sexual trait in male Midas cichlid fishes that is strongly preferred by females, indicating a trade-off between physiological efficiency and reproductive success.

The use of gene expression profiles to study ecological speciation has increased over the past decade and can be used to reveal the link between morphology, physiology and adaptation. In some cases, differences between conspecific populations or between recognized species correlate with processes that underlie adaptive divergence. For instance, populations of the North American lake whitefish Coregonus clupeaformis display two morphotypes: normal and dwarf. Using microarrays to study sympatric populations in two separate lakes in parallel, Derome, Duchesne, and Bernatchez (2006) revealed similar patterns of differential gene expression in white muscle tissue of the two morphotypes. They found significant over-expression of genes involved in metabolism and regulation of muscle contraction in dwarf whitefish in both lakes. Raffini et al. (2020) take this a step further by examining gene expression in individuals immediately after exercise. They showed significant differences in gene expression profiles of limnetic and benthic species during both rest and exercise phases, with the greatest number of affected genes in gills during exercise. Some of the differentially expressed genes they identified have been conclusively linked with vital functions in fish. In particular, during exercise, three genes (fh11b, tph1a and and cart2) were down-regulated in the gills of limnetic $A$. zalio-
sus when compared to its benthic counterpart. Calcium uptake has been shown to be negatively correlated with the expression of fh11b in gills, where calcium regulation occurs in fish (Pillar et al., 2017). During hypoxic conditions, such as in the benthic environment of Lake Apoyo, tph1a is down-regulated. This gene mediates oxidative stress responses, including the expression of serotonin, which in turn activates branchial vasoconstriction in their gills to conserve oxygen (Rahman & Thomas, 2014). Finally, the cart2 gene is an appetite and metabolic regulatory gene which has been reported to be up-regulated after feeding and down-regulated during fasting in many fish species (Rønnestad et al., 2017). The limnetic $A$. zaliosus of Lake Apoyo feed on fish and insects, as well as their larvae, which are evasive and patchily distributed. The variation in gene expression and the associated differences in O$_2$ demand and optimal cruising speeds documented by Raffini et al. (2020) may serve as adaptations to the specific diets and microhabitats of these two morphotypes. By demonstrating transcriptional differences, their study provides new evidence that the demonstrated physiological changes may be heritable traits with adaptive significance toward increased feeding efficiency for each species’ respective environmental and ecological role.

The integrative approach used by Raffini et al. (2020) suggests that the benthic/limnetic specializations resulting from morphological and physiological trade-offs have probably contributed to the establishment of reproductive isolation in less than 2,000 generations (Kautt et al., 2016). However, the level of morphological divergence and degree of ecological adaptation probably reflect a long list of processes driven by gene flow, environmental gradients and selection. Translating these microevolutionary patterns and processes to a macroevolutionary scale is not a trivial task. Yet, the authors make a good start, and there is an opportunity to use similar approaches in other systems to test hypotheses concerning the correlation between morphological and physiological divergence. By characterizing the physiological drivers that have been hypothesized to play a role in the divergence of these species, they have begun to uncover a potential answer as to why adaptation was able to occur in such a young and small lake.

**AUTHOR CONTRIBUTIONS**

All authors contributed to the writing of this manuscript.

**ORCID**

Michelle R. Gaither [https://orcid.org/0000-0002-3711-5621](https://orcid.org/0000-0002-3711-5621)

Samuel Greaves [https://orcid.org/0000-0001-7299-2991](https://orcid.org/0000-0001-7299-2991)

Pavithiran Amirthalingam [https://orcid.org/0000-0003-0517-458X](https://orcid.org/0000-0003-0517-458X)

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