



## SYMPOSIUM

# Is the Medium the Message? Functional Diversity Across Abiotic Gradients in Freshwater Electric Fishes

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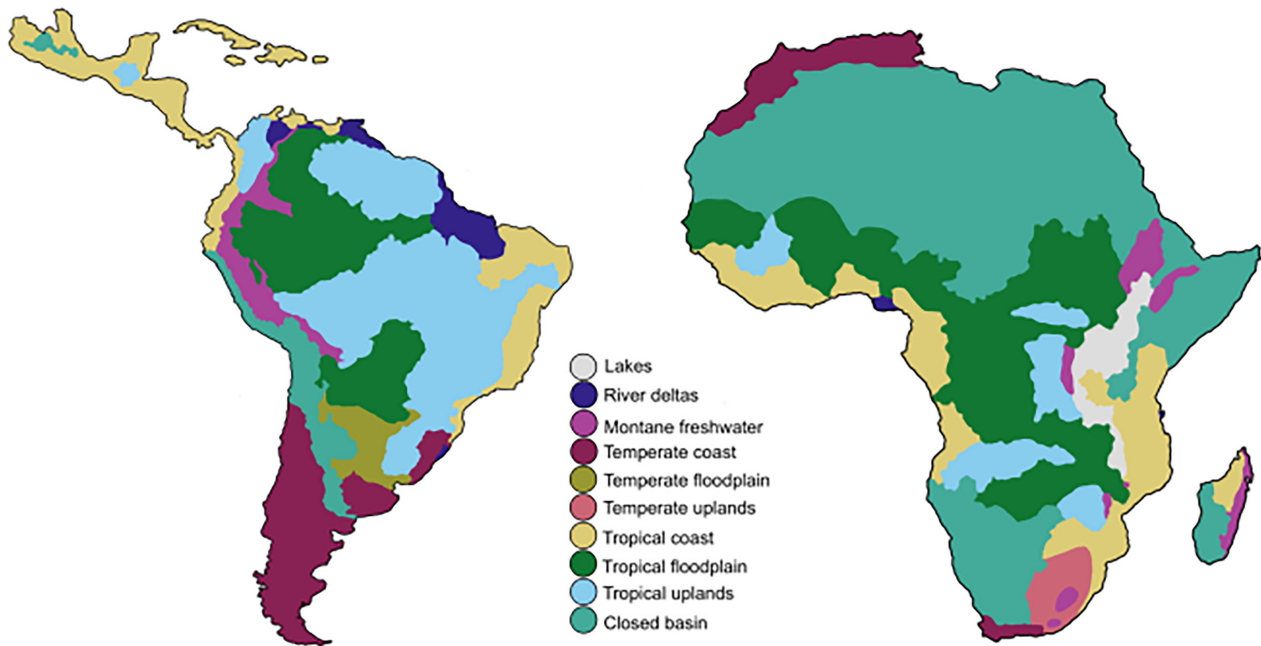
**Synopsis** Evolutionary transitions across abiotic gradients can occur among habitats at multiple spatial scales, and among taxa and biotas through a range of ecological and evolutionary time frames. Two diverse groups of electric fishes, Neotropical Gymnotiformes, and Afrotropical Mormyroidea, offer interesting examples of potentially convergent evolution in aspects of morphological, physiological, and life history traits. We examined biogeographical, morphological, and functional patterns across these two groups to assess the degree of convergence in association with abiotic environmental variables. While there are superficial similarities across the groups and continents, we found substantially more differences in terms of habitat occupancy, electric signal diversity, and morphological disparity. These differences likely correlate to differences in biogeographical histories across the Neotropics and Afrotropics, biotic factors associated with aquatic life and electric signals, and sampling issues plaguing both groups. Additional research and sampling are required to make further inferences about how electric fishes transition throughout diverse freshwater habitats across both microevolutionary and macroevolutionary scales.

## Introduction

Freshwater habitats account for just 0.01% of the Earth's water supply, but they provide area for nearly 50% of fish species (Lundberg et al. 2000, Albert et al. 2020, Lavoué 2020, Eschmeyer's Catalogue of fishes). Continental river and lake basins include a wide range of freshwater habitats, from torrential mountain rivers to meandering lowland river channels and their flanking floodplains, ancient tectonic lakes, a vast network of small streams flowing under a closed-forest canopy, hypogean caves and aquifers, interior wetlands, and coastal estuaries (Fig. 1; van der Sleen & Albert 2017). Tropical freshwater habitats exhibit strong longitudinal gradients by stream order, climate and soil chemistry, that control abiotic habitat properties like water velocity, water volume, and water chemistry (Vannote et al. 1980, Larsen et al. 2019). The two largest and most diverse freshwater regions of the world are the Neotropics and Afrotropics, which together are home to more than 9300 (or 51%) of the c. 18,000 valid species of freshwater

fishes on Earth (Fig. 1; Albert et al. 2020, Lavoué 2020, Eschmeyer's Catalogue of fishes).

Two diverse groups of freshwater electric fishes, Gymnotiformes and Mormyroidea, inhabit Neotropical, and Afrotropical freshwaters, respectively. These fishes have historically been considered an example of convergent evolution (Roberts 1972, Lowe-McConnell 1975, Bullock & Heiligenberg 1986, Marrero & Winemiller 1993, Kirschbaum 1995, Winemiller & Adite 1997, Bullock et al. 2005, Zakon et al. 2006). More recent research has shown there are more differences than similarities in these fishes (Tagliacollo et al. 2015, Ford et al. *in press*, Ford et al. *in review*). Studies on genetics, electric organ discharges (EOD), physiology, diet, habitat occupancy, and morphology show examples of divergence or incomplete convergence, with few examples of complete or total convergence (Gallant et al. 2014, Ford et al. *in review*). While many of these studies focused on biotic factors and variables, this study looks at several abiotic factors as potential explanations for electric fish



**Fig. 1** Habitat diversity across the Neotropics and Afrotropics. Maps of the Neotropics (Central and South America) and the Afrotropics (continental Africa) with labels for habitat types. The Neotropics are dominated by Tropical uplands and tropical lowlands, while the Afrotropics are dominated by Closed basins + Xeric basins and Tropical lowlands. There are more prominent river deltas in the Neotropics and more lakes in the Afrotropics. Habitats include: lakes, river deltas, montane freshwater, temperate coast, temperate floodplain, temperate uplands, tropical coast (dry), tropical coast (wet), tropical lowlands, tropical uplands, and closed basins + xeric basins. Based on Rios-Touma et al. and Fouchy et al. figures.

diversity patterns. In context of “abiotic transitions at an evolutionary level”, we assessed similarities across Gymnotiformes and Mormyroidea using biogeographical patterns, habitat utilization, species diversity, EODs, and morphological characteristics.

## Methods

We obtained habitat data for all 261 valid species of Gymnotiformes and 199/234 (85.0%) valid species of Mormyroidea from museum collection records and the published literature reports (Corbet 1961, Greenwood 1966, Ita 1978, Banister & Bailey 1979, Møller et al. 1979, Balon & Stewart 1983, Gosse 1984, Lévêque et al. 1991, Bailey 1994, Paugy et al. 1994, Kirschbaum 1995, Sanyanga et al. 1995, Ikomi 1996, van der Bank & Kramer 1996, Bigorne 2003a, Bigorne 2003b, Seegers et al. 2003, Lavoué et al. 2004, Sullivan & Hopkins 2005, Konan et al. 2006, Hopkins et al. 2007, Lavoué et al. 2010, Albert & Reis 2011, Lavoué 2011, Lavoué 2012, Kramer 2013, Monsembula Iyaba et al. 2013, Lavoué & Sullivan 2014, Lamanna et al. 2016, Lavoué 2016, Sullivan et al. 2016, Rich et al. 2017, Albert et al. 2020, Mulelenu et al. 2020, Fricke et al. 2021, gbif.org). We used primary literature when available for all species, but there is more primary literature available for Gymnotiformes than Mormyroidea. We supple-

mented the primary literature with data from GBIF for other species.

We recorded the presence and absence of each species based on seven habitat types following the classification of tropical freshwater habitats by Albert et al. (2020): (1) deep (5–100 m) river channels; (2) high-gradient upland streams; (3) low-gradient lowland streams; (4) floodplains; (5) ancient tectonic (rift) lakes; (6) rapids; and (7) caves/aquifers. These data were used to graph the number of habitats occupied by each genus and species, along with the diversity of species in each habitat type. We compiled a list of species for which we have EOD, habitat, and skull morphology data. Three-dimensional geometric morphometrics were performed on 62/261 (23.7%) gymnotiform species in 3D-Slicer using the landmark scheme found in Ford et al. *in press*, with representatives from 23/29 (79.3%) gymnotiform genera (Supplemental Tables 1 and 2; Federov et al. 2012). We also sampled 42/234 (17.9%) mormyroid species, with representatives from 17/20 (85%) mormyroid genera and used the landmark scheme found in Ford et al. *in press* and Ford et al. *in review* (Supplemental Tables 1 and 2). Procrustes superimpositions and a principal components analyses were performed in *geomorph* (Collyer and Adams 2018, Adams et al. 2021, Collyer and Adams 2021, RStudio Team 2021). We highlighted the overall habitat distribution by color for each individ-

ual sampled for each group. Finally, we outlined genus representatives for the groups and grouped by habitat distribution to examine trends of body-shape diversity.

## Results

### Habitat utilization

There are contrasting patterns of habitat utilization across genera and species of Gymnotiformes and Mormyroidea (Fig. 2). In the Neotropics, the majority of gymnotiform genera occupy a single habitat type (19 of 35 genera, 54.2%), while only two genera occupy five or more habitat types. Most species in Gymnotiformes also occupy a single habitat type (192 of 261 species, 73.5%), while no single species occupies five or more habitat types. The overall pattern of habitat utilization in this group is a power function in which most genera and species occupy very few habitat types, while few genera and species occupy many. Several genera include species that occupy vastly different habitat types, e.g., species of *Brachyhyopomus* and *Sternarchella* inhabit either small streams or deep river channels, respectively (Supplementary Table 3). The same pattern is not found in Mormyroidea, where the highest proportion of genera occupy five or more habitat types (10 of 20 genera, 50%), while only two genera are restricted to a single habitat type. Most mormyroid species occupy at least two habitat types (157 of 198 species, 79%). The result is a much more even distribution of habitat occupancy.

### Habitat species diversity

The Neotropics and Afrotropics have differing patterns of gymnotiform and mormyroid species diversity across habitats (Fig. 3). In the Neotropics, the deep river channels and lowland rainforest streams have the highest species diversity with dramatically fewer species found in floodplains, and even fewer in rapids. In the Afrotropics, there is a more even distribution of species across river channels, floodplains, and lowland and upland streams. There are fewer mormyrid species found in rapids or the rift/tectonic lakes in eastern Africa.

### Habitat EOD diversity

Across Gymnotiformes and Mormyroidea, the distribution of EOD diversity across habitat types follows different patterns (Fig. 4). In the Neotropics, the majority of wave-type gymnotiform species (i.e., Apterontidae and Sternopygidae) inhabit swiftly moving river channels ( $n = 86$ ), while a minority inhabit slowly flowing streams ( $n = 27$ ). By contrast, the majority of pulse-type gymnotiform species (i.e., Gymnotidae, Hypopomidae, Rhamphichthyidae) inhabit slower-moving waters ( $n = 61$ ), while a minority inhabit larger channels ( $n = 14$ ).

In the Afrotropics, there is only one wave-type mormyroid species (*Gymnarchus niloticus*), which inhabits all our listed habitat types (Gosse 1984, Bigorne 2003a). All other mormyroid species have a pulse-type EOD. The majority of mormyroids are pulse-type species found in large river channels ( $n = 124$ ), while the minority are found in slower-moving waters ( $n = 78$ ).

### Snout and EOD diversity

In both Gymnotiformes and Mormyroidea, there are more short-snouted (i.e., brachycephalic) species than species with intermediate-length or elongate (i.e., dolichocephalic) snouts (Fig. 5). Among Gymnotiformes, both wave- and pulse-type species exhibit extreme brachycephalic and dolichocephalic morphologies. In Mormyroidea, the only wave-type species (*G. niloticus*), has an intermediate-length snout. All known aspects of diversity in mormyroid head and jaw shapes are observed in pulse-type mormyroid species.

### Skull diversity across habitats

There are different patterns of skull shape diversity across gymnotiform and mormyroid species, especially when species are grouped by habitat occupancy (Fig. 6). In the Neotropics, the species that occupy the largest portion of the morphospace are those found in the fewest number of habitat types ( $< 3$  habitats). This region of the morphospace is dominated by Apterontidae, a morphologically diverse family that primarily inhabits deep (5–100 m) river channels in lowland Amazonia. There is also a large area of the morphospace that includes gymnotiform species occupying five or more habitat types. In the Afrotropics, most mormyroid species are found in multiple habitat types (Figs 2 and 3). The largest portion of the morphospace includes species that inhabit five or more habitat types (Fig. 6). Taxa occupying fewer habitat types occupy a smaller area of the PCA space.

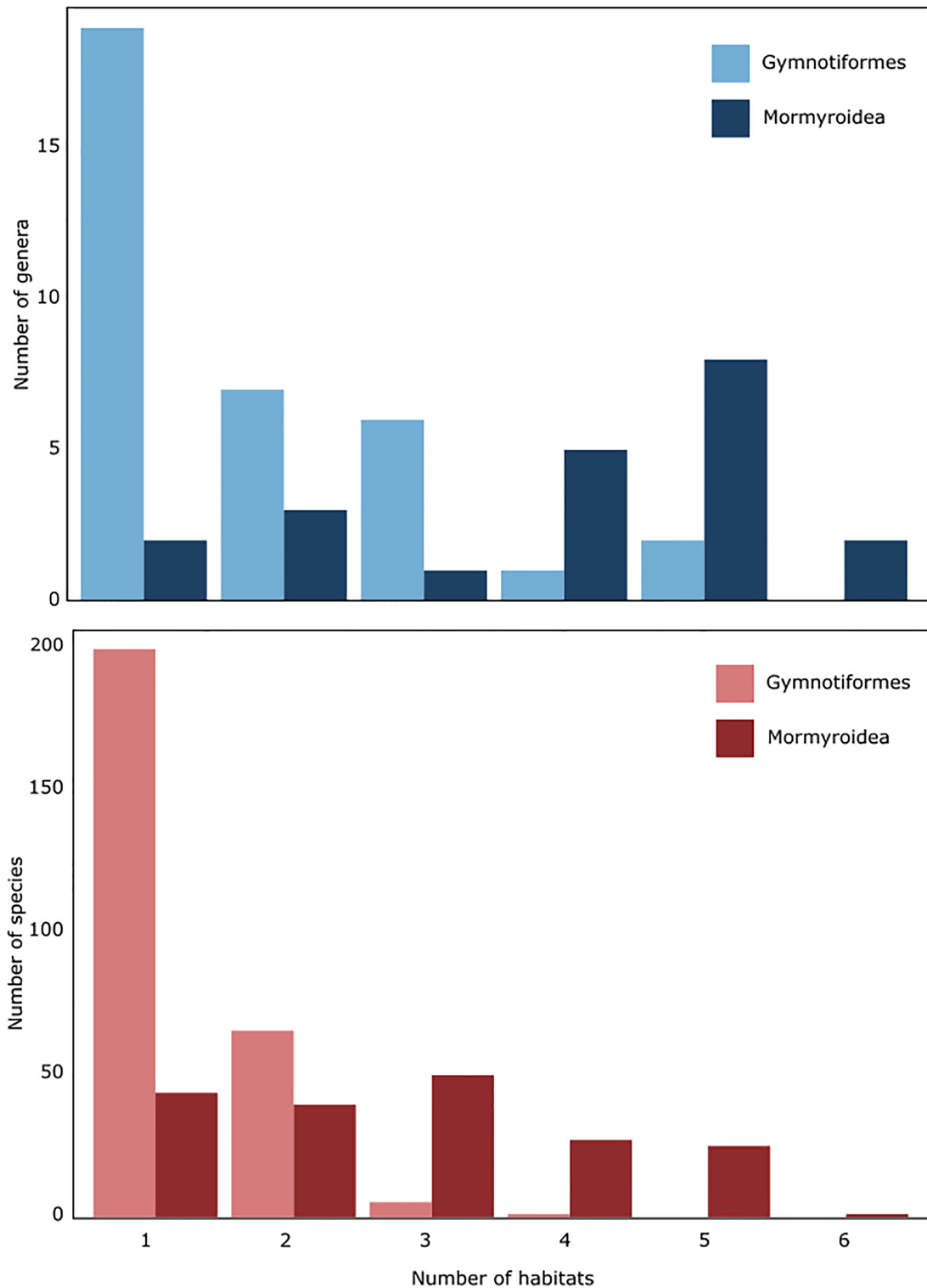
### Body morphology diversity

Patterns of body shape (i.e., body depth) differ between Gymnotiformes and Mormyroidea (Fig. 7). In Gymnotiformes, the largest diversity of body shapes is found in the deep channels; a pattern that makes sense due to the morphological diversity of apteronotids. There is a large amount of body shape diversity in Mormyroidea, regardless of habitat occupancy.

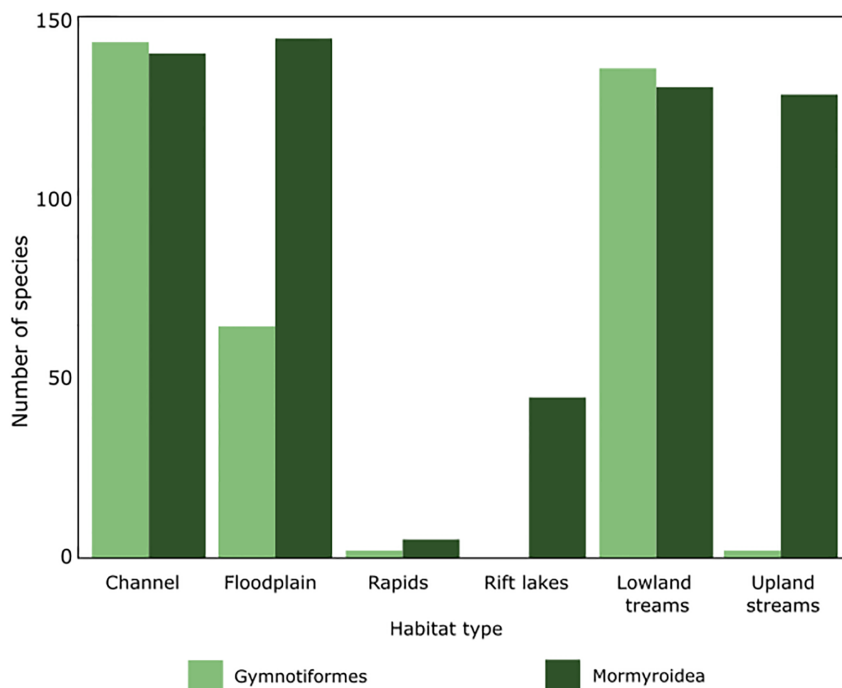
## Discussion

### Physical geography

We observed similarities and substantial differences in the distribution of habitat types among biogeographic



**Fig. 2** Species and genera habitat utilization. **(A)** The distribution of habitat utilization by the genera in Gymnotiformes (light) and Mormyroidea (dark). The highest number of gymnotiform genera occupy a single habitat type, while most mormyroid genera occupy 5 habitats. **(B)** The distribution of habitat utilization by the species in Gymnotiformes (light) and Mormyroidea (dark). Most gymnotiform species occupy a single habitat, while the distribution of mormyroid species is more even across 1–4 habitats. The habitat utilization patterns are different across the two groups of interest.



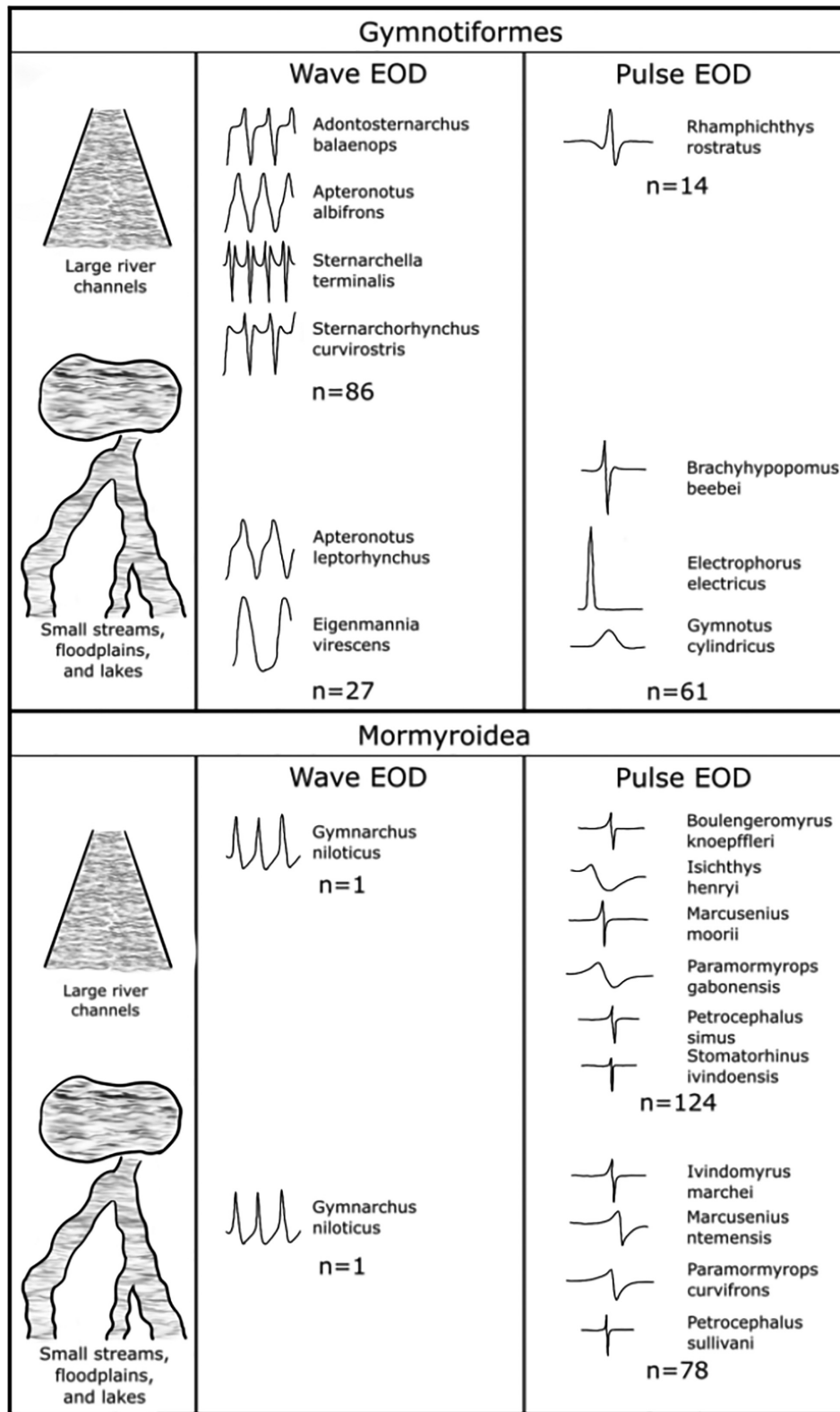
**Fig. 3** Species diversity by habitat type. The distribution of gymnotiform (light) and mormyroid (dark) species diversity across six habitat types: channels, floodplains, rapids, rift lakes, lowland streams, and upland streams. In Gymnotiformes, channels and lowland streams are most species rich, while rapids and rift lakes have the lowest species diversity. In Mormyroidea, the channels, floodplains, lowland streams, and upland streams have similar amounts of species richness. The rapids and rift lakes are also the least species rich. There are some similarities across groups, but also some clear differences in continental habitat diversity.

regions (Fig. 1). Both the Neotropics and Afrotropics include large areas of tropical lowlands, floodplains and wetlands, humid coastal plains, and tropical upland savannas (Fouchy et al. 2018, Rios-Touma et al. 2018). However, the Afrotropics has many more endorheic and xeric river and lake basins, and smaller rivers and river deltas (Fouchy et al. 2018). African ecosystems are more dominated by large arid desert areas in the northern and southwestern regions (Fouchy et al. 2018). In contrast, South American ecosystems are dominated by large, lowland tropical rainforests and wetlands (i.e., Amazon, Orinoco, La Plata) and tropical savannas of upland shields (Brazilian and Guiana) (Rios-Touma et al. 2018).

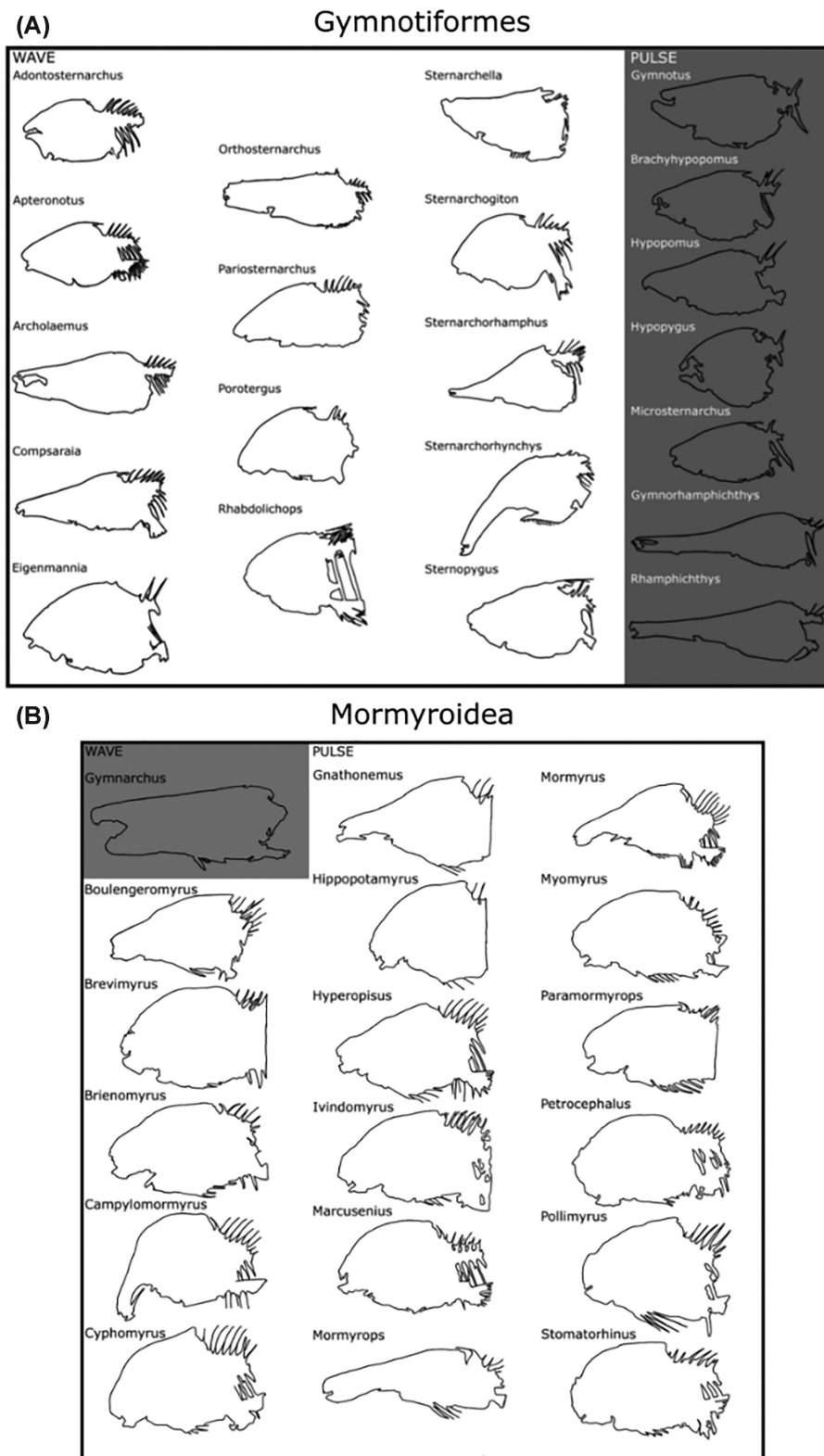
It is also important to consider the different climatic and geological histories of these two biogeographic regions. The modern Amazon river basin is not only much larger than the river basins in Afrotropics (in terms of total aquatic habitat volume and surface area), but Amazonian habitats have also been more climatically stable over evolutionary time (Albert & Reis 2011, Albert et al. 2020), and have been exposed to larger-scale and biotically impactful river network rearrangements (Albert et al. 2021). The Pebas Megawetland likely contributed to high speciation and extinction rates of aquatic taxa in the paleo-Amazon dur-

ing the early and middle Miocene (c. 22–10 Ma), and portions of that diversity have persisted into modern times (Albert & Reis 2011, Albert et al. 2020). Further, the South American platform has lower average topographic relief (is flatter) than the African platform and has likely had the influence of river capture to both divide and connect portions of the watershed (Albert & Reis 2011, Val et al. 2022). The Afrotropics experienced higher extinction and speciation rates during Neogene than the Neotropics, primarily due to aridification and the conversion of tropical forests to savannas (Sepulchre et al. 2006). These differences likely contribute to the overall diversity patterns seen across these two groups, with temporal continental changes being just as important as other abiotic factors. Gymnotiformes have speciated over longer amounts of time across the Neotropics compared to the more rapid speciation of Mormyroidea (Albert & Reis 2011, Peterson et al. 2022). Today, the continents have significantly different flooding regimes, with Amazonia having many large, seasonally flooded wetlands (Albert & Reis 2011). The Afrotropics does not have wetlands of the same size, but instead has multiple large, rift lakes that are absent from the Neotropics (Sepulchre et al. 2006, Fouchy et al. 2018).

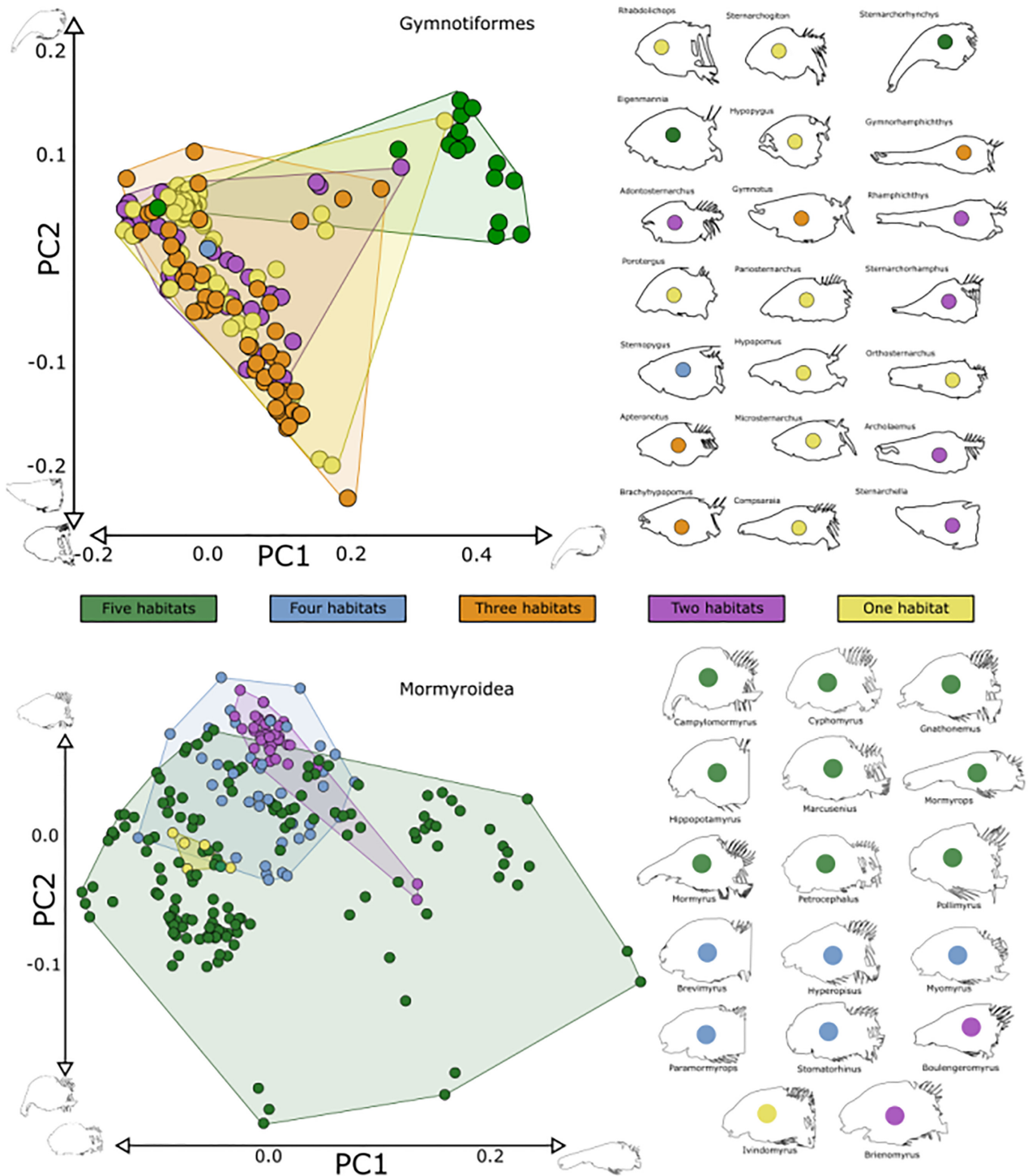




**Fig. 4** Electric organ discharge diversity across habitat type. The EOD diversity across habitat types for both Gymnotiformes and Mormyroidea. For Gymnotiformes, most wave-type species are found in large river channels ( $n = 86$ ), while most pulse-type species are found in small streams, floodplains, and lakes ( $n = 61$ ). In Mormyroidea, there is only one species of wave-type EOD, *Gymnarchus niloticus*, which is found in all habitat types. More pulse-type species live in deep river channels ( $n = 124$ ) than in slower-moving waters ( $n = 78$ ). The patterns across these two groups are noticeably different. Note that data are incomplete and based on a combination of literature review and distribution data from gbif.com

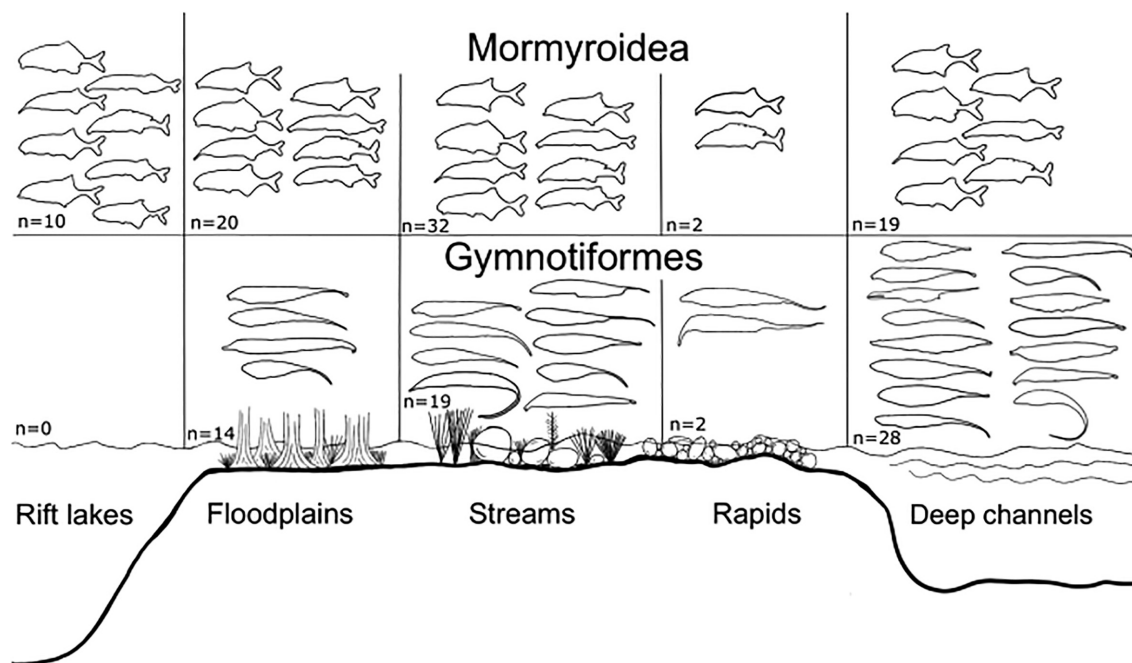


**Fig. 5** Head and skull shape diversity across EOD types. Skull outlines depict the overall head and skull shape diversity across Gymnotiformes and Mormyroidea, separated by EOD type. **(A)** In Gymnotiformes, there are short (brachycephalic), intermediate, and long (dolichocephalic) species in both wave- and pulse-type species. **(B)** In Mormyroidea, the only wave-type species (*Gymnarchus niloticus*) has an intermediate-length snout. All other head and skull shape diversity is found in the pulse-type species. There are clear differences in the patterns across these two groups.



**Fig. 6** Principle Components Analysis of skull shape with habitat information. **(A)** A PCA of gymnotiform species colored by habitat occupancy numbers. There is a lot of overlap across species, but the largest portion of the morphospace is occupied by species that are found in only one habitat (yellow polygon). PC1 represents 45.9% of the morphological variation, while PC2 represents 16.2% for Gymnotiformes. **(B)** A PCA of mormyroid species, colored by habitat occupancy numbers. The largest portion of the morphospace is occupied by species that are found in five habitats (green polygon). PC1 represents 35% of the morphological variation, while PC2 represents 17.7% for Mormyroidea. These patterns are different across the two groups.





**Fig. 7** Body shape diversity across habitats. There are body outlines of both gymnotiform and mormyroid genera that are found in each habitat type. While there are not clear patterns of traits like body depth across habitats in Mormyroidea, there are some indications that deeper-bodied Gymnotiformes are found in deeper river channels. There do not appear to be any patterns in terms of traits like tail length or snout length for either group.

### Abiotic versus biotic factors

We also observed stark differences in the relationships between gymnotiform and mormyroid EODs and factors such as habitat type and morphology. While gymnotiform EOD diversity is greatest in large and deep river channels, more mormyroid species are known in slowly moving waters of rainforest streams and lakes (Figs 3 and 4). When comparing head shape diversity and EOD diversity, both wave- and pulse-type gymnotiform fishes exhibit high amounts of craniofacial diversity. This may be phylogenetically linked; the most specious clade of Gymnotiformes is Apterontidae, a morphologically diverse family largely found in deep river channels (Fig. 5). Most craniofacial diversity in Mormyroidea is found in the pulse-type fishes (Fig. 5). Again, this is likely phylogenetically linked as *G. niloticus*, the only wave-type mormyroid, is the sister clade to all other Mormyroids. Mosaic evolution in the rates of the ecophysiological traits underlying phylogenetic niche conservatism may allow some traits and clade to diversify morphologically and ecologically faster than others. Phylogenetic inertia may be playing a role, allowing certain portions of each clade to diversify while other portions remain less morphologically and ecologically diverse.

While these differences between Gymnotiformes and Mormyroidea could be explained in terms of abiotic factors such as water type and flow-speed, we cannot ig-

nore the biotic factors that likely play a large role in the diversity patterns across these groups. It is likely that one factor leading to the evolution of EODs is the ability to navigate, communicate, and hunt during nocturnal hours in water systems (Møller et al. 1979). EODs in weakly electric fishes are also considered species- and sex-specific in both groups, leading to strong sexual selection (Albert & Crampton 2005, Arnegard et al. 2010, Ho et al. 2010). Other morphologies, including those of head and skull shape, are also sexually dimorphic in some gymnotiform species (Fernandes et al. 2002, Albert & Crampton 2009, Santana & Fernandes 2012, Hilton & Cox Fernandes 2017, Evans et al. 2019, Keeffe et al. 2019). Functional traits, such as EOD and skull shape, are also multi-functional and important for behaviors such as feeding and fighting (Albert & Crampton 2005, Evans et al. 2018, Evans et al. 2019). In electric fishes, head shape also plays an important role in electroreception (Xu-Friedman & Hopkins 1999, Albert & Crampton 2005). We therefore conclude that lineage and phenotypic diversification of electric fishes occur under the influence of both abiotic and biotic factors, as they do in other diverse clades of tropical organisms (Arnegard et al. 2010, Albert et al. 2020).

### Taxonomic and sampling factors

There are clear differences across habitats in terms of utilization, diversity, and morphology of

Gymnotiformes and Mormyroidea. While many Gymnotiformes occupy a single habitat type and few occupy many, most mormyroids occupy more than one habitat type (Fig. 2). The deep river channels in the Neotropics dominate gymnotiform species diversity, while there is more homogeneity of species diversity among mormyroids across the Afrotropics (Fig. 3). The skull shape diversity patterns across these groups show some similarities, but overall, the patterns remain largely distinct (Fig. 6). The most craniofacially diverse group of mormyroid fishes occupy five or more habitats, while the most craniofacially diverse gymnotiform fishes occupy a single habitat.

While these patterns appear robust, there are some taxonomic issues that may skew these results. The species-level taxonomy of Mormyroidea remains poorly resolved. The majority of taxonomic papers about Mormyroidea involve naming newly identified species and resolving phylogenetic relationships and naming inaccuracies. The gymnotiform literature is also focused on identifying new species but has also expanded to studies of functional, biogeographical, and physiological topics, as well as analysis of within-species variation (Craig et al. 2017, Evans et al. 2017), ontogenetic and sexual dimorphism (Albert & Crampton 2009, Fronk et al. 2019, Garcia and Zuanon 2019), and cryptic species (Milhomen et al. 2008, Waltz 2019). There are also far more data on biogeographic distributions in Gymnotiformes (and across the Neotropics in general) than in Mormyroidea. Despite recent advances in mormyroid taxonomy and biogeography (e.g., Picq et al. 2020, Mutizwa et al. 2021), substantially more efforts will be required to obtain comprehensive and complete distributional datasets.

## Conclusions

Electric fish clades exhibit more phenotypic divergence than convergence along abiotic gradients of elevation, climate, and habitat type. In gymnotiform and mormyroid taxa, phenotypic differences in head, mouth, and body shape, are not directly correlated with these simple abiotic gradients. Inferences on trophic position from craniofacial morphology, behavioral observations, gut-contents, and stable isotope data indicate a broader range of trophic roles for brachycephalic than dolichocephalic gymnotiform species, but not for mormyroids (Evans et al. 2019). Only dolichocephalic mormyroids are thought to be top predators (e.g. *Mormyrops*) (Kouamelan et al. 2000). While extreme brachycephalic and dolichocephalic head shapes have evolved in each group multiple times, closer examination of Gymnotiformes and Mormyroidea show more examples of divergence or incomplete convergence than

complete convergence (Ford et al. *in press*, Ford et al. *in review*).

The effects of abiotic environmental gradients on diversification in weakly electric teleosts are complex. We found no simple direct links between morphological disparity or EOD diversity and any single trophic, habitat, or abiotic variable. Both clades evolved over a lengthy time-period of tens of millions of years, and across a continental-scale arena of millions of square km, and yet that geographical separation appears to have led to differences in biogeographical and diversity patterns (Albert & Reis 2011). Each clade encompasses many distinct evolutionary lineages, all evolving under the influences of multiple external environmental (habitat utilization, trophic specialization, sexual communication), and internal organismal (chromosomal and developmental constraints) factors. Comprehensive studies of these groups need to incorporate integrative and interdisciplinary methods to answer these complex questions of diversity patterns. Our work in this study shows that patterns of phenotypic evolution in freshwater electric fishes is at best weakly correlated with those abiotic factors available to us to evaluate. Different patterns of evolution are more pronounced than commonalities in the two weakly electric teleost radiations.

## Author contributions

K.L.F. and J.S.A. conceived the ideas and designed the methodology. K.L.F. collected the data, analyzed the biogeographical and morphological data, completed the literature review, and led the writing of the manuscript. All authors contributed to the drafts and gave final approval for publication of the manuscript.

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## Supplementary data

Supplementary data available at [ICB](#) online.

## Data availability

CT scans of all individuals are being made freely available through the open-source web program MorphoSource.

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