Neotropical Riverine Cichlids: Adaptive Radiation and Macroevolution at Continental Scales

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Abstract Neotropical cichlids include over 550 species from Central and South America and the Caribbean and are increasingly recognized as models for studying evolutionary diversification. Cichlinae's great morphological, ecological, and behavioral diversity is concentrated in the tribes Geophagini, Heroini, and Cichlasomatini. Feeding and swimming morphology broadly fit two gradients of ecomorphological differentiation: An "elongation axis" follows a ram–suction feeding gradient of deep-bodied fishes with diverse diets at one end and mostly predatory shallow-bodied taxa at the other end. Body and fin configurations correspond with habitats spanning open substrate to structured areas. A second gradient of morphology spans suction feeders and biters with benthic-feeding or complex three-dimensional habitats. Several body configurations reflect specializations to live in rapids. Rates of Cichlinae ecomorphological disparity and lineage diversification often showed early, rapid acceleration followed by a slowdown. Early divergence in South America was likely dominated by the radiation of Geophagini. Rapid geophagin diversification into new niches may have precluded divergence in other South American cichlids, particularly Heroini and Cichlasomatini. Further lineage and morphological divergence in Heroini increased after colonization of Central America. Cichlinae appear to have repeatedly radiated by taking advantage of ecological opportunity in novel environments across the Neotropics, resulting in widespread convergence.

Keywords Ecomorphology · Convergent evolution · Adaptive landscapes · Ecological opportunity · Geophagini · Heroini

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1 Neotropical Cichlids Then and Now

Our knowledge of Neotropical cichlids has grown vastly since the publication of Keenleyside's (1991) edited volume. At the time, most work on South and Central American cichlids had been focused on taxonomy, ecology, and behavior, but little was known about phylogeny or the evolutionary biology of the group. Perhaps understandably eclipsed by the stunning diversity and breakneck speed of divergence of the East African radiations, Neotropical cichlids were not widely thought about as subjects of diversification studies. The decades since then have seen an enormous increase in interest on the evolution of Neotropical cichlids that is beginning to offer a valuable complement to the study of East African radiations.

   In the first chapter of Keenleyside's book, Stiassny (1991) presented the first phylogeny for cichlids and established the reciprocal monophyly of the African and Neotropical clades. Her phylogeny set the stage for a flood of subsequent interest in reconstructing the relationships of cichlids, and the Neotropical clade in particular. A few years later Kullander (1998) and Farias et al. (1998), respectively, pioneered morphological and molecular phylogenetic analyses of Neotropical cichlids that eventually led to an increasingly solid base for studying the timing and mode of divergence in the clade. Also in the Keenleyside volume, Lowe-McConnell (1991) provided the only chapter dedicated to the riverine cichlids of the Neotropics and Africa: a brief summary of ecology that brought up the importance of studying the ecological and functional diversity of cichlids outside of the African Great Lakes. Lowe McConnell had pioneered the study of the ecology of riverine cichlids in both continents and published some of the first studies of South American cichlid ecology working in Guyana (1964, 1969). Her book "*Fish communities in tropical freshwaters*" set the stage for innumerable studies of fish ecology in the Neotropics and elsewhere (Lowe-McConnell 1975). By the 1980s and early 1990s, parallel but as yet separate advances in ecological and systematic studies started to converge through the emergence of comparative methods aimed at studying the evolution of ecological traits in a phylogenetic context (e.g., Felsenstein 1985; Grafen 1989; Harvey and Pagel 1991; Brooks and McLennan 1991). The first study linking ecology and an early expression of the phylogeny of cichlids looked at ecomorphology and convergent evolution in the Neotropics and Africa (Winemiller et al. 1995). Winemiller and colleagues used Stiassny's (1991) tree as a backbone and taxonomic classifications as a proxy for relationships; then they mapped an extensive dataset of morphometrics and diet on their tree. In that first comparative macroevolutionary study of riverine cichlids, they found extensive ecomorphological convergence between South and Central America, as well as convergence between Neotropical and African cichlid communities and taxa. Since then, extraordinary advances in molecular phylogenetics and an explosion of newly developed comparative methods have opened entirely new avenues for studying diversification and macroevolution.

   The study of African lake cichlids consolidated the image of cichlids as classic examples of vertebrate "adaptive radiations" (e.g., Kornfield and Smith 2000;

Verheyen et al. 2003; Kocher 2004; Seehausen 2006; Salzburger et al. 2014). A concept originally defined by Simpson (1953), the modern "ecological theory of adaptive radiation" (Schluter 2000) studies a process by which the ancestor of a clade diversifies into a number of functionally distinct lineages. As new lineages emerge, ecological niches (together representing *ecological opportunity*, Schluter 2000; Yoder et al. 2010; Gavrilets and Losos 2009) are progressively occupied until eventually new lineages fail to become established due to the absence of further unfulfilled ecological opportunity. Adaptive radiation thus leaves a characteristic phylogenetic signature reflected in lineage and phenotypic divergence patterns (e.g., Gavrilets and Losos 2009; Glor 2010; Losos and Mahler 2010). Essentially, increasing diversity during adaptive radiation is evidenced by the rapid accumulation of lineages and of ecologically relevant (i.e., functional) phenotypic traits. This early increase or "early burst" of divergence is followed by a slowdown in rates of divergence as ecological opportunity wanes and lineages can no longer diversify into new niches. Simpson (1944, 1953) envisioned the niches occupied by successful, newly emerged lineages as *adaptive zones,* which together formed an *adaptive landscape* with peaks of high fitness and valleys of low fitness separating different lineages. Evolving lineages can invade new adaptive zones as they adapt to utilize niches within them. In this context, convergent evolution results from independent lineages being subject to similar selective pressures that drive them toward the same adaptive zone or *adaptive peak*. The concept of adaptive landscape allows envisioning the direction and strength of selection during macroevolutionary divergence as it would occur in adaptive radiation.

Until recently, the empirical study of adaptive radiations and adaptive landscapes was greatly limited by a lack of tools to analyze macroevolutionary patterns in a phylogenetic context. The rise of modern molecular phylogenetics and phylogenetic comparative methods has greatly expanded the study of adaptation and adaptive radiations at macroevolutionary scales. Comparative methods provide tools for two broad types of evolutionary inference: (1) establishing evolutionary correlations among characters (e.g., morphology, diet, habitat use) while accounting for lack of statistical independence due to common ancestry, and (2) fitting models of evolution to infer the processes under which diversity might have evolved (O'Meara 2012; Pennell and Harmon 2013). Both approaches use models of evolution, but while the former corrects for phylogeny (e.g., Felsenstein 1985) the latter uses phylogenetic patterns to delimit plausible hypotheses about the evolutionary process (e.g., Harmon et al. 2003; Rabosky and Lovette 2008; Mahler et al. 2010; Pennell and Harmon 2013; Slater and Pennell 2014). Emerging evolutionary models are also being developed to estimate the adaptive landscape of a clade by modeling selection on traits along the branches of a phylogeny (e.g., Beaulieu et al. 2012; Harmon 2018; Harmon et al. 2008; Ingram and Mahler 2013; Mahler et al. 2013; Mahler and Ingram 2014).

Until these new tools and increasingly strong hypotheses of phylogenetic relationships became available, the patterns of divergence and possible mechanisms that originated the functional and ecological diversity of Neotropical cichlids remained all but unknown. Recent work supports the idea that (1) functional divergence in

Neotropical cichlids is compatible with early adaptive radiations at continental scales, generally followed by stasis in functional and ecological innovation; (2) that convergence among clades has been extensive; and (3) that at least some of this convergence was driven by renewed ecological opportunity in novel environments. Further research is needed in determining whether and how the processes associated with the early adaptive radiations of tribes and genera may continue to play a role in more recent, species-level divergence. The exact timing and environmental context of Neotropical cichlid radiation still need much clarification. Nevertheless, the origin of Neotropical cichlid diversity is increasingly emerging as a continent-wide case of ecologically driven adaptive radiation that gave origin to the functionally and ecologically distinct lineages at the deeper levels of the phylogeny. Recent discoveries suggest that some Neotropical cichlids also have undergone radiations in geographically restricted riverine environments and relatively recent time frames (e.g., Burress et al. 2018; Piálek et al. 2018).

In this chapter, I attempt to offer a brief review of some of the recent advances in our understanding of Neotropical cichlid evolution. Due to space limitations and because I find them of particular interest, this review focuses on macroevolutionary patterns as perceived through the analysis of ecological, ecomorphological, and functional morphological data. I concentrate on describing the emerging understanding of patterns and possible mechanisms of higher-level adaptive diversification throughout South and Central America. Unfortunately, this focus requires leaving much of interest out from the chapter. I encourage readers interested in topics such as historical biogeography, behavior, or systematics to peruse the extensive literature available on those and related subjects.

2   The Riverine Neotropical Cichlid Fauna

Neotropical cichlids (subfamily Cichlinae) encompass over 550 described species plus an uncertain, but probably large, number that remain undescribed. Cichlid diversity in the Neotropics remains incompletely sampled, with new species being discovered frequently, either by reanalysis of previously established taxonomies (e.g., Maza-Benignos and Lozano-Vilano 2013; Schmitter-Soto 2007), study of established collection materials (Kullander and Varella 2015; Malabarba et al. 2015) or by field-based discovery, particularly in previously unexplored regions (e.g., López-Fernández et al. 2012a; Varella and Moreira 2013). Moreover, it is likely that our view of Neotropical cichlid diversity will continue to change as our understanding of geographic distributions and genetic variation increase (e.g., Amado et al. 2011; Colatreli et al. 2012; Willis et al. 2012, 2014; Willis 2017).

2.1 Taxonomic Diversity and Geographic Distribution

Neotropical cichlids are distributed from the southern United States where the Texas Cichlid (*Herichthys cyanoguttatus*) represents the northern-most lineage, to the northern edge of Patagonia in Argentina. Cichlids also naturally occur in the Pacific slopes of Colombia, Peru, and Ecuador, the Antillean islands of Cuba and Hispaniola, and the island of Trinidad (Fig. 1). Cichlinae diversity is not uniformly distributed either phylogenetically or geographically. Three monophyletic groups classified as tribes contain most taxa of Cichlinae: Geophagini, Heroini, and Cichlasomatini, with four additional tribes—Cichlini (1 genus, 16 described species), Retroculini (1, 4), Astronotini (1, 2), and Chaetobranchini (2, 4)—accounting for a much smaller but distinct number of taxa that occur only in South America east of the Andes.

The tribe Geophagini includes 16 genera and more than 260 described species at the time of this writing, and many more in need of description. Geophagini is the most species-rich Neotropical clade and ranges from southern Panama to northern Argentina, including the Pacific slope and Magdalena basin of Colombia, plus one drainage in the Guajira peninsula of Venezuela. Geophagin diversity reaches its peak in the Amazon and Orinoco basins, but the northwestern Andes, the Guiana Shield, and the Paraná basin also hold endemic genera or species with unique evolutionary and biogeographic significance (e.g., Burress et al. 2018; Kullander and Nijssen 1989; López-Fernández et al. 2012a; Piálek et al. 2012, 2018; Malabarba et al. 2015).

The tribe Cichlasomatini largely overlaps in distribution with Geophagini and includes 11 genera and 77 described species. Cichlasomatins are present further south on the Pacific slope of the Andes, reaching central Peru, but are most diverse in the lowlands of the Amazon and the Orinoco, as well as in the slopes of the eastern Andes (Kullander 1986; Musilová et al. 2008, 2009).

The only Neotropical cichlid clade broadly distributed in both South and Central America is Heroini, with a total of 183 described species in up to 38 named genera (Říčan et al. 2016). As a consequence of taxonomic revision of the genus *Cichlasoma* (Kullander 1983), to which most Heroini were once assigned, this group has remained in taxonomic flux for an extended period. Several lineages with long unrecognized generic status are now being assigned to either previously available or newly proposed names (e.g., Kullander 1983, 1996; Kullander and Hartel 1997; Schmitter-Soto 2007). Very recent work has made major revisions to heroin classification (McMahan et al. 2015; Říčan et al. 2016), but given the long history of taxonomic instability, it is likely that additional changes will occur as further taxonomic and phylogenetic understanding of Central American heroines continues to emerge. Phylogenetic analyses have revealed that several heroin genera with South American distributions have originated in Central America (e.g., Hulsey et al. 2004; Říčan et al. 2008; López-Fernández et al. 2010; McMahan et al. 2013; Říčan et al. 2016; Ilves et al. 2018) but our understanding of the historical biogeography linking South and Central American cichlids is far from definitive (e.g.,
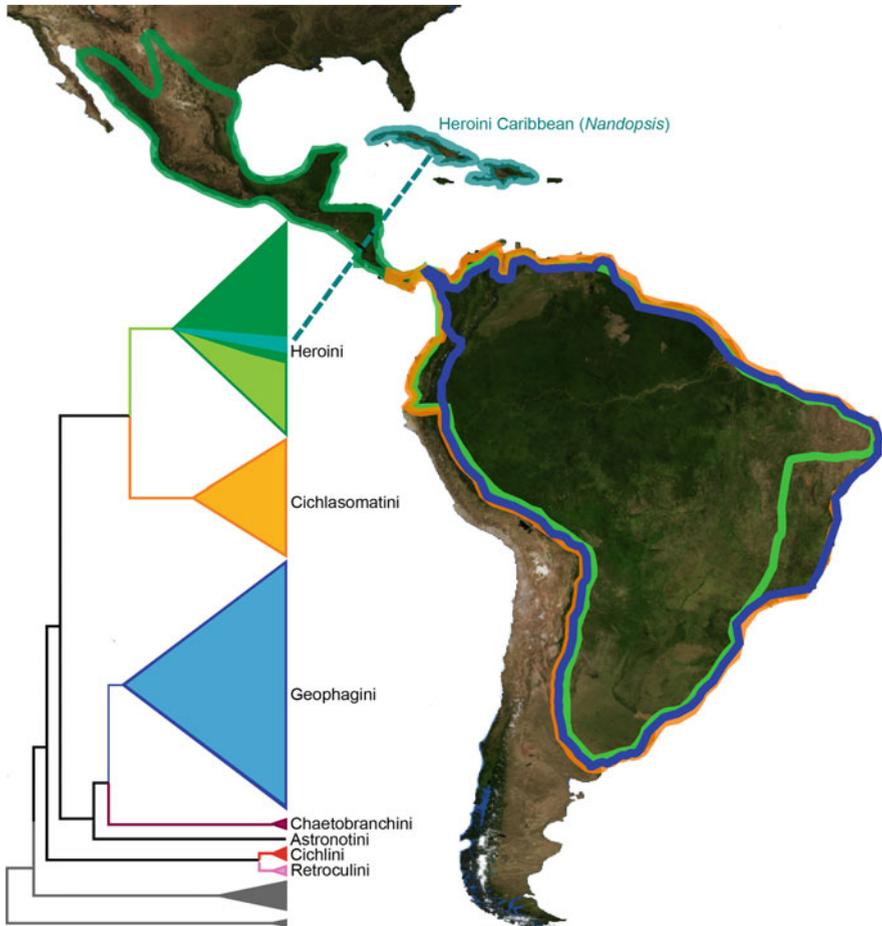
Fig. 1 Phylogeny and distribution of Neotropical cichlids (subfamily Cichlinae). A simplified version of the phylogeny of Cichlinae highlights each of the seven tribes, size of triangles represents approximate proportional species richness; see text for actual diversity. Heroini (Green, light green depicts taxa with South American distribution, dark green are taxa with Mesoamerican distribution, teal shows the genus *Nandopsis*, restricted to Cuba and Hispaniola in the Caribbean); Orange: Cichlasomatini; Blue: Geophagini; Purple: Chaetobranchini; Black: Astronotini; Red: Cichlini; Pink: Retroculini. Lineages in gray depict African, Malagasy, and Indian outgroups. Colored lines on the map represent the approximate distribution of the three main tribes in South and Central America. (Modified from López-Fernández et al. 2013; Satellite image courtesy of NASA: Neo Earth Observations)

Chakrabarty et al. 2011; Říčan et al. 2013; Tagliacollo et al. 2017; Ilves et al. 2018). South American heroines are comprised of two non-monophyletic sets of taxa: seven basal lineages which originated in South America (primary South American heroines, sensu Arbour and López-Fernández 2016, *Heros*, *Hoplarcus*, *Hypselecara*, *Mesonauta*, *Pterophyllum*, *Symphysodon,* and *Uaru*) and several others with South

American distributions but phylogenetically nested within the Central American clade (*Australoheros*, *Caquetaia*, *Heroina*, *Kronoheros* [= formerly *Caquetaia umbrifera*], and *Mesoheros*). Together, these two groups are broadly distributed in the Amazon, Orinoco, Paraná, and Pacific Andean basins from Colombia to northern Peru but are relatively species-poor—with the exception of *Australoheros* from the Paraná-La Plata. Finally, the only Caribbean cichlids belong in the genus *Nandopsis*, distributed in Cuba and Hispaniola with three described species and a putative fossil taxon (Chakrabarty 2006a, b).

2.2 Phylogeny, Times of Divergence, and Macroevolutionary Analyses

Neotropical cichlids (subfamily Cichlinae) are a monophyletic clade sister to a monophyletic African sister group (subfamily Pseudocrenilabrinae). In turn, the Neotropical-African clade is sister to a paraphyletic assembly of Indian and Malagasy taxa (Stiassny 1991; Kullander 1998; Farias et al. 2000; Sparks and Smith 2004; Smith et al. 2008). While species-level phylogenies are not established for most lineages and a few genus-level relationships remain elusive, relationships among the seven recognized Neotropical cichlid tribes and most genera within them are generally well established and supported (e.g., Hulsey et al. 2004, 2011; Říčan et al. 2008, 2016; López-Fernández et al. 2010; McMahan et al. 2013; Ilves et al. 2018, Fig. 1).

Relationships among most genera are reasonably well established within Cichlasomatini (Musilová et al. 2008, 2009, 2015; Smith et al. 2008; López-Fernández et al. 2010), and Geophagini (Kullander 1998; López-Fernández et al. 2005a, b, 2010; Ilves et al. 2018). The phylogenetic relationships among heroines are becoming increasingly resolved, particularly with the publication of recent phylogenomic analyses, but further study is needed to clarify some relationships (e.g., Říčan et al. 2008, 2013, 2016; López-Fernández et al. 2010; Hulsey et al. 2010; McMahan et al. 2015; Matschiner et al. 2017; Ilves et al. 2018). Basal heroins from South America form a paraphyletic arrangement sister to the rest of the clade. Whereas all studies find two large subclades among Middle American heroins, the exact composition of these groups and the relative position of some genera within them can vary depending on the analysis. This is particularly true of the relationships within the amphilophins clade; a clearly monophyletic group for which species assignment to different genera has been contentious due to often poorly resolved or ambiguously supported basal relationships. Even recent analyses based on extensive taxon sampling and genome-wide phylogenomic approaches still reveal some ambiguity in the relationships within amphilophins and a few other heroins (Říčan et al. 2016; Ilves et al. 2018). The position of the Antillean genus *Nandopsis* and of South American lineages within the Middle American phylogeny can also vary across studies. Due to such phylogenetic uncertainty, to differences in methods

and to incongruence among age estimates, the historical biogeography of Middle American colonization and recolonization of South America by heroins remains an active area of study (e.g., Chakrabarty and Albert 2011; Hulsey et al. 2011; Říčan et al. 2013; Tagliacollo et al. 2017; Musilová et al. 2015, and see discussions in Matschiner 2018; Ilves et al. 2018).

Correctly estimating the age of cichlids affects much more than our understanding of Central American biogeography. The distribution of cichlids across the southern hemisphere coincides with that of many of the landmasses of Gondwana, making the family important in the study of historical biogeography of both fishes and other taxa. The age of cichlids also is critical in understanding the timeline of diversification and the environmental context in which Neotropical cichlids diversified. Despite the importance of having reliable estimates of cichlid ages, considerable debate persists, with current age estimates ranging from the early Cretaceous to the Eocene (e.g., Genner et al. 2007; Azuma et al. 2008; Friedman et al. 2013; López-Fernández et al. 2013; Říčan et al. 2013; Tagliacollo et al. 2017, and see the detailed review by Matschiner 2018). There are multiple reasons for such lack of consensus, including the limited information available from the fossil record, the varying sets of assumptions required to date molecular phylogenies, the molecular data used in different studies (e.g., nuclear vs. mitochondrial), and whether estimates come from analyses aimed at dating cichlids per se (e.g., Genner et al. 2007; López-Fernández et al. 2013; Tagliacollo et al. 2017; Matschiner et al. 2017; Irisarri et al. 2018) or from broader studies dating large clades of fishes that include cichlid taxa but may (Betancur-R et al. 2013, 2017b; Hughes et al. 2018) or may not include cichlid fossils (Near et al. 2012; Friedman et al. 2013).

Ultimately, the only way to reliably estimate the age of any clade is by using robust fossil calibrations. Although the cichlid fossil record is limited, there are some fossils with excellent preservation that should help accurately date cichlids. Particularly relevant in the context of this chapter are recently described fossils from the Eocene Lumbrera formation in Argentina. These fossils include the geophagin †*Gymnogeophagus eocenicus (the dagger symbol denotes a fossil taxon throughout the chapter)*, which phylogenetic analysis supports as part of the extant geophagin genus *Gymnogeophagus* (Malabarba et al. 2010; 2014). The Lumbrera fossils also include the putative heroin †*Plesioheros chauliodus* (Alano-Pérez et al. 2010) and the equivocally placed †*Proterocara argentina* (Malabarba et al. 2006). With an age of at least 40 Ma (del Papa et al. 2010; Malabarba et al. 2014), these fossils provide minimum ages for two of the main clades of Neotropical cichlids. The putative cichlasomatin †*Tremembichthys garciae* of Eocene–Oligocene age (Malabarba 2008; Alano-Pérez et al. 2010) may provide a minimum age for the third-largest clade of Cichlinae. A Miocene fossil assigned to the Antillean heroin genus *Nandopsis* is also available, although poorly preserved (Tee-Van 1935; Chakrabarty 2006a). Additionally, extraordinarily preserved African cichlid fossils in the genus †*Mahengechromis*, of Eocene age, are also available, but their phylogenetic placement is not clearly established (Murray 2001; Sparks 2004). Ongoing and future studies using expanded datasets and new methods for dating phylogenies have much to contribute to the currently controversial age of cichlids.

Despite the relatively poor state of our understanding of cichlid ages, using phylogenies for comparative analyses of Neotropical cichlid macroevolution is still a valid and powerful approach, especially when analyses focus on higher levels of divergence, such as tribes and genera. For the purposes of this chapter, whenever phylogenetic correction is used, most analyses are based on the phylogeny published by López-Fernández et al. (2010) and time-calibrated in López-Fernández et al. (2013). More recent analyses that have expanded both on numbers of loci and taxon sampling (e.g., Říčan et al. 2013, 2016) or used different molecular markers (e.g., Friedman et al. 2013) continue to support most of the higher-level relationships found in that study. Furthermore, the López-Fernández et al. (2010) phylogeny remains the most thoroughly sampled single analysis of Neotropical cichlid lineages throughout the subfamily. Recent exon-based phylogenomic analysis with comparable taxon sampling corroborated and strengthened most of the relationships found in that study (Ilves et al. 2018). Simulation analyses (Arbour and López-Fernández 2016) have shown that the macroevolutionary studies described in the rest of this chapter should remain robust to potential disagreements among phylogenetic hypotheses or potential identification problems pointed out elsewhere (e.g., Říčan et al. 2013 and see Ilves et al. 2018). When performing comparative analyses using phylogenies it is essential not to base all analyses on one tree, but rather to employ a distribution of trees that allows establishing credibility intervals and accounting for the possible biases introduced by phylogenetic uncertainty and branch length variation (e.g., Rabosky 2014; Slater and Pennell 2014). Time-calibration of phylogenies using Bayesian methods, as have been applied to Neotropical cichlids (e.g., López-Fernández et al. 2013; Říčan et al. 2013; McMahan et al. 2013; Tagliacollo et al. 2017), generate distributions of chronograms that span the range of variation in both phylogenetic relationships and in time estimates. These distributions of trees include ranges of age estimates with chronograms of correspondingly different total lengths (i.e., total ages). Meaningful statistical comparisons of trait evolution and distribution analyses among a sample of chronograms, however, are more easily obtained and interpreted if all trees have the same total length. This is achieved by adjusting all trees to an arbitrary total length, usually 1, which eliminates variation in tree length due to varying time estimates while keeping the proportionality of branch lengths among trees (e.g., López-Fernández et al. 2013). Such comparative analyses facilitate robust interpretations of evolutionary patterns along the distribution of trees, but due to the rescaling of tree length, they are based on "relative-time" and do not directly provide information regarding the absolute timing of evolutionary events. In an unexpected way, this is a fortunate circumstance because it allows for valid macroevolutionary analyses even in the presence of extensive disagreement in time estimates.

2.3   Ecological and Morphological Diversity: Cichlinae Functional Morphospace

Neotropical cichlids encompass a tremendous diversity of morphological, ecological, and behavioral adaptations. An extensive literature is available that includes ecological analyses, ecomorphological correlations, and functional morphological models that describe cichlid ecology. Trophic diversity in Neotropical cichlids is strongly associated with morphological variation. Ecomorphological and biomechanical studies have outlined the main axes of functional variation in trophic specialization and linked both ecomorphological and biomechanical traits with diet composition, prey attributes, or more rarely, foraging behavior (e.g., Burress 2016; Burress et al. 2013; Cochran-Biederman and Winemiller 2010; Hulsey and García De León 2005; López-Fernández et al. 2012b, 2014; Montaña and Winemiller 2013; Waltzek and Wainwright 2003; Winemiller et al. 1995). Despite all these studies, detailed dietary data are lacking for many taxa and their trophic preferences must often be inferred based on closely related but better-studied species or functional morphology (e.g., Arbour and López-Fernández 2014). Moreover, among existing analyses, units of measurement are often not comparable across studies (e.g., some use percent volume and others use frequency of occurrence of diet items), limiting our ability to integrate ecological and functional information on Neotropical cichlids.

Ecomorphological and functional convergence among clades of Cichlinae is widespread, in most cases making it difficult to constrain descriptions of trophic ecology to a particular clade. Cichlid communities generally share ecotypes across regions such that the functional groups present in a community are common across assemblages (e.g., Winemiller et al. 1995; Seehausen 2015). Most ecomorphological and behavioral diversity in Neotropical cichlids is concentrated in the three major clades, Geophagini, Heroini, and Cichlasomatini. Nevertheless, the smaller tribes encompass significant and sometimes unique sets of Cichlinae ecological specializations, most notably two specialized plankton-feeding genera in Chaetobranchini (*Chaetobranchus*, *Chaetobranchopsis*) and the exclusively piscivorous Cichlini (genus *Cichla*). Using phylogenetic corrections (see previous section for details), several recent studies of Cichlinae or Geophagini have summarized variation in ecologically meaningful external morphology (López-Fernández et al. 2012b, 2013; Feilich 2016), feeding biomechanics (Arbour and López-Fernández 2013, 2014), swimming functional morphology (Astudillo-Clavijo et al. 2015) and the lower pharyngeal jaw (Burress 2016). Other studies have directly correlated ecomorphology or functional morphology with stomach contents analyses in a phylogenetic context (Winemiller et al. 1995; López-Fernández et al. 2012b; Burress 2016). Because feeding and habitat use (related to swimming morphology) are among the most relevant axes of ecomorphological divergence in cichlids and other fishes (Collar et al. 2008; Price et al. 2011; Claverie and Wainwright 2014), these studies provide insight into some of the main drivers of Neotropical cichlid diversification within a generalized Cichlinae *functional morphospace* on which analyses and discussions of macroevolutionary patterns can be grounded.

With or without phylogenetic correction, Principal Components Analysis of external morphology, oral jaw mechanics and swimming attributes of Cichlinae result in two significant Principal Components (PC1, PC2) delimiting a two-dimensional morphospace dominated by variation in morphological traits associated with feeding and swimming (e.g., Montaña and Winemiller 2010; Cochran-Biederman and Winemiller 2010; López-Fernández et al. 2012b, 2013; Pease et al. 2012; Arbour and López-Fernández 2013, 2014; Astudillo-Clavijo et al. 2015). While not identical, the commonalities among morphospaces defined by these two axes allow them to be meaningfully joined into a diagrammatic representation that describes general patterns of ecomorphological specialization among Neotropical cichlids as we understand them today, particularly in regard to traits associated with feeding and swimming performance (Fig. 2). Variation in the pharyngeal jaws does not appear to follow the same pattern as this generalized space (Burress 2016), but this lack of correspondence adds to our understanding of cichlid trophic specialization and further supports the idea of a decoupling between oral and pharyngeal jaws in cichlid feeding biology (see below, and Liem 1973; Hulsey et al. 2006a, 2010).

2.3.1 Elongation or Ram–Suction Feeding Axis

Regardless of the variables analyzed, functional morphospace in Cichlinae is dominated by an "elongation axis" along PC1. This axis ranges between very elongate fishes with shallow bodies and heads and low positioned eyes (negative [left] end of horizontal axis on Fig. 2; e.g., the geophagin *Crenicichla*, and to a lesser degree *Cichla*, *Retroculus* and the heroins *Petenia* and *Parachromis*) versus taxa with deep bodies and heads and eyes displaced dorsally of which the most extreme examples are all within Heroini (positive [right] end of horizontal axis on Fig. 2, (e.g., *Symphysodon*, *Pterophyllum* and *Paraneetroplus* [= *Vieja* in recent taxonomic revisions]; throughout this chapter, I refer to the taxon names used in the original publications to facilitate the reading of earlier literature. Current generic names are given in brackets when pertinent). Functionally, the elongation axis represents a gradient between ram-feeding and suction or biting feeders. The ram-feeding end of the gradient (Fig. 2, left) includes lineages with highly protrusible oral jaws, fast opening and closing of lower jaws with even occlusion (gripping bite), relatively strong pharyngeal crushing potential and comparatively low suction force. These are attributes that generally characterize predatory fishes but can also include taxa specialized to living in rapids regardless of their feeding habits (e.g., *Teleocichla*, *Crenicichla*, *Theraps*, Arbour and López-Fernández 2013, 2014). This configuration allows both fast-start accelerations and turns associated with predation on elusive prey and maintaining position in high currents (Astudillo-Clavijo et al. 2015); often both are combined in various species of *Crenicichla* (Zuanon 1999).

Diet analyses show that many taxa in the elongate end of the axis are at least partially piscivorous and include the tribes Cichlini (Genus *Cichla*), Geophagini (*Crenicichla*), Cichlasomatini (*Acaronia*), and Heroini (*Petenia*, *Caquetaia*, *Parachromis*, and "*Cichlasoma*" (= *Mayaheros*] *urophthalmus*) (e.g., Winemiller
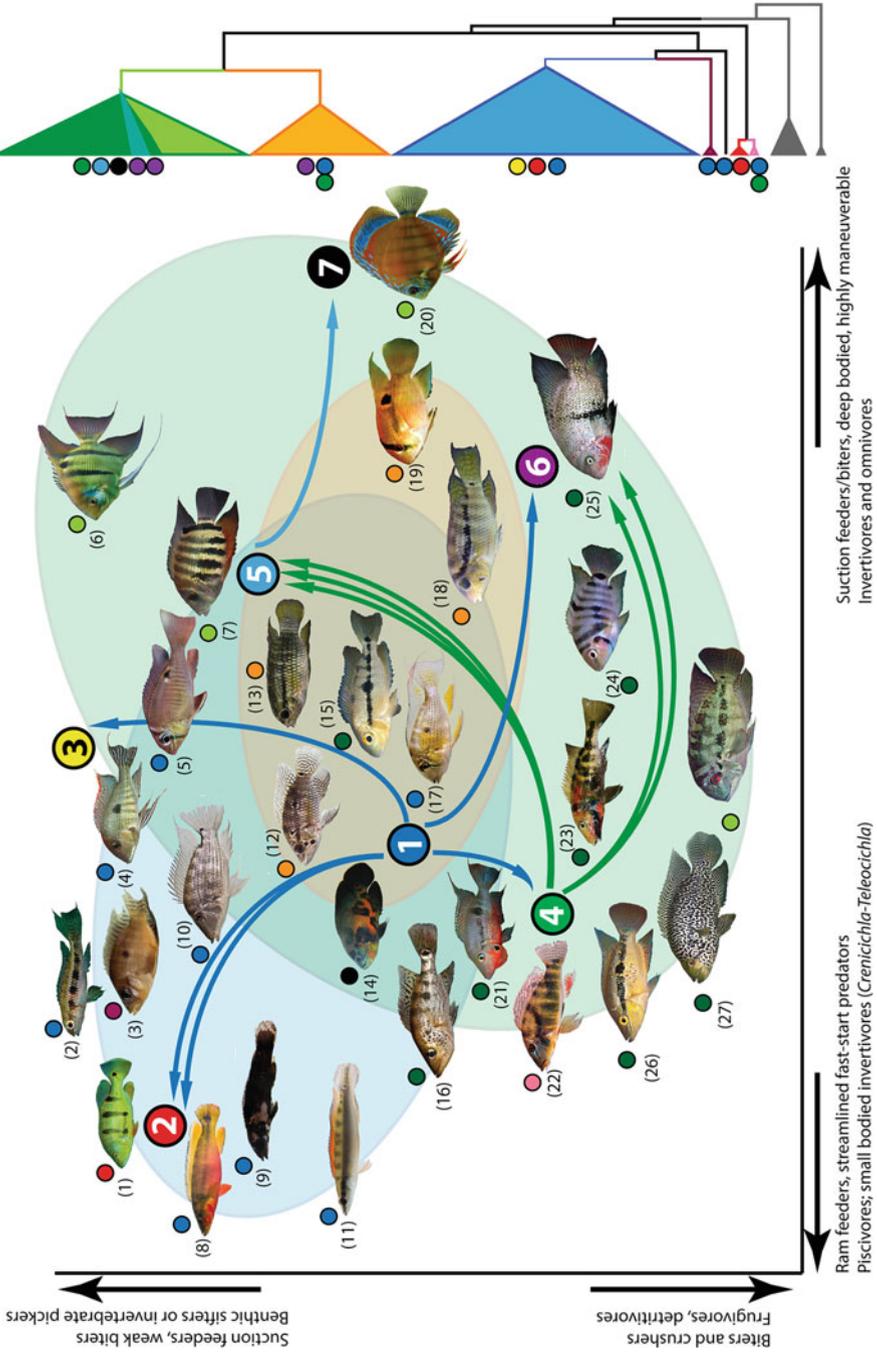
Fig. 2 Cichlinae functional morphospace and adaptive landscape—*Left*: A diagrammatic representation summarizes the ecomorphological and functional morphospace of Neotropical cichlids based on the first two axes of phylogeny-corrected Principal Components Analyses (see López-Fernández et al. 2013;

Arbour and López-Fernández 2014; Astudillo-Clavijo et al. 2015 for description of the original analyses and the actual PCA-based morphospaces). Ellipses depict generalized representations of morphospace for the main Cichlinae clades: Geophagini (blue), Heroini (light green: South America; dark green: Mesoamerica), and Cichlasomatini (orange). Numbered colored circles depict the approximate placement of feeding mechanics adaptive peaks (Arbour and López-Fernández 2014). Peak 1 (Blue) represents the most likely ancestral adaptive optimum for South American cichlids; Peak 4 (Green) is the most likely adaptive optimum for Central American cichlids. Arrows depict transitions between peeks; multiple arrows represent independent (convergent) moves between adaptive peaks. *Right:* Phylogeny showing the adaptive peaks (circles) detected for each of the Neotropical cichlid clades (triangles). Peak and clade colors in the phylogeny correspond to the peak and clade colors in the adjacent morphospace. Two peaks side by side (blue and green) represent an ambiguous reconstruction of the ancestral peak for a clade (i.e., blue and green for Cichlasomatini and Retroculini). Peak 6 (purple) evolved twice independently within Heroini; peak 2 (red) evolved independently in Cichlini and in the geophagine genus *Crenicichla*. See text and Arbour & López-Fernández for details and methods. Photographs depict representative genera/species and their approximate position in morphospace. See text for details of morphospace interpretation. Genera identification: (1) *Cichla*, (2) *Dicrossus*, (3) *Chaetobranchus*, (4) *Geophagus*, (5) *Biotodoma*, (6) *Pterophyllum*, (7) *Heros*, (8) *Crenicichla* (large, piscivores), (9) *Teleocichla*, (10) *Satanoperca*, (11) *Crenicichla* (small, invertivores), (12) *Acaronia*, (13) *Laetacara*, (14) *Astronotus*, (15) *Hypsophrys*, (16) *Petenia*, (17) *Acarichthys*, (18) *Bujurquina*, (19) *Cleithracara*, (20) *Symphysodon*, (21) *Thorichthys*, (22) *Retroculus*, (23) *Theraps*, (24) *Amatitlania*, (25) *Vieja*, (26) *Trichromis*, (27) *Parachromis*, (28) *Hoplarchus*. Species do not necessarily depict those utilized in the original analyses. Colored dots by each image depict the clade to which each genus belongs (and see Fig. 1): Blue = Geophagini, Orange = Cichlasomatini, Green = Heroini, Red = Cichlini, Black = Astronotini, Purple = Chaetobranchini, Pink = Retroculini (Photo credits: H. López-Fernández, J. Arbour, K. M. Alofs, M. H. Sabaj-Pérez)

1989; Winemiller et al. 1995; Montaña and Winemiller 2009, 2010; Cochran-Biederman and Winemiller 2010; Kullander and Ferreira 2006; López-Fernández et al. 2012b; Soria-Barreto et al. 2019). Despite having a diet dominated by fish, piscivory among Neotropical cichlids is achieved through a variety of functional configurations in different clades (see next section and Fig. 2). At the most elongate end of the gradient, the geophagin *Crenicichla* clade represents a unique set of functional and morphological configurations that is not found in any other clade of Neotropical cichlids (López-Fernández et al. 2013; Arbour and López-Fernández 2013, 2014; Astudillo-Clavijo et al. 2015). However, the highly specialized morphology of *Crenicichla* is not always associated with piscivorous diets or sit-and-wait predation, with some taxa having become benthic invertebrate feeders (e.g., Montaña and Winemiller 2009; López-Fernández et al. 2012b; Varella et al. 2016), frequently in association with body size reduction (Steele and López-Fernández 2014). The *Crenicichla* configuration is the most versatile of Neotropical cichlid morphologies and has been associated with its own adaptive zone. The only exception is the piscivorous genus *Cichla,* which has convergent feeding and swimming morphology with *Crenicichla* (Arbour and López-Fernández 2014; Astudillo-Clavijo et al. 2015). Another unique predatory configuration convergent among Neotropical cichlids is that of the "basket mouth" cichlids in the heroin genera *Petenia* and *Caquetaia* and the cichlasomatin *Acaronia*. These highly specialized predators combine ram attacks with extreme jaw protrusion, presumably as a way to increase closing speed when attacking elusive prey (Waltzek and Wainwright 2003).

The suction–biting end of the PC1 gradient (Fig. 2, right) includes taxa with strong but comparatively slower opening and closing of the oral jaws, uneven occlusion (quadrate offset resulting in "scissors"—like biting), and strong suction and/or biting ability. These taxa also tend to have larger caudal and pectoral fins as well as pelvic and unpaired fins placed comparatively far from the center of mass, resulting in elevated maneuverability presumably compatible with feeding on benthic or attached prey (Arbour and López-Fernández 2013, 2014; Astudillo-Clavijo et al. 2015). Diet among the suction–biting taxa includes invertebrates, plant material, fruits, detritus, and in some cases mollusks and other hard prey (e.g., Crampton 2008; Winemiller 1990; Winemiller et al. 1995; Cochran-Biederman and Winemiller 2010; López-Fernández et al. 2012b; Soria-Barreto et al. 2019).

The elongation gradient appears to be a widespread axis of morphological variation in fishes; for example, this gradient is very apparent among coral reef fishes (Claverie and Wainwright 2014). The strong functional morphological correlates of the gradient as described above in cichlids supports the idea that the association between the elongation axis and both swimming and feeding may be a major determinant of fish diversification. Interestingly, while the deep-bodied end of the axis in Cichlinae is consistent with findings in coral reef-fishes and supports interpretations of increased benthic habits and suction feeding, the elongated extreme of the gradient appears to diversify in less constrained ways and maybe more clade-specific (see Claverie and Wainwright 2014 for further discussion). In
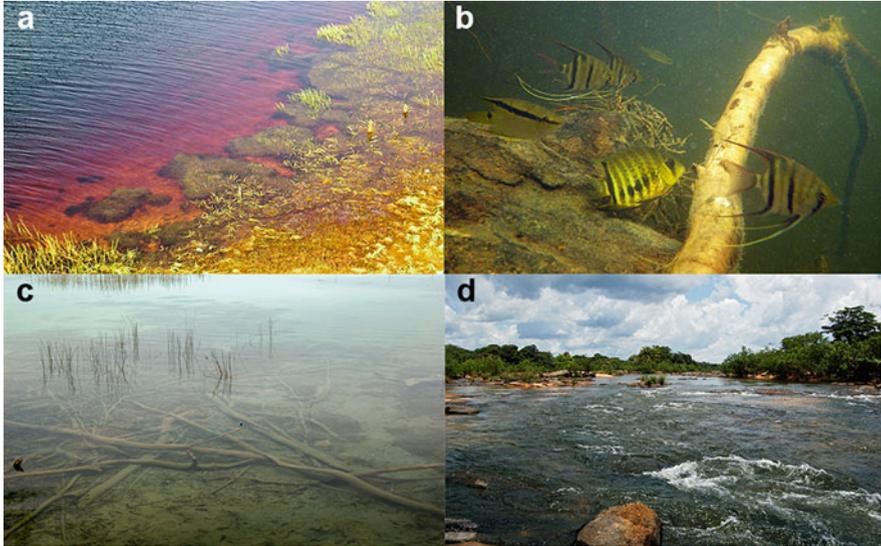
Fig. 3 (**a**) A black water stream with sandy bottom and some shoreline structure formed by vegetation and gallery forests (not visible in photograph) in the Venezuelan Orinoco River floodplain. These habitats tend to be dominated by substrate sifting Geophagini in *Geophagus*, *Satanoperca*, *Biotodoma*, *Apistogramma*, *Biotoecus* and predatory *Crenicichla* as well as the piscivorous Cichlini genus *Cichla*; Heroini genera *Heros*, *Hypselecara*, *Hoplarchus* and *Mesonauta* and the Cichlasomatini *Aequidens* and *Acaronia* are also present but are generally less abundant. (**b**) South American heroin taxa in a complex Amazonian habitat. The picture shows the Heroini genera *Pterophyllum*, *Mesonauta,* and *Heros* feeding among the branches of a fallen tree in a clear-water creek, Rio Negro basin, Brazil. Body shape in these genera, as well as *Symphysodon* and *Uaru*, do not overlap with any of those in the South American Geophagini and Cichlasomatini (López-Fernández et al. 2013). The South American Heroini includes some of the most extreme body shape, feeding, and swimming adaptations among Neotropical cichlids (Arbour and López-Fernández 2014; Astudillo-Clavijo et al. 2015). Presumably, competition limited the ability of Heroini to occupy niches already occupied during the early diversification of Geophagini, resulting in highly specialized South American heroin genera. Later invasion of Mesoamerica by heroins renewed ecological opportunity and triggered the diversification of Heroini into niches previously unavailable. See text for details. (**c**) A sandy bottom shore in the Usumacinta River basin in Mexico. Central American environments with sandy or muddy bottoms are frequently occupied by substrate sifting *Thorichthys*, *Astatheros,* and *Cribroheros* which are broadly convergent with South American geophagines; detritivorous lineages such as *Vieja* and *Cincelichthys* in Central America occupy niches not available to cichlids in South America, presumably due to the presence of detritivorous characiforms in families such as Prochilodontidae. (**d**) The Xingu River basin is rich in rapids where species of *Crenicichla*, *Teleocichla*, *Retroculus,* and others represent specialized rheophilic cichlid lineages. Convergent rheophilic Central American taxa include *Theraps*, *Wajpamheros,* and *Rheoheros* (Photo credits: (**a**, **c**, **d**) H. López-Fernández, (**b**) K. M. Alofs)

the case of cichlids, both locomotion and feeding correlates of elongation appear to be associated with an increasingly predatory lifestyle, and in some cases, with the evolution of rapids-adapted (rheophilic) lineages.

2.3.2 Suction–Biting and Maneuverability Axis

Variation along PC2 involves a gradient between suction feeders and biters, both frequently associated with feeding in or near the benthos, or in complex, highly three-dimensional habitats (Figs. 2 and 3). Taxa along this gradient share laterally compressed, deep bodies with relatively small mouths capable of generating strong, directed suction (Winemiller et al. 1995; Hulsey and García De León 2005; López-Fernández et al. 2012b, 2014; Arbour and López-Fernández 2013, 2014). Nevertheless, these adaptions encompass a wide variety of dietary specializations with an equally diverse combination of feeding mechanics involving suction and biting (Fig. 2). Although contrasts between extremes of the suction–biting gradient are not as strong as the elongation axis, PC2 separates largely substrate sifting taxa from species that feed on a variety of benthic or substrate-attached food items (e.g., algae, vegetation, or epibenthic invertebrates). Even though all taxa along axis 2 are to some extent suction feeders, it is clear that some employ biting or scraping in order to obtain food resources such as algae (*Hypsophrys*), fruits (*Tomocichla*), or detritus (e.g., *Paraneetroplus* [=*Vieja*]), whereas others extract benthic invertebrates from within the substrate or from its surface (substrate-sifting geophagins and heroins). These diverse feeding modes combine morphological attributes with behavioral components that are not reflected in morphological analyses (e.g., Hulsey and García De León 2005; López-Fernández et al. 2014; Weller et al. 2017). For example, substrate sifters ingest a mixture of inorganic substrate particles and food items (e.g., invertebrates, seeds) and methodically remove inedible particles through the gill openings by coordinated movements of the hyoid, the oral jaws, and the pharyngeal basket. This "winnowing" behavior separates food from debris, with the gill rakers acting like sieves directing food toward the esophagus and debris ejected through the gills. Although superficially similar to behavior in surfperches (Drucker and Jensen 1991), a pioneering biomechanical study recently showed winnowing is a functionally unique and underexplored axis of specialization among geophagins (Weller et al. 2017). Substrate sifting morphology is broadly similar but not identical across benthic-feeding taxa, which tend to have deep heads, large and dorsally placed eyes, wide mouth gapes, and longer snouts, but display an assortment of oral jaw mechanics that suggests a variety of functional configurations for food acquisition (Hulsey and García De León 2005; Arbour and López-Fernández 2014; López-Fernández et al. 2014; Weller et al. 2017). Consistent with their varied morphology, substrate sifters display a large diversity of diets (e.g., Winemiller et al. 1995; Hulsey and García De León 2005; Montaña and Winemiller 2009; Cochran-Biederman and Winemiller 2010; López-Fernández et al. 2012b; Soria-Barreto et al. 2019).

Analysis of the lower pharyngeal jaws in Neotropical cichlids revealed two different pharyngeal jaw configurations among substrate sifters, suggesting yet further diversification in prey manipulation modes (Burress 2016). The functional separation between the oral and pharyngeal jaw of cichlids has been long proposed as a key adaptive innovation (e.g., Liem 1973; Hulsey et al. 2006a, b, 2010; Burress 2016 and references therein). Among substrate sifters, this jaw independence may affect the efficiency of prey acquisition depending on the type of substrate (e.g.,

sand, mud, hard surfaces), location of food items with respect to the substrate (e.g., benthic infauna, epibenthic invertebrates, or detritus) or whether food items are attached or loose.

Most discussions of pharyngeal specialization tend to focus on dentition and force of the lower pharyngeal jaw (e.g., Hulsey et al. 2006b; Burress 2016), whereas comparatively little attention has been given to the functional role of broader pharyngeal variation on winnowing performance, prey capture, or prey selection (but see Galis and Drucker 1996; Burress 2016; Weller et al. 2017). Likewise, we know very little about the role of pharyngeal structures other than the potential influence of tooth plates on winnowing (but see Weller et al. 2017). In the case of Geophagini, it is possible that the "epibranchial lobe," an anteroventrally directed laminar expansion of the first epibranchial, could also be involved in enhancing the efficiency of substrate sifting or the evolution of mouthbrooding behavior (e.g., Lowe-McConnell 1991; López-Fernández et al. 2012b). Analogous structures to the epibranchial lobe of geophagins are present in the South American genus *Retroculus* and some African cichlids, but to the extent that I am aware, no functional analyses have been performed on the pharyngeal lobes of any of these groups. Given the ubiquity of winnowing and the functional diversity of oral jaws in sifting cichlids (particularly Geophagini), it would be interesting to explore associations between oral and pharyngeal jaws and consumption of benthic food. Such studies could enhance understanding of the functional morphology of the pharyngeal basket, discerning how different substrate-sifting taxa actually perform winnowing, and establishing whether differences in winnowing behavior and mechanics facilitate interspecific dietary divergence.

The functional complexity of the suction–biting axis is also reflected in the swimming attributes of suction feeders and biters. Within Geophagini variation along this axis suggests diversification in both habitat and swimming attributes associated with a benthic/epibenthic adaptive zone (Astudillo-Clavijo et al. 2015, and see below). Variation in swimming morphology is associated with divergence in fin size, shape, and position within the deep-bodied end of the elongation axis, which ecological studies suggest is congruent with variation in habitat preferences (e.g., Claverie and Wainwright 2014; Willis et al. 2005; Soria-Barreto and Rodiles-Hernández 2008; Cochran-Biederman and Winemiller 2010; Montaña and Winemiller 2010, 2013). Interpretation of this vertical axis suggests that substrate sifters (top end of axis, Fig. 2, e.g., *Geophagus, Satanoperca*) may have body and fin shapes optimized for hovering or maneuvering with precision while searching for, biting at, or scooping and winnowing food items on or within substrates. The negative end of the axis (center to bottom of Fig. 2, e.g., *Guianacara, Apistogramma, Teleocichla*) tends to be associated with fishes having paddle-like paired fins inserted relatively far from the center of mass that presumably enhance maneuverability within structurally complex habitats such as vegetation, rocky reefs, and submerged wood debris. Despite the distinctions made above, however, trait combinations that enhance maneuverability can be found all along axis 2, albeit some of them involve different aspects of locomotion. These swimming attributes

are expected to relate to different habitat preferences, but further study is needed to test that assumption (Astudillo-Clavijo et al. 2015; Feilich 2016).

In summary, much of the functional morphological and ecological variation in Neotropical cichlids can be placed along two main axes of adaptive divergence. These axes are defined by functional trait combinations affecting feeding and swimming performance and indicate strong trade-offs between diet and habitat use. A dominant elongation axis is shared with most other fishes and represents a gradient between elongate, fast-swimming, or sit-and-wait predators that use ram feeding, and deeper-bodied fishes capable of maneuvering with precision while searching for and consuming food attached to or buried within substrates. All fishes along this gradient are capable of using a variety of habitats, from open water to structurally complex with variable current velocity, but rely on different strategies to maneuver through them and access food resources (Fig. 3). A second axis of functional variation describes further specialization between biting and substrate sifting taxa, and consumption of attached or buried prey. Neotropical cichlids exhibit specializations along the length of this suction–biting gradient, and diversity is impressive even just among substrate-sifting taxa.

2.3.3 Adaptive Landscape of Neotropical Cichlid Evolution

The axes of the Cichlinae functional morphospace, as currently understood, describe adaptive suites for distinct ecological roles (niches) and reveal repeated instances of ecomorphological convergence. Modeling selection on functional traits along the branches of the phylogeny allows inferring an *adaptive landscape*. Although methods continue to evolve and results must be read with caution, recent work based on 10 variables associated with feeding biomechanics and 75 species representing all Cichlinae tribes estimated an adaptive landscape with seven adaptive peaks and 11 regime shifts among peaks (Fig. 2). In this context, "peaks" represent ecomorphological configurations assumed to maximize fitness and to be favored by selection, whereas "adaptive shifts" represent ecomorphological changes from one peak to another via a novel ecomorphological configuration. Seven of these shifts correspond with convergence on the same three adaptive peaks (Fig. 2, peaks 2, 5, and 6). Two additional shifts correspond with the invasion of new, non-convergent adaptive zones restricted to one clade (Fig. 2, peaks 3 and 7 and see Arbour and López-Fernández 2014). Analyses of simulations without convergence and models that vary the regime shifts both indicated that some of the observed peaks could consist of multiple non-convergent peaks, suggesting that additional adaptive peaks may exist (Arbour and López-Fernández 2014).

Peaks 1–3 include all tribes except Cichlini and Heroini, with peak 1 estimated as the ancestral regime for Cichlinae (Fig. 2). Within Cichlasomatini, the genus *Cleithracara* is the only genus outside adaptive peak 1, as it has converged toward peak 6, a strong biting adaptive zone otherwise restricted to South American Heroini and possibly one Central American lineage. Within the ancestral peak 1, functional optimization tends toward improved oral jaw velocity transmission and reduced jaw opening and closing force, hypothesized to be associated with the substrate sifting

behaviors of geophagins (see above, and Arbour and López-Fernández 2014). This view is congruent with the finding of a geophagin adaptive peak of swimming morphology optimized for maneuverability and associated with substrate sifting taxa (Astudillo-Clavijo et al. 2015). Despite their shared adaptive regime, there is a large variation in feeding modes among lineages in peak 1 (e.g., planktivory in Chaetobranchini, substrate sifting in Geophagini, omnivory in Cichlasomatini). Interestingly, a recent analysis of Cichlinae adaptive landscape as defined by pharyngeal jaw shape variation using the same phylogenetic context found a non-convergent regime within substrate sifting geophagines of the genera *Geophagus* sensu *lato* and *Gymnogeophagus* (Burress 2016) that was not detected in our analysis as different from peak 1. Likewise, the same analysis found a convergent peak in pharyngeal jaws that includes the piscivores *Cichla* and *Petenia* and the planktivorous *Chaetobranchus*, which in our analysis belong in three different adaptive peaks (see below, and Fig. 2). Given the likely functional decoupling of oral and pharyngeal jaws, the difference in estimated adaptive landscapes based on each set of jaws is not surprising and provides a broader understanding of the multidimensional nature of adaptive divergence in Neotropical cichlid early diverging lineages (i.e., recognized as tribes and genera, and see next section).

The geophagin clade *Crenicichla/Teleocichla* and the tribe Cichlini (genus *Cichla*) convergently occupy adaptive peak 2, which is jaw-velocity optimized and congruent with the predatory tendencies of many of these taxa. This feeding adaptive peak is consistent with a unique adaptive peak described by Astudillo-Clavijo et al. (2015) for the swimming morphology of Geophagini. Adaptive peak 3 includes *Biotodoma-Dicrossus-Crenicara* (although a less favored reconstruction included those genera plus *Geophagus* sensu lato and *Gymnogeophagus*). This latter peak includes several specialized benthic and epibenthic feeders in Geophagini that bite, suck, or scoop and sift for prey (López-Fernández et al. 2012b, 2014).

Adaptive peaks 4–7 are dominated by Heroini and tend to be optimized for high suction potential or strong biting force (i.e., toward the right portion of PC1 and the lower half of PC2 in ecomorphospace, Fig. 2). Peak 4 was reconstructed as the ancestral adaptive zone in Heroini, with the South American genera *Pterophyllum*, *Mesonauta*, *Uaru,* and *Heros* showing a convergent shift toward peak 5, and *Symphysodon* shifting uniquely toward peak 7 with the strongest suction potential of any Neotropical cichlid. Mesoamerican cichlids all remain within adaptive zone 4 except for the convergent *Herotilapia* and *Paraneetroplus* (= *Vieja*) which shifted toward peak 6, with strong biting forces and presumably associated with diets that include plant material and vegetative detritus (Winemiller et al. 1995).

Interestingly, South American Heroini are confined to their own adaptive zones (peaks 4, 5, and 7), and most Central American heroines diversified within adaptive zones 4 and 6. In contrast, geophagines diversified within the confines of peaks 1, 2, and 3, with cichlasomatins largely restricted to peak 1. This suggests that, despite the large convergence in morphospace occupation (Fig. 2) and diet, the adaptive regime shifts between South and Central American cichlids have been largely independent from each other, with their evolutionary trajectories following clade-specific paths.

This interpretation of the adaptive landscape is supported by ecomorphological and functional variables in morphospace, which suggest that both the timing of origin of Cichlinae tribes and the presence of non-cichlid clades contributed to shape the evolution of Neotropical cichlids. In the following section, I broadly discuss how the timing of divergence, ecology, and biogeographic shifts, by affecting ecological opportunity, may have influenced the evolution of the adaptive landscape and driven convergence among the main clades of Neotropical cichlids.

3 Neotropical Cichlids as Ancient, Continental Adaptive Radiations

Cichlids are among the most celebrated and studied adaptive radiations, mostly because of intense interest in the remarkable species flocks of the East African Great Lakes (Kornfield and Smith 2000; Verheyen et al. 2003; Kocher 2004; Seehausen 2006; Salzburger et al. 2014) and the smaller crater lakes radiations in Africa and Central America (Schliewen et al. 1994, 2001; Barluenga et al. 2006; Elmer et al. 2010; Martin et al. 2015). These lake radiations generally share a relatively recent origin of a few tens of thousands to a few million years (e.g., Seehausen 2002; Genner et al. 2007; Day et al. 2008; Elmer et al. 2010). In contrast, diversification of the much older, continentally distributed, river-dwelling cichlids of Africa and the Neotropics is much less understood. We have only recently started addressing the question of whether riverine cichlid divergence might follow processes analogous to the adaptive radiation paradigm widespread among their lake-dwelling kin. These studies increasingly suggest that diversification processes in Neotropical cichlid lineages have not been uniform through time or across the phyletic history of the clade. Rather, phylogenetic, comparative, and fossil evidence suggest that diversification of the modern Neotropical cichlid fauna is the result of accumulated episodes of evolution with potentially different drivers through evolutionary time. Moreover, at least in some cases, diversification of Neotropical riverine cichlids appears to have followed a pattern consistent with early adaptive radiations resulting in most of the modern functional and higher-level phylogenetic diversity, followed by a relative deceleration of adaptive diversification. Nevertheless, in at least two cases, it appears that pike cichlids in the genus *Crenicichla* may have diversified through much more recent riverine adaptive radiation.

3.1 Decoupled Divergence Patterns: Temporal and Phylogenetic Scale of Divergence in Neotropical Cichlids

We have referred to the earlier stages of Neotropical cichlid diversification as "ancient continental adaptive radiations" (López-Fernández and Albert 2011;

López-Fernández et al. 2013; Arbour and López-Fernández 2016), which appear to have given origin to most of the functionally and ecologically distinct lineages spanning modern Neotropical cichlids at the taxonomic levels of tribes and genera. This initial period of adaptive divergence generally appears to have been followed by widespread adaptive stasis, with lineage-level divergence dominated by speciation within genera and often resulting in high species richness but low ecomorphological divergence. Ecomorphological variation within living genera is often negligible compared to variation among genera (López-Fernández et al. 2012b), with the exception of *Crenicichla* and perhaps a few others (e.g., Kullander et al. 2009; Piálek et al. 2018; Burress et al. 2013; Burress et al. 2018). This proposed phenotypic stasis within genera is evident in at least one fossil cichlid, †*Gymnogeophagus eocenicus*, an Eocene taxon that can be unambiguously placed within a living genus (Malabarba et al. 2010, 2014). With few known exceptions such as species of *Amphilophus* in Central American crater lakes (e.g., Barluenga et al. 2006) and some *Crenicichla* in localized areas of the Uruguay and Paraná river basins (Burress et al. 2018; Piálek et al. 2018), recent or ongoing species-level diversification in Neotropical cichlids appears to be broadly driven by nonadaptive forces and biogeographic happenstance (e.g., Farias and Hrbek 2008; López-Fernández and Albert 2011; Argolo et al. 2020). Whether adaptive divergence plays a larger role in recent Neotropical cichlid divergence is poorly understood. In the following paragraphs, I describe recent analyses of the early origin of Neotropical cichlids at the tribe and genus level. Disparity among these older lineages encompasses the vast majority of the functional and ecological diversity of cichlids in modern South and Central American assemblages.

3.2   South America: Early Burst of Divergence in Lineages and Phenotypes

All clades of Neotropical cichlids originated in South America. Although the temporal framework of divergence of Cichlinae and its subclades remains unclear and controversial (see Sect. 1), the order in which clades originated is relatively well established by a number of phylogenetic analyses that include all tribes (e.g., Smith et al. 2008; López-Fernández et al. 2010; McMahan et al. 2013; Ilves et al. 2018). Patterns of lineage diversification based on Lineage Through Time analysis (LTT plots, Pybus and Harvey 2000) were compatible with early and rapid lineage diversification followed by a decrease in the rate of lineage accumulation in Geophagini, and to a lesser extent the entire Cichlinae (López-Fernández et al. 2013). A similar pattern in Cichlasomatini was statistically nonsignificant, and patterns in Heroini indicated linear accumulation of lineages. Further, the comparison of models with constant and variable rates of lineage accumulation favored processes with variable rates, including diversity-dependent models for Cichlasomatini and Geophagini. López-Fernández et al. (2013) interpreted these

combined results as compatible with early, diversity-dependent lineage diversification in Geophagini, and evidence that the origin of geophagin genera is compatible with the ecological model of adaptive radiation. McMahan et al. (2013) found significantly fast rates of lineage accumulation in the African cichlid clade containing the East African radiations (Schwarzer et al. 2009), as well as some evidence of fast lineage accumulation in Heroini (contra Hulsey et al. 2010; López-Fernández et al. 2013), but not Geophagini. The studies, however, focused on different timelines of divergence: whereas López-Fernández et al. (2013) focused on the early two-thirds of the evolutionary history of the clade and genus-level divergence to account for incomplete species-level sampling, McMahan et al. (2013) interpreted the entire length of Cichlinae diversification, including modern diversity, making the two studies not directly comparable. Regardless, lineage diversification patterns are apparently compatible with early, diversity-dependent lineage diversification within Geophagini and possibly Heroini, a pattern theoretically congruent with adaptive radiation. These patterns need to be reexamined with more densely sampled phylogenies that span all times of divergence and more accurately reflect diversity across cichlid clades (and see Burress and Tan 2017).

In the ecological model of adaptive radiations, theory predicts that early bursts of lineage diversification should be paralleled by concomitant early bursts of phenotypic divergence (Gavrilets and Losos 2009; Glor 2010; Schluter 2000; Yoder et al. 2010). Analyses of phenotypic disparity through time (DTT plots, Harmon et al. 2003) using the axes of Cichlinae functional morphospace (see above, Fig. 2) with external ecomorphological characters (López-Fernández et al. 2013), feeding biomechanics (Arbour and López-Fernández 2013) and swimming functional morphology (Astudillo-Clavijo et al. 2015) all reveal a significant decline in phenotypic diversification through time for Geophagini. This pattern, however, is not found for diversification within Heroini or Cichlasomatini. In addition, Arbour and López-Fernández (2016) found declining feeding biomechanics disparity through time for all basal lineages of Cichlinae in South America, indicating early adaptive divergence and suggesting that divergence of lineages now recognized as tribes was also consistent with an adaptive radiation. Therefore, disparity through-time and lineage-through-time analyses coincide in finding an early burst in basal divergence of Neotropical cichlids. These results, particularly those based on morphological disparity, suggest that both the initial divergence of Neotropical cichlid tribes (Arbour and López-Fernández 2016) and subsequent diversification within Geophagini in South America are consistent with adaptive radiation (López-Fernández et al. 2013; Arbour and López-Fernández 2013; Astudillo-Clavijo et al. 2015). The pattern of early niche divergence followed by a reduced diversification rate suggests there was a progressive filling of adaptive zones and niche partitioning among ancestors of contemporary tribes and genera. We have interpreted these patterns as evidence of early ecological opportunity for cichlid diversification in South America.

Although evidence suggests all main lineages of Cichlinae may have diversified in an early adaptive burst involving the ancestral forms leading to the modern tribes, diversification within the tribes clearly did not occur at a uniform rate. Early divergence in South America was likely dominated by the radiation of Geophagini.

Rapid diversification into new niches by geophagins may have precluded divergence in other lineages of South American cichlids, particularly Heroini and Cichlasomatini, which did not undergo phyletic and functional diversification until later (e.g., Fig. 1, and see López-Fernández et al. 2013). Geophagins occupy a vast swath of South American cichlid functional morphospace (Fig. 2, and see López-Fernández et al. 2013; Arbour and López-Fernández 2014). Other tribes in South America tend to show little overlap with geophagins (Fig. 2, e.g., South American Heroini, Cichlasomatini, Retroculini, Cichlini), or when they do overlap, tend to do so toward the center of morphospace where both morphology and ecology tend to be generalized (e.g., most Cichlasomatini). This morpho-functional segregation is most notable among the basal South American heroin lineages *Pterophyllum*, *Symphysodon*, *Uaru*, *Heros,* and *Mesonauta*. These genera display extreme morphologies both for feeding and swimming (Fig. 2) and often (although not always) can be found coexisting with each other in structurally complex habitats where geophagins tend to be uncommon (e.g., Fig. 3b). Lineages of South American heroins may have been under selective pressure to move into adaptive zones unoccupied by geophagins (e.g., peaks 5 and 7, Fig. 2 and see above). These heroin zones are characterized by strong suction or biting forces and deep bodies optimized for complex habitats that are not broadly occupied by substrate sifting or predatory geophagins that occupy zones 1, 2, and 3 (Fig. 2). Available niches would have been further limited by the presence of a potentially high diversity of non-cichlid fishes (e.g., Winemiller et al. 1995; Albert and Reis 2011, and see Sects. 3.3 and 4), resulting in the highly specialized basal South American Heroini.

3.3   *Central America: Renewed Ecological Opportunity and Convergence*

Analysis of rates of phenotypic divergence (as opposite to the pattern of change in phenotypic disparity) among South and Central American lineages of Cichlinae, controlling for biogeographic origin, reveals an intriguing pattern. Using Node Height Tests (Freckleton and Harvey 2006; Slater and Pennell 2014) to correlate the rate of phenotypic divergence and time or branch lengths in a tree, Arbour and López-Fernández (2016) compared rates of phenotypic evolution between two groups formed by South and Central American lineages of Cichlinae, respectively. These analyses revealed a significant effect of biogeography on rates, showing a decrease in phenotypic divergence in South American cichlids on both PC1 and PC2 of feeding morphospace (Fig. 2). The Central American heroin lineages initially showed high morphological evolutionary rates followed by a decrease along PC1. Both the initial rate and the subsequent rate of decrease mirrored those for South American lineages along the ram–suction gradient of morphospace (Fig. 4). Likewise, the initial increase in evolutionary rates following the colonization of Central America suggests that Heroini experienced ecological release (i.e., renewed
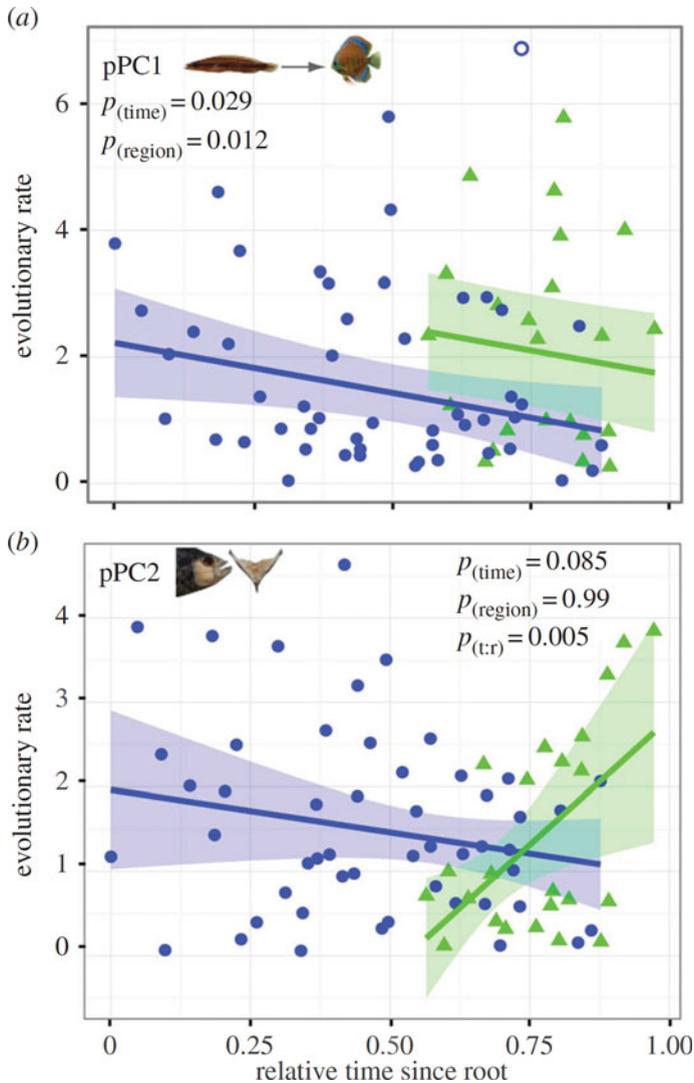
Fig. 4 Changes in evolutionary rates of ram–suction morphology in South and Central America (top row, PC1; bottom row, PC2) on a relative-time chronogram of 75 species of Neotropical cichlids based on López-Fernández et al. (2013). Evolutionary rate estimates (absolute value of standardized independent contrasts) through time for South American (blue, circles) and Central American (green, triangles) taxa, including the regression line (shaded region = 95% CI) from a Node Height Test using a robust regression of standardized independent contrasts against distance from the root for each node (Reproduced with permission from Arbour, J. H., & López-Fernández, H. (2016). Continental cichlid radiations: functional diversity reveals the role of changing ecological opportunity in the Neotropics. *Proceedings of the Royal Society B: Biological Sciences*, *283* (1836), 20160556)

ecological opportunity) in the absence of competitors. This conclusion is further supported by the extensive overlap between South American Geophagini and Central American Heroini morphospace (Fig. 2, López-Fernández et al. 2013; Arbour and López-Fernández 2014), suggesting that, once released from competition, heroins were able to diversify into similar morphospace and ecological niches as those of geophagins. Interestingly, divergence in ecomorphology was paralleled by increased rates of vision protein molecular evolution (Hauser et al. 2018). At the lineage level, these findings may also be congruent with the increased rate of divergence found by McMahan et al. (2013) within Heroini. A recent study analyzing purely lineage divergence suggests that diversification shifts across cichlids may be frequently related to renewed ecological opportunity after colonization of new biogeographic regions (Burress and Tan 2017).

It is important to highlight that the observed decline in evolutionary rates in Central America is not mirrored by an equivalent reduction in phenotypic disparity through time (see above). This suggests either that (a) Central American heroins may be undergoing an adaptive radiation that has not yet reached the point at which niches are saturated and therefore there is no evidence of a decline in the rate of functional diversification (e.g., Hulsey et al. 2010), (b) different processes drove functional divergence between South and Central America, or (c) either the methods or datasets yield insufficient statistical power to detect a decline in morphological differentiation among Central American heroins (and see Arbour and López-Fernández 2016).

While rates of evolution along PC1 for Central American lineages declined, rates started low and continually increased along PC2, the suction/biting gradient (Figs. 2 and 4). This result, fundamentally different from the observations in South American lineages, suggests that variation toward larger oral jaw muscles and pharyngeal tooth plates in Central American cichlids may be associated with access to biting/crushing adaptive zones not occupied by cichlids in South America (Arbour and López-Fernández 2014, 2016; Burress 2016). Variation in the suction/biting axis further highlights the expansion of the functional morphological and ecological repertoire of heroins in Central America. On the one hand, the clade invaded adaptive zones otherwise restricted to geophagins (e.g., piscivory, substrate sifting), but it also evolved into the use of entirely novel adaptive zones among Neotropical cichlids. This is particularly notable in the appearance of frugivorous and detritivorous niches, which in South American rivers are restricted to Characiformes, Siluriformes, and other non-cichlid fishes (e.g., Curimatidae, Prochilodontiade, Serrasalmidae, Loricariidae, Winemiller et al. 2006; Correa et al. 2007, 2015; Sidlauskas 2008; Lujan et al. 2012). Thus, evidence continues to accumulate supporting the idea that cichlid diversification in South America was limited by interactions among clades within the family (e.g., Geophagini) as well as non-cichlids (e.g., Characiformes). The increasing rates of evolution in Central American heroines along the suction/biting axis suggests that ecological release from these South American competitors may have played a large role in the functional expansion experienced by the clade (e.g., Winemiller et al. 1995; López-Fernández et al. 2013; Arbour and López-Fernández 2014, 2016; Burress 2016).

4 Divergence in Rivers and Lakes: Are Processes the Same?

Despite the current uncertainty regarding the age of cichlids, it is indisputable that Neotropical and most African riverine cichlid taxa belong to older lineages than those present in lake radiations of both Africa and Central America (e.g., Verheyen et al. 2003; Koblmüller et al. 2008; Elmer et al. 2009; Schwarzer et al. 2009, 2011; Betancur-R et al. 2017a; López-Fernández et al. 2013; McMahan et al. 2013; Friedman et al. 2013, Matschiner 2018). An obvious "null" hypothesis to explain the comparatively limited diversity of cichlids in rivers is that lineage and phenotypic divergence may have occurred at a constant rate over a long period of time, whereas diversity in the East African lakes resulted from a recent "explosion" of diversification. However, this constant-rate hypothesis is repeatedly rejected by comparative analyses of Neotropical cichlids, indicating more complex processes were involved in generating modern diversity. Ecological and functional diversity in riverine Cichlinae appears to have originated early in the South American divergence of cichlids, followed by a slowdown in phenotypic diversification (see Sect. 3). Such morphological stasis within the clade suggests that ecological selective pressures that shaped the early functional diversification of Neotropical cichlids have remained active for an extended period of time. In combination, comparative analyses point toward a clear division of the timeline into an early period of South American adaptive radiation that originated early diverging lineages (tribes and genera), followed by a more recent but prolonged period during which diversification appears to have been dominated by speciation within the ecomorphological boundaries of genera (Argolo et al. 2020). Phenotypic stasis in South America, however, has not been uniform across all clades, with some clearly undergoing much later adaptive diversification, particularly within *Crenicichla* (e.g., Burress et al. 2013, 2018; López-Fernández et al. 2013). A second major period of adaptive divergence resulted from renewed ecological opportunity following the invasion of Central America by heroins (Arbour and López-Fernández 2016; Hauser et al. 2018), but the phylogenetic signal of adaptive radiation is much less clear. It appears that this adaptive diversification process may be ongoing, at least in terms of further specialization along the suction–biting gradient. Clearly defining these different periods of divergence will be essential to circumscribe episodes in Neotropical cichlid evolution and to identify underlying forces that drove their divergence through the long and complex history of the Neotropical region.

With the exception of the incipient radiations of the heroin genus *Amphilophus* in Nicaraguan crater lakes (e.g., Barluenga et al. 2006; Elmer et al. 2010, and see Torres-Dowdall and Meyer 2021), the vast majority of modern Neotropical cichlids are adapted to live in rivers and floodplains. Therefore, beyond differences in age and tempo of evolution, the environmental and ecological "stage for evolution" in which the continental cichlid radiations unfolded may be essentially different from that provided by insular lakes. Lakes where recent cichlid radiations have evolved are generally island-like: they provide ecological opportunity within a restricted area and are largely, although not exclusively (e.g., Day et al. 2009), dominated by

cichlids, with limited influence of other fish taxa. In that sense, the adaptive radiations of lacustrine cichlids are much more like those of Caribbean *Anolis* (Losos 2009) or Galápagos finches (Grant and Grant 2008). In contrast, Neotropical cichlids, particularly in South America, evolved largely within riverine systems with long-established non-cichlid fish communities and frequent environmental disturbances that reshaped the landscapes, fluvial connectivity, and ecological conditions over tens of millions of years. Much evidence suggests (see above) that the ecological roles played by non-cichlid taxa influenced ecological opportunities for cichlids (e.g., Winemiller et al. 1995; López-Fernández and Albert 2011; Albert and Carvalho 2011). Recent work has modeled cichlid radiations in lakes on the basis of spatial and ecological multidimensionality combined with the influence of sexual selection (e.g., Wagner et al. 2012; Aguilée et al. 2013; Seehausen 2015). Although multiple niche dimensions are involved in the diversification of cichlids in both lakes and fluvial systems, certain factors seem to be more influential in lakes and others in rivers. For example, depth and sexual selection play a dominant role in lake radiations (Seehausen et al. 2008; Wagner et al. 2012; Seehausen and Wagner 2014), whereas community assembly and species interactions seem to have strongly influenced fish evolution in the Neotropical fluvial systems (Albert and Reis 2011; Bower and Winemiller 2019).

Ecological opportunity, or lack thereof, for cichlid diversification in the Neotropics was undoubtedly shaped by abiotic elements such as sea-level changes, orography, and associated changes in hydrology and fluvial geomorphology in South and Central America. Unfortunately, the complexity of this history makes it difficult to ascertain the environmental context for early Neotropical cichlid diversification. In South America, for example, extensive paleo-lakes or mega-wetlands that persisted for prolonged periods of time (e.g., Paleo Amazonas-Orinoco, Lago Pebas, Lundberg et al. 1998, 2010; Hoorn et al. 2010; Albert and Reis 2011) undoubtedly influenced fish evolution. However, compared to present-day lakes containing cichlid species flocks, these ancient South American mega-wetland systems were less insular and with different environmental conditions than closed lakes; they received water from huge drainage basins and probably were more similar to the vast floodplains of the modern South American Pantanal and Llanos. Consequently, these systems were almost certainly much more dynamic than an African Rift Valley lake. From the late Cretaceous to the end of the Miocene, South American mega-wetlands shifted between riverine, shallow lacustrine, and estuarine conditions under the influence of climate change, marine incursions and transgressions, and tectonic activity (Lundberg et al. 1998; Hoorn and Wesselingh 2010; Albert and Reis 2011). Thus, even assuming the mega-wetlands were an important setting for Neotropical cichlid evolution, we must remember that they were part of even larger fluvial systems. In such a context, and given the vast time expanses involved, it may be impossible to determine whether processes affecting early cichlid evolution in the South American mega-wetlands were similar to those in modern lakes. Ultimately, understanding Neotropical cichlid diversification requires analyses of historical biogeography in the context of repeated reconfigurations of river drainage networks

and the coevolution of large, complex assemblages of phylogenetically diverse fish species (e.g., Winemiller et al. 1995; Albert and Reis 2011).

The cichlid fossil record is, expectedly, moot on whether sexual selection or depth (both associated with coloration and visual cues, see Seehausen et al. 2008; Hauser et al. 2018) played a strong role in early Cichlinae divergence as they do in cichlid flocks within modern lakes. Most Neotropical rivers do not have major depth gradients, but rather are affected by dendritic spatial connectivity and dynamic responses to seasonal flow and flood regimes. Depth may be a major driver of cichlid divergence in lakes (Seehausen 2015), whereas, for river-dwelling cichlids, habitat fragmentation within fluvial networks promotes allopatric speciation (e.g., Dias et al. 2013 and see Seehausen and Wagner 2014). In riverine cichlids, the combined effects of hydrological disturbance (e.g., Albert et al. 2011; Crampton 2011), drainage capture (Ribeiro 2006; Albert et al. 2018), population fragmentation (e.g., Fagan 2002; Campbell Grant et al. 2007; Campbell Grant 2011), and river network architecture (e.g., Thomaz et al. 2016) are likely dominant elements influencing genetic structure and rates of speciation and extinction.

Several features of Neotropical cichlids suggest that sexual selection may be less influential when compared to its role in the evolution of cichlid species flocks in African lakes. Although sexual dimorphism is present in Cichlinae, it tends to be subtle and not as widespread as in African lake lineages. This may be a result of different light conditions in rivers compared to lakes. Vision-associated molecular evolution has been shown to be habitat-specific and is at least partially related to adaptation to dim light (e.g., Terai et al. 2006; Schott et al. 2014; Torres-Dowdall et al. 2015; Hauser et al. 2018). Although it seems indisputable that ecological and morphological specializations are prominent in cichlid evolution in both lakes and rivers, it is possible that ecological conditions in rivers limit the complementary role of sexual selection in adding to species diversity. It is perhaps telling that the two Neotropical genera with the greatest species richness, the geophagins *Apistogramma* and *Crenicichla*, each with about 100 species, show marked sexual dimorphism. Interestingly, while *Crenicichla* species display a considerable amount of functional diversity (e.g., Piálek et al. 2012, 2018; Burress et al. 2013, 2018; Arbour and López-Fernández 2014; Astudillo-Clavijo et al. 2015), *Apistogramma* seems to display much more limited morphological differentiation. It remains unclear whether sexual selection has a widespread role in speciation among these or other sexually dimorphic riverine Neotropical cichlids. For instance, Ready et al. (2006) demonstrated that color differences are associated with prezygotic reproductive isolation in populations of *Apistogramma caetei*, but the studied color forms were allopatric, suggesting that the principal driver of speciation was a response to local environments in allopatry rather than color-based assortative mating in sympatry as is the case in most lake cichlids (Ready et al. 2006; Seehausen et al. 2008).

Finally, despite the differences between lake and riverine environments, there is extensive convergence among cichlid assemblages in South American rivers and African rivers and lakes, which often harbor similar coexisting ecotypes or functional groups (e.g., Winemiller et al. 1995; Seehausen 2015). Seehausen (2015) suggested that the difference between lake and riverine cichlids in Africa often is one

of species richness and not necessarily of functional diversity. Regardless of their phylogenetic relations or ecological circumstances, cichlids tend to repeatedly evolve into certain niches and assemble into communities that contain similar sets of functional groups. These patterns suggest that local species interactions may constrain community structure (Montaña et al. 2014) and possibly limit niche diversification in rivers (Winemiller et al. 1995; Seehausen 2015). Conversely, as more species assemble into local communities, species interactions could intensify and thereby promote niche diversification. This generalization, however, can only be taken so far because there is a non-trivial number of niches occupied by East African lake cichlids that, to my knowledge, are not present in riverine cichlids of any continent. These include specialized ecologies such as eye-biting [Lake Malawi's *Dimidiochromis compressiceps* (e.g., Fryer and Iles 1972)] or scale predation [Lake Tanganyika's *Perissodus* (e.g., Hori 1993; Kusche et al. 2012)], among others. The availability of these niches to cichlids may be determined by available ecological opportunity. For instance, fin-nipping and scale feeding in South America is observed in several piranhas (Serrasalmidae) that frequently coexist with cichlids, and detritivory and frugivory, although present in Central American cichlids, is absent from South American lineages presumably because these feeding habitats are widespread among characiforms (Winemiller et al. 1995, and see above). Unfortunately, these patterns of niche occupation and exclusion, while suggestive of a historical role for species interactions in adaptive divergence, cannot be easily linked to actual drivers of speciation.

In contrast to our emerging understanding of the interplay between ecology, morphology, sexual selection, and genomic structure in the evolution of lake cichlids (e.g., Kocher 2004; Santos and Salzburger 2012; Brawand et al. 2014; Seehausen 2015; Malinsky et al. 2015), our knowledge of the evolutionary forces driving divergence of cichlids in the older and more dynamic fluvial systems of South and Central America remains limited. Revealing the processes that originated the modern ecomorphological diversity of Neotropical cichlids requires integrating two major types of elements affecting their divergence. Firstly, we must clarify the timing and extent to which environmental and biogeographic events of continental and regional scale affected diversification. Secondly, we must assess the evolving historical role of ecological interactions among fish clades. Together, environmental transformation and ecological coexistence through time shaped ecological opportunity and modulated the adaptive diversification of cichlids and other fishes in the Neotropics.

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