UNTANGLING FOOD WEBS: IDENTIFICATION OF DRIVERS AND MAJOR PATTERNS IN PREDATOR-PREY INTERACTIONS

A Dissertation

by

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ABSTRACT

Identification of the main factors (e.g., species traits, environmental conditions) underlying predator-prey interactions is an important step to reveal species organization within food webs, potentially improving our predictions and management of natural ecosystems. Using a large and detailed dataset of freshwater and estuarine fishes, I explored how body size and other functional traits of consumers are linked with their trophic position, trophic niche width, and food item size. I also explored the degree to which phylogenetic relatedness and morphological similarity predict similarity of consumer species in terms of diet and stable isotopic ratios (δ^{15}N and δ^{13}C), two common descriptors of the trophic niche. Functional traits were significantly associated with phylogeny, and both morphological traits and phylogeny were significantly associated with fish diets and isotopic ratios; however, functional traits were stronger predictors of dietary and isotopic ratios than phylogenetic relationships. I inferred that functionally relevant morphological traits of fish can be used to infer trophic niches for certain kinds of questions and analyses when trophic data are lacking. Trophic position–body size relationships were weak and only statistically significant for predatory fishes at the species level. Gut length was considered a better predictor of trophic position than body size. At the intraspecific level, trophic position – body size correlations varied from negative to positive depending on other functional traits (e.g., body depth, tooth shape, mouth width). Food item size and trophic niche width were all positively related to body size and negatively associated with gut length at the species level; mouth width was positively associated with food item size. Therefore, the incorporation of functional traits and their intermediate pathways is critical for understanding size-based trophic relationships of animal groups that encompass diverse feeding strategies. Given the diverse ecological strategies encompassed by fishes, organism trophic positions and food web patterns and processes cannot be inferred based solely on body size. Research that integrates multiple functional traits with trophic ecology will improve understanding and predictions about food web structure and dynamics.

DEDICATION

To my beloved Dani that embarked on this journey with me, and my family that was extremely supportive and understanding along these five long years of Ph.D.

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Contributors

This work was supervised by a dissertation committee consisting of Professors Kirk O. Winemiller (Advisor) and Masami Fujiwara of the Department of Wildlife and Fisheries Science, Professor Micky Eubanks of the Department of Entomology, Professor David Hoeinghaus of the Department of Biological Sciences at University of North Texas, and Professor Roger P. Mormul of the Graduate Program in Ecology of Inland Water Ecosystems at Maringá State University, Brazil.

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1. INTRODUCTION

Food webs, networks of consumer-resource interactions, have long interested ecologists because they affect population dynamics as well as ecosystem functioning (Massol *et al.*, 2011). Trophic interactions create fluxes of nutrients and energy on spatial scales ranging from local habitats to the entire biosphere (Polis & Winemiller, 1996; McCann, 2011). These fluxes affect other ecosystem processes, such as primary-secondary production and decomposition (Polis & Winemiller, 1996; McCann, 2011). In a fast-changing world, there is an increasing need to understand which factors underlie the structure and stability of food webs and how we could mitigate human impacts on food webs in order to maintain ecosystems services (Thompson *et al.*, 2012).

Over the last several decades, there has been a great effort to catalog a diversity of natural food webs worldwide (e.g., Beaver, 1985; Hildrew *et al.*, 1985; Winemiller, 1990; Thompson & Townsend, 2004) and to seek general patterns that could be associated with ecosystem stability and functions (e.g., Gross *et al.*, 2009; Johnson *et al.*, 2014; Yen *et al.*, 2016). Some regularities have been reported, most of which are related to organism body size (Woodward *et al.*, 2005). Body size often has been claimed to be related to important food web components, including vertical trophic structure (Riede *et al.*, 2011), trophic niche width (Costa, 2009; Arim *et al.*, 2010) and consumption rates (Kleiber, 1947; Brown *et al.*, 2004). Moreover, the removal of large organisms from a food web may lead to severe changes in the stability of ecosystems (McCann *et al.*, 2005; Estes *et al.*, 2011) and the loss of important ecosystem functions, such as seed dispersal (Caughlin *et al.*, 2014). Consequently, the study of patterns and processes related to body size is a subject of intense interest among ecologist and conservationists.

Body size is one of the most important organismal features determining the architecture of food webs, but the predictive power of statistical models describing food webs has shown to improve considerably with the addition of other functional traits (Eklöf *et al.*, 2013; Brose *et al.*, 2019). For example, the low trophic level of many large herbivorous and detritivores species may be explained better when other functional traits, such as gut length and dentition, are included in the model. Given that ecological performance and functional traits often have strong phylogenetic signals (Losos 2008), phylogeny has also been used as a proxy to predict predator-prey interactions (Cattin *et al.*, 2004; Bersier & Kehrli, 2008; Brousseau *et al.*, 2018). The use of phylogeny as a predictor of trophic interactions is particularly important when it is difficult to measure potential influential functional traits, such as digestive enzymes of predators (Feyereisen, 1999) and chemical compounds used for defense (Eisner *et al.*, 2005). Several studies have proposed that species traits and phylogenetic relationships are suitable proxies for ecological niches when analyzing community ecological structure (e.g., Cooper *et al.*, 2008; Kraft *et al.*, 2008; Côte *et al.*, 2019), and yet, relationships between species phylogenetic and trait similarity with ecological performance remain poorly understood (Gerhold *et al.*, 2015; Cadotte *et al.*, 2017, 2019; Funk *et al.*, 2017).

The main goal of this dissertation was to explore patterns of trophic ecology in fish assemblages and to determine how these patterns are associated with functional traits and phylogeny. Datasets for freshwater and estuarine fishes from three zoogeographic regions (Neartic, Neotropical and Afrotropical) were analyzed for the second dissertation chapter, whereas fishes from two freshwater systems located in the Neotropical region were analyzed for the third and fourth chapters. The diet dataset of freshwater/estuarine fishes used in this dissertation was collected by field research projects conducted over the past 36 years by Dr. Kirk Winemiller and members of his lab. This is one the most detailed diet datasets ever compiled for fishes, encompassing around 367 species, 220 genera, 75 families and 20 orders of fishes from a variety of sizes and trophic guilds.

The second chapter addressed the hypothesis that body size is strongly and positively associated with trophic level. I expanded previous studies by assessing how the trophic level-body size relationship is mediated by functional traits at intraspecific and interspecific levels. In the third chapter, I developed a structural equation model to link consumer body size with food items, mouth gape and gut length of consumers, trophic niche width of consumers, and trophic level. This research filled a gap left by previous studies regarding the incorporation of potential indirect effects, interactions, and collinearity in trophic level-body size relationships, improving our capability to infer mechanistic processes in food webs. Phylogenetic relatedness among species also was incorporated into the analysis conducted in chapters 2 and 3. This approach rarely has been applied in studies of the trophic level-body size relationship. The use of phylogenetic statistical procedures was made possible by a recent study by Rabosky *et al*. (2018) that provides a super tree containing ca. 30,000 fish species.

The fourth chapter explores the capability of phylogeny and morphological traits to predict patterns of trophic interactions. This is a highly relevant subject for food web ecology, because species interactions are difficult to quantify, and, consequently, many studies have used species traits and phylogeny as proxies under an assumption of niche conservatism (e.g., Cooper *et al.*, 2008; Kraft *et al.*, 2008; Côte *et al.*, 2019). However, few studies have explored whether niches are actually conserved across communities, a limitation that my study investigates.

1.1. References

Arim M., Abades S.R., Laufer G., Loureiro M. & Marquet P.A. (2010) Food web structure and body size: trophic position and resource acquisition. *Oikos*, 119, 147–153. https://doi.org/10.1111/j.1600-0706.2009.17768.x

Beaver R.A. (1985) Geographical variation in food web structure in Nepenthes pitcher plants. *Ecological Entomology*, 10, 241–248. https://doi.org/10.1111/j.1365-2311.1985.tb00720.x

Bersier L-F. & Kehrli P. (2008) The signature of phylogenetic constraints on food-web structure. *Ecological Complexity*, 5, 132–139. https://doi.org/10.1016/j.ecocom.2007.06.013

Brose U., Archambault P., Barnes A.D., Bersier L-F., Boy T., Canning-Clode J., Conti E., Dias M., Digel C., Dissanayake A., Flores A.A.V., Fussmann K., Gauzens B., Gray C., Häussler J., Hirt M.R., Jacob U., Jochum M., Kéfi S., McLaughlin O., MacPherson M.M., Latz E., Layer-Dobra K., Legagneux P., Li Y., Madeira C., Martinez N.D., Mendonça V., Mulder C., Navarrete S.A., O'Gorman E.J., Ott D., Paula J., Perkins D., Piechnik D., Pokrovsky I., Raffaelli D., Rall B.C., Rosenbaum B., Ryser R., Silva A., Sohlström E.H., Sokolova N., Thompson M.S.A., Thompson R.M., Vermandele F., Vinagre C., Wang S., Wefer J.M., Williams R.J., Wieters E., Woodward G. & Iles A.C. (2019) Predator traits determine food-web architecture across ecosystems. *Nature Ecology and Evolution*, 3, 919–927. https://doi.org/10.1038/s41559-019-0899-x

Brousseau P-M., Gravel D. & Handa I.T. (2018) Trait matching and phylogeny as predictors of predator-prey interactions involving ground beetles. *Functional Ecology*, 32,192–202. https://doi.org/10.1111/1365-2435.12943

Brown J.H., Gillooly J.F., Allen A.P., Savage V.M. & West G.B. (2004) Toward a metabolic theory of ecology. *Ecology*, 85, 1771–1789. https://doi.org/10.1890/03-9000

Cadotte M.W., Carboni M., Si X. & Tatsumi S. (2019) Do traits and phylogeny support congruent community diversity patterns and assembly inferences? *Journal of Ecology*, 107, 2065–2077. https://doi.org/10.1111/1365-2745.13247

Cadotte M.W., Davies T.J., & Peres-Neto P.R. (2017) Why phylogenies do not always predict ecological differences. *Ecological Monographs*, 87, 535–551. https://doi.org/10.1002/ecm.1267

Cattin M.F., Bersier L.F., Banasek-Richter C., Baltensperger R., Gabriel J.P. (2004) Phylogenetic constraints and adaptation explain food-web structure. *Nature,* 427, 835–839. https://doi.org/10.1038/nature02327

Caughlin T.T, Ferguson J.M., Lichstein J.W., Zuidema A., Bunyavejchewin S., Levey D.J. & Caughlin T.T. (2014) Loss of animal seed dispersal increases extinction risk in a tropical tree species due to pervasive negative density dependence across life stages. *Proceedings of the Royal Society B*, 282, 20142095. https://doi.org/10.1098/rspb.2014.2095

Cooper N., Rodríguez J. & Purvis A. (2008) A common tendency for phylogenetic overdispersion in mammalian assemblages. *Proceedings of the Royal Society B*, 275, 2031–2037. https://doi.org/10.1098/rspb.2008.0420

Costa G. (2009) Predator size, prey size, and dietary niche breadth relationships in marine predators. *Ecology*, 90, 2014–2019. https://doi.org/10.1890/08-1150.1

Côte J., Kuczynski L. & Grenouillet G. (2019) Spatial patterns and determinants of trait dispersion in freshwater fish assemblages across Europe. *Global Ecology and Biogeography*, 28, 826–838. https://doi.org/10.1111/geb.12896

Eisner T., Eisner M. & Siegler M. (2005) *Secret weapons: defenses of insects, spiders, scorpions, and other many-legged creatures*, Harvard University Press, Cambridge.

Eklöf A., Jacob U., Kopp J., Bosch J., Castro-Urgal R., Chacoff N.P., Dalsgaard B., de Sassi C., Galetti M., Guimarães P.R., Lomáscolo S.B., González A.M.M., Pizo M.A., Rader R., Rodrigo A., Tylianakis J.M., Vázquez D.P. & Allesina S. (2013) The dimensionality of ecological networks. *Ecology Letters*, 16, 577–583. https://doi.org/10.1111/ele.12081

Estes J.A., Terborgh J., Brashares J.S., Power M.E., Berger J., Bond W.J., Carpenter S.R., Essington T.E., Holt R.D., Jackson J.B.C., Marquis R.J., Oksanen L., Oksanen T., Paine R.T., Pikitch E.K., Ripple W.J., Sandin S.A., Scheffer M., Schoener T.W., Shurin J.B., Sinclair A.R.E., Soulé M.E., Virtanen R. & Wardle D.A. (2011) Trophic downgrading of planet Earth. *Science*, 333: 301–306. https://doi.org/10.1126/science.1205106

Feyereisen R. (1999) Insect P450 enzymes. *Annual Review of Entomology*, 44, 507–533. https://doi.org/10.1146/annurev.ento.44.1.507

Funk J.L., Larson J.E., Ames G.M., Butterfield B.J., Cavender-Bares J., Firn J., Laughlin D.C., Sutton-Grier A.E., Williams L. & Wright J. (2017) Revisiting the Holy Grail: using plant functional traits to understand ecological processes. *Biological Reviews*, 92, 1156–1173. https://doi.org/10.1111/brv.12275

Gerhold P., Cahill J.F., Winter M., Bartish I.V. & Prinzing A. (2015) Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Functional Ecology*, 29, 600–614. https://doi.org/10.1111/1365-2435.12425

Gross T., Rudolf L., Levin S.A. & Dieckmann U. (2009) Generalized models reveal stabilizing factors in food webs. *Science*, 325, 747–750. https://doi.org/10.1126/science.1173536

Hildrew A.G., Townsend C. & Hasham A. (1985) The predatory Chironomidae of an iron-rich stream: feeding ecology and food web structure. *Ecological Entomology*, 10, 403–413. https://doi.org/10.1111/j.1365-2311.1985.tb00738.x

Johnson S., Domínguez-García V., Donetti L. & Muñoz M.A. (2014) Trophic coherence determines food-web stability. *Proceedings of the National Academy of Sciences*, 111, 17923-17928. https://doi.org/10.1073/pnas.1409077111

Kleiber M. (1947) Body size and metabolic rate. *Physiological Reviews*, 27, 511–541. https://doi.org/10.1152/physrev.1947.27.4.511

Kraft N.J.B., Valencia R. & Ackerly D.D. (2008) Tree community assembly in an Amazonian Forest. *Science*, 322, 580–582. https://doi.org/10.1126/science.1160662

Losos J.B. (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters*, 11, 995–1003. https://doi.org/10.1111/j.1461-0248.2008.01229.x

Massol F., Gravel D., Mouquet N., Cadotte M.W., Fukami T. & Leibold M.A. (2011) Linking community and ecosystem dynamics through spatial ecology. *Ecology Letters*, 14, 313–323. https://doi.org/10.1111/j.1461-0248.2011.01588.x

McCann K.S. (2011) *Food webs*, Princeton University Press, New Jersey.

McCann K.S., Rasmussen J.B. & Umbanhowar J. (2005) The dynamics of spatially coupled food webs. *Ecology Letters*, 8, 513–523. https://doi.org/10.1111/j.1461-0248.2005.00742.x

Polis G.A. & Winemiller K.O. (eds) (1996) *Food webs: integration of patterns and dynamics*, Chapman and Hall, New York.

Rabosky D.L., Chang J., Title P.O., Cowman P.F., Sallan L., Friedman M., Kaschner K., Garilao C., Near T.J., Coll M. & Alfaro M.E. (2018) An inverse latitudinal gradient in speciation rate for marine fishes. *Nature*, 559, 392–395. https://doi.org/10.1038/s41586-018-0273-1

Riede J.O., Brose U., Ebenman B., Jacob U., Thompson R., Townsend C.R. & Jonsson T. (2011) Stepping in Elton's footprints: a general scaling model for body masses and trophic levels across ecosystems. *Ecology Letters*, 14, 169–178. https://doi.org/10.1111/j.1461-0248.2010.01568.x

Thompson R.M., Brose U., Dunne J.A., Hall R.O., Hladyz S., Kitching R.L., Martinez N.D., Rantala H., Romanuk T.N., Stouffer D.B. & Tylianakis J.M. 2012. Food webs: reconciling the structure and function of biodiversity. *Trends in Ecology and Evolution*, 27, 689–697. https://doi.org/10.1016/j.tree.2012.08.005

Thompson R.M. & Townsend C.R. (2004) Land-use influences on New Zealand stream communities: effects of species composition, functional organisation, and food-web structure. *New Zealand Journal of Marine and Freshwater Research*, 38, 595–608. https://doi.org/10.1080/00288330.2004.9517265

Winemiller K.O. (1990) Spatial and temporal variation in tropical fish trophic networks. *Ecological Monographs*, 60, 331–367. https://doi.org/10.2307/1943061

Woodward G., Ebenman B., Emmerson M., Montoya J., Olesen J., Valido A. & Warren P. (2005) Body size in ecological networks. *Trends in Ecology & Evolution*, 20, 402–409. https://doi.org/10.1016/j.tree.2005.04.005

Yen J.D.L., Cabral R.B., Cantor M., Hatton I., Kortsch S., Patrício J., Yamamichi M. (2016) Linking structure and function in food webs: maximization of different ecological functions generates distinct food web structures. *Journal of Animal Ecology*, 85, 537–547. https://doi.org/10.1111/1365-2656.12484

2. THE RELATIONSHIP BETWEEN TROPHIC LEVEL AND BODY SIZE IN FISHES DEPENDS ON FUNCTIONAL TRAITS [*]

2.1. Introduction

Body size varies many orders of magnitudes in nature and has long been recognized as an important trait influencing not only fitness, but also species interactions and community dynamics (Elton, 1927; Cohen *et al.*, 1993). Animal body size affects many important aspects of physiology and ecological performance, including metabolism (Kleiber, 1932), movement and home range (Reiss, 1988), foraging and predation vulnerability (Peters, 1983), fecundity (Roff, 1992), and longevity (Speakman, 2005). Body size distributions therefore can affect population, community and ecosystem dynamics (Brown *et al.*, 2004; Caughlin *et al.*, 2014; Ripple *et al*., 2017). Recent studies have suggested that overharvest (Pauly *et al*., 1998), deforestation (Ilha *et al*., 2018), global warming (Tseng *et al*., 2018), and other human impacts are reflected in population and community size structures. Given the many ways body size affects ecological processes, it should not be surprising that size relationships have been a major research focus in ecology (Cohen *et al*., 2003; Jonsson *et al*., 2005; Woodward *et al*., 2005; Petchey *et al*., 2008; McLaughlin *et al*., 2010; Gilljam *et al*., 2011).

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A major body of research concludes that predators (here excluding parasites and parasitoids) are typically larger than their prey (Warren & Lawton, 1987; Cohen *et al*., 1993; Jennings *et al*., 2002; Barnes *et al*., 2010; Nakazawa, 2017). Small predators are limited to capturing and handling large prey, whereas large predators often feed on the largest prey available in order to meet their higher energetic demand (Werner & Hall, 1974; Mittelbach, 1981). Therefore, it is expected that trophic level is positively correlated with body size (Elton, 1927). Evidence for a positive relationship between trophic level and body size in predators has been found for both aquatic (Jennings *et al.*, 2007; Arim *et al*., 2010; Barnes *et al*., 2010; Gilljam *et al*., 2011; Riede *et al*., 2011; Reum & Marshall, 2013) and terrestrial organisms (Riede *et al*., 2011), encompassing invertebrates as well as ectothermic and endothermic vertebrates. Furthermore, the structure of entire communities has been shown to be strongly size based (Jennings *et al*., 2002; Al-Habsi *et al*., 2008; Romero-Romero *et al*., 2016), with most studies to date conducted in the marine realm. At a global scale, fishes apparently show a positive relationship between trophic level and body size (Pauly *et al*., 1998; Romanuk *et al.*, 2011). As a result, a growing number of food web models have been built under the assumption of a positive trophic level-body size relationship (McCann *et al.*, 2005; Rooney *et al.*, 2008; McCann, 2011), and some have derived model parameters assuming certain size-based relationships among interacting species (Otto *et al.*, 2007; Berlow *et al*., 2009; Schneider *et al.*, 2016). These models have succeeded in simulating the structure and dynamics of simple systems (Berlow *et al*., 2009; McCann, 2011), but their predictive power seems to decrease as systems become more complex (Jonsson *et al*., 2018).

Despite numerous claims of a strong positive relationship between trophic level and body size, this pattern does not always hold. Potapov *et al*. (2019) found positive relationships between trophic level and body size in consumers of aquatic ecosystems, but not in terrestrial ones. Layman *et al.* (2005) found a flat relationship between trophic level and body size of carnivorous freshwater fishes from a tropical river. Similarly, no relationship was found between trophic level and body size in terrestrial and marine mammals (Tucker & Rogers, 2014). The trophic level-body size relationship can even be negative, as exemplified in cyprinids, a diverse freshwater fish family (Burress *et al.*, 2016). Arim, Bozinovic, and Marquet (2007) hypothesized the existence of hump-shaped trophic level-body size relationships, such as the one found for animals from the coast of the southwestern Atlantic (Segura *et al*., 2015). This pattern arose, in part, because small organisms are restricted to feed at relatively high trophic levels due to morphological limitations (e.g., mouth gape size), whereas adults are limited by the amount of energy available. The inconsistences found in trophic level-body size relationships indicate that factors in addition to body size play significant roles in determining trophic level.

Body size is an important factor determining food web structure (e.g., feeding interactions, trophic niche width, trophic position), but the prediction power of models has been shown to increase greatly with the inclusion of other functional traits (Eklöf *et al*., 2013; Brose *et al*., 2019). For instance, the largest animals on land (e.g., elephants, rhinos, giraffes and hippos) and many large tropical freshwater fishes (e.g., frugivorous tambaqui, *Colossoma macropomum*, of the Amazon) are herbivores. These animals are usually not included in trophic level-body size analyses, often being dismissed as outliers. In these cases, characteristics of dentition and the gastrointestinal tracts are more indicative of trophic level than body size. Burress *et al*. (2016) suggested that many herbivorous fishes evolved large body size to accommodate a long gastrointestinal tract required to process a cellulose-rich diet. Carnivores have protein-rich diets and tend to have relatively short gastrointestinal traits, something that can be achieved at any body size (Wagner *et al*., 2009). Similar associations may be observed for other traits, such as tooth shape (e.g., in mammals, presence of canines and sharp molars in carnivores vs. absence of canines with flat molars in herbivores) and claws (e.g., raptorial talons in birds of prey vs. grasping claws in perching songbirds). Surprisingly, few studies have examined traits other than body size to predict trophic level and other features of food webs (e.g., trophic niche width, food item size).

Several food web studies have emphasized how intraspecific variation in body size and trophic ecology affects dynamics of populations and communities (Werner & Gilliam, 1984; Ingram *et al.*, 2011; Klecka & Boukal, 2013; Nakazawa *et al.*, 2013; Rudolf *et al.*, 2014). Ontogenetic shifts in trophic levels are common (Werner & Gilliam, 1984). Anuran amphibians provide an extreme example, with tadpoles of most species feeding on algae and detritus, and most adult frogs and toads consuming terrestrial arthropods. Major ontogenetic dietary shifts (e.g., invertivory to piscivory, omnivory to carnivory) are observed in many other vertebrates and invertebrates, including fishes, crocodilians and spiders (Werner & Gilliam, 1984; Nakazawa, 2015; Sánchez-Hernández *et al*., 2019). Given that intraspecific variation is known to influence population dynamics and species interactions (Bruno & O'Connor, 2005; Rudolf, 2008), improved understanding of trophic level-body size relationship at the species level should facilitate development of more realistic food web models.

Here, I investigated the relationship between trophic level and body size at both interspecific and intraspecific levels by analyzing a large dataset for freshwater and estuarine fishes. The relationship was assessed for both carnivorous and non-carnivorous fish guilds. I also explore how the trophic level-body size relationship at the species level varies according to seven morphological traits: body depth, body width, mouth width, mouth position, tooth shape, gill raker length and number, and gut length. Because these morphological attributes influence fish feeding performance (as well as fitness, indirectly, via effects on growth, survival and reproduction) (Villéger *et al*., 2017), I consider them to represent functional traits (Violle *et al*., 2007). Body depth and width influence maneuverability and swimming speed and therefore are strongly associated with habitat use (Keast & Webb, 1966; Gatz Jr., 1979) and indirectly linked to foraging (Webb, 1984a). Mouth gape limits the size of prey that can be ingested whole (Nilsson & Brönmark, 2000), and mouth position influences the efficiency of feeding at vertical positions within the water column (Helfman *et al*., 2009). Tooth shape affects food acquisition and processing (Winemiller, 1991b), gill rakers affect processing and selection of particles within the orobranchial chamber (Helfman *et al*., 2009), and gut length affects digestion and nutrient absorption (Horn, 1989; German & Horn, 2006).

I expected that trophic level is positively correlated with body size, especially for carnivorous fishes; and that the strength and direction of the trophic level-body size relationship at the species level is mediated by other functional traits.

2.2. Methods

2.2.1. Fish samples and trophic level estimation

I compiled new and previously published data for freshwater and estuarine fish diets based on examination of 30,341 specimens (excluding specimens with empty stomachs) and encompassing 367 species, 220 genera, 75 families and 20 orders (Table A.1). Dietary data originated from six field research projects conducted over the past 36 years by Dr. Kirk Winemiller and members of his lab in temperate and tropical freshwater systems, including two floodplain rivers (Tarim, 2002; Robertson *et al.*, 2008; Montaña & Winemiller, 2013) and an estuary in Texas (USA) (Akin & Winemiller, 2006), two coastal streams in Costa Rica (Winemiller, 1990), four streams in Venezuela (Winemiller, 1990; Peterson *et al.*, 2017), and a floodplain river (Upper Zambezi River and Barotse Floodplain) in Zambia (Winemiller, 1991a; Winemiller & Kelso-Winemiller, 1994, 1996, 2003). In each of these systems, fishes were collected throughout one year using experimental gillnets, seines, cast nets and dipnets, in order to acquire a good representation of the local fish assemblage and any seasonal variation in composition. Surveys were conducted during all seasons: Winter-Spring-Summer-Fall seasons in temperate regions and Rainy/Flood-Dry/Low-water seasons in tropical regions. Thus, samples contain broad ranges of species body sizes based on temporal patterns of reproduction, recruitment and dispersal at the sites (e.g., Winemiller, 1989; Zeug & Winemiller, 2007).

For all specimens, dietary analysis followed a protocol described by Winemiller (1990). Prey categories were assigned within trophic levels according to information reported in literature sources (Table A.2). The trophic level of each fish specimen (herein referred as TL) was calculated using the formula proposed by Adams, Kimmel, and Ploskey (1983):

$$TL_i = 1.0 + \sum_{j=0}^{n} (T_j * p_{ij}),$$

where, T_j is the trophic level of a prey taxon *j* and p_{ij} is the fraction of prey taxon *j* ingested by predator *i*. The mean trophic level (herein referred as MTL) of each fish species was calculated as the arithmetic mean of the weighted mean trophic levels (TL) of every analyzed specimen of a species, and based on MTL, I classified each fish species in one of two groups: carnivorous or non-carnivorous. Carnivorous species were those that included more animal than non-animal material in their diets, resulting in MTL > 2.5 (N= 223), whereas non-carnivorous species were omnivores, herbivores and detritivores that included minor fractions of animal material in their diets with MTL < 2.5 (N=52).

2.2.2. Functional traits

Standard length (SL) was used as the main descriptor for body size. SL (mm) was measured for all specimens examined for dietary analysis. Given that SL is an imperfect index for fish body mass because of the diverse body shapes of teleost fishes (ranging from anguilliform to gibbose to compressiform), I converted SL to weight (g) using the allometric formula (Keys, 1928):

$$W_i = aL_i^b$$

where, W_i is the predicted weight of individual i, L_i is the length of individual i, and log (a) and b are the intercept and slope, respectively, of the logarithmic form of the length-weight relationship of individual i*'s* population. The values of the parameters a and b for each species were estimated by posterior modes (i.e., kernel density estimation) generated by the Bayesian hierarchical approach proposed by Froese, Thorson, and Reyes Jr. (2014). This Bayesian method generates posteriori distributions for parameters a and b for a target species using priors based on body shape classifications and length-weight data (i.e., a and b estimates from other studies) available for the species of interest and/or closely related species in FishBase (Froese & Pauly, 2019).

Morphological measurements, including maximum body depth (maximum distance from ventrum to dorsum; mm), maximum body width (maximum horizontal distance from side to side; mm), gut length (mm), tooth shape (absent, unicuspid, multicuspid, conical, triangular serrated), gill raker shape (absent, short/blunt/toothlike, intermediate/long and sparse, long and comb-like), mouth orientation (superior, terminal, sub-terminal, inferior) and mouth width (mm), were made on adult specimens (i.e., body length exceeding the minimum size of maturation reported for the species or most closely related species for which data are reported) based on the protocol described by Winemiller (1991b). For most species, I measured 3 individuals, although in a few cases this number was higher or lower depending on availability of preserved specimens from the field studies (Table A.3). Three specimens per species was deemed sufficient for reliable mean values for body size-standardized measures (Winemiller, 1991b), and facilitated detection of outlier values caused by measurement error. In all cases, measurements were made on formalin-fixed and alcohol-preserved (70% EtOH) specimens, including specimens deposited in ichthyology collections at Texas A&M University (Biodiversity Research and Teaching Collections - BRTC) and The Texas University at Austin (Texas Natural History Collections - THNC). In few cases, specimens from the original field studies were unavailable, and I measured specimens collected from nearby locations.

Maximum body depth, maximum body width, gut length, and mouth width were converted to body proportions to remove the effect of body size differences. Following Winemiller (1991b), I used SL as the denominator for ratios involving body depth, body width, and gut length, and I used maximum body width as the denominator for the ratio of mouth width. The measurements were then averaged for each species. Although intraspecific variation in body shape and other morphological traits caused by sexual dimorphism, ontogeny and polymorphism is common in fish (Bolnick *et al*., 2011), I only estimated species averages of morphological traits ratios based on adult specimens with the objective of analyzing how interspecific variation may influence MTL and the TL- body size relationships. Standardization based on proportions can introduce allometric biases in morphometric analyses (Albrecht *et al.*, 1993), however, this source of potential bias should have little influence for broad interspecific comparisons (Winemiller, 1991b). Moreover, body size ratios have straightforward ecological and functional interpretations (Winemiller, 1991b; Montaña & Winemiller, 2013; Villéger *et al*., 2017) and have been widely used in functional ecology studies (e.g., Toussaint *et al*., 2018; Su *et al.*, 2019). Standard length, body mass (both indicators of body size), and relative gut length for all species were log transformed prior to analysis.

2.2.3. Data analysis

I used two approaches to test the relationship between trophic level and body size and its association with other functional traits. One approach analyzed trophic level and body size averages per species (using MTL, herein called *averaged data*) while the second approach analyzed data for individual specimens and encompassed within-species variation (using TL, herein called *raw data*). The analyses were conducted using a Bayesian framework that has advantages over traditional frequentist approaches, including a capability to generate exact confidence intervals for the parameters and to account for uncertainty at multiple levels of the model, independent of sample size (Kéry, 2010; Reum & Marshall, 2013). No evidence of non-linearities (Segura *et al.*, 2015) was detected in my data; consequently, statistical analyses were based on linear models. The lack of independence among species due to shared ancestry was considered by adding phylogenetic components in the analyses (see details below). To do that, I used a hundred different phylogenetic hypotheses generated by a recent study that analyzed ca. 30,000 fish species (Rabosky *et al*., 2018). The backbone of these super trees is based on molecular data of ca. 15,000 fish species and time-calibrated with fossil records. Rabosky *et al.* (2018) placed the remaining unsampled species (i.e., those lacking molecular data) in the backbone tree using stochastic polytomy resolution in order to generate consistent taxonomic resolution through a conservative constant-rate birth-death process.

2.2.3.1. Average data

I used average values per species to examine patterns of interspecific variation. Species with less than 5 specimens having gut contents were removed from my dataset to reduce the potential for outliers to skew dietary data. The remaining species (n= 275) in the dataset were analyzed using Bayesian phylogenetic linear mixed models in which MTL was the response variable and the arithmetic mean of body size (SL or body mass) was the main factor. In addition to analysis of the full fish dataset, the relationship of MTL with body size was examined separately for carnivorous and non-carnivorous fishes. Consistency of the MTL-body size relationships were assessed using three models: 1) NULL model, which was run without any explanatory variable, 2) SUB model, which used the main factor alone (body size), and 3) FULL model, which used the main factor (body size) along with 7 co-variables (body depth, body width, mouth orientation, mouth width, tooth shape, gill raker shape, gut length). To account for non-independence, species phylogeny was included in the models as a random term (forming what is called an animal model; Hadfield 2010). To account for uncertainty from shared ancestry (i.e., multiple phylogenetic hypotheses), I performed analyses on all phylogenetic trees published by Rabosky et al. (2018) (N= 100) and calculated a combined posterior distribution of the model parameters using the R package mulTree (Guillerme & Healy, 2018). I used non-informative priories (variance= 0.5, belief parameter= 0.002) for both fixed and random effects (Hadfield, 2010) and conducted three chains for 240,000 interactions with a thinning value of 100 and burning of 40,000. The strength of the phylogenetic component to explain the trait variance was accessed using Lynch's phylogenetic heritability index (H^2) (Lynch, 1991), which is comparable to Pagel's lambda (Pagel, 1999) and varies from 0, when the trait is evolving independently of the phylogeny, to 1, when the trait is evolving according to Brownian motion (Hansen & Orzack, 2005). Convergence of the model chains was verified using the Gelman-Rubin Statistic (Gelman & Rubin, 1992). Potential scale reduction values were lower than 1.1, and autocorrelations of posterior probabilities were lower than 0.1. The effective sample sizes of the models were all greater than 1,000. QQ-plots of the posterior density of parameter estimates indicated that Gaussian was an adequate probability distribution for the response variable. Multicollinearity was tested prior to Bayesian analyses using the Variance Inflation Factor (VIF), but no evidence of autocorrelation among the traits was found (VIF<2). I considered a variable significant when the 95% credible intervals did not encompass zero. I also compared the NULL, SUB and FULL models using the deviance information criterion (DIC), which is a hierarchical generalization of Akaike's Information Criterion (AIC) for Bayesian models (Spiegelhalter *et al*., 2002). Marginal R^2 and conditional R^2, which represent the variance explained by the fixed factors and by both fixed and random factors, respectively, were calculated according to Nakagawa and Schielzeth (2013).

2.2.3.2. Raw data

The second approach used data for individual specimens to test for intraspecific variation in TL-body size relationships and employed two steps. First, I conducted

Bayesian semi-parametric generalized mixed models on a Dirichlet Process Mixtures (DPM, family= Gaussian, nit= 240,000, thin= 100, burning= 40,000, chains= 3) using non-informative priors (alpha= 1, tau1= 0.01, tau2= 0.01, nu0= 4.01, tinv= 10, nub= 4.01, tbinv= 10, mb= 0, Sb= 1000; see Jara et al. 2011 for more details), with TL used as the response variable, body size (SL or body mass) as the main factor, and fish species as a random variable (random slope and intercept). For this model, I used data from all dissected specimens for those species for which at least 30 specimens contained food items in the gut, which reduced the number of observations to 28,710 and the number of species to 179. The threshold of 30 specimens was necessary to allow the mixed models to estimate the relationship between body size and TL for individual species. In contrast to other studies (e.g., Arim *et al.*, 2010), I did not split body size into size categories. The use of size categories is usually justified on the basis of reducing uncertainty in TL estimation, but exploratory analyses indicated that splitting body size into size categories did not consistently reduce uncertainty nor changed the parameter estimates. I used a semi-parametric mixed model because of its modeling flexibility and robustness to deviance from parametric assumptions, including multivariate normal distribution of random effects (Escobar & West 1995; Jara *et al.*, 2011; Müeller *et al.*, 2018).

Second, I extracted the random slopes generated for species from the Bayesian semi-parametric generalized mixed model in step 1. These slopes describe the relationship between body size (SL or body mass) and TL for each species and allowed us to explore how this relationship may vary according to species functional traits. Thus, I conducted another series of Bayesian phylogenetic linear mixed models (nit= 240,000, thin= 100, burning= 40,000, chains= 3) using: i) the random slopes as a response variable, ii) mean body size (SL or body mass), body depth, body width, mouth orientation, mouth width, tooth shape, gill raker shape and gut length as main factors, iii) phylogenetic trees (N= 100) as random components, and iv) non-informative priors (variance= 0.5 and belief parameter= 0.002). Similar to the first approach, the posterior distribution of each variable parameter generated here accounts for the uncertainty associated with species shared ancestry. I compared the FULL model (i.e., with all explanatory variables) with the NULL model (i.e., a model without any explanatory variables) using the DIC to test the importance of these functional traits in explaining TL-body size relationships. All diagnostic techniques applied to approach 1 were repeated for approach 2. Furthermore, generalized linear models (GLM) based on the binomial distribution were performed to explore whether species with consistent relationships between TL and body size (i.e., species with a random slope CI not encompassing zero) were those that had larger sample sizes and wider body-size ranges. Body-size range was estimated by dividing the body-size range observed in my samples by the total body-size range, which is the distance between minimum and maximum body size of a given species. Maximum body size of each species was obtained from FishBase (Froese & Pauly, 2019), and minimum body size was set to 1 mm for SL and 0.001 g for body mass; although arbitrary, these minimum values were necessary because newly hatched or liveborn fishes are always larger than 0 mm and heavier than 0 g. Given the lack of maximum body size information reported as SL for many species, the effect of body size range on the consistency of the TL-body size relationship was tested using only 87 species.

A Bayesian phylogenetic linear mixed models with non-informative priors was also performed to explore the possibility that the relationship between TL-body size becomes positive at positions higher in the food web. The random slopes generated by the Bayesian semi-parametric generalized mixed models served as the response variable, MTL was used as the main factor, and the phylogenetic trees constructed by Rabosky *et al.* (2018) were used as the random components. I did not introduce co-variables for this analysis (e.g., relative gut length) because of high levels of multicollinearity (VIF > 10). These models (herein named SUB-MTL models) also were compared with the FULL and NULL models (described above) using the DIC.

Hypothesis 1 (trophic level is positively correlated with body size) was rejected if the relationship between trophic level and body size was not consistently positive (credible intervals of slopes encompassing 0) according to approach 1 (species averages data) and the first step of approach 2 (individual specimen data). Hypothesis 2 (strength of the TL-body size relationship is mediated by functional traits) was supported if any of the seven functional traits affected the slope of the TL-body size relationship, and this was assessed based on results from step 2 of approach 2.

Bayesian phylogenetic linear mixed models were performed in R (R Core Team, 2019) using the packages MCMCglmm (Hadfield, 2010). Bayesian semi-parametric generalized mixed models were performed in DPpackage (Jara *et al*., 2011), and model comparisons and VIF were done using the packages MuMIn (Barton, 2019) and fmsb

(Nakazawa, 2018), respectively. Length-weight data were obtained from the FishBase database using the R package rfishbase (Boettiger *et al.*, 2012).

2.3. Results

2.3.1. Averaged data

Mean SL was not a consistent predictor of MTL when all fishes were analyzed together (FULL: slope of the MTL-SL relationship= 0.06 [Lower CI= -0.01, Upper CI= 0.13]; SUB: slope of the MTL-SL relationship= 0.04 [Lower CI= -0.05, Upper CI= 0.13]; Figure 2.1a, Figure 2.2a). Models with only SL (SUB model) reached a maximum conditional R^2 lower than 1% and had lower performance on average when compared to models with other functional traits (FULL model) and without any explanatory variable (NULL model; Table 2.1). Both large and small fishes fed at low and high trophic levels, but at intermediate MTL (~2.5) there was a tendency for fishes to have small body sizes (Figure 2.1a; Table A.4). The fixed variables in the FULL model explained 35% of MTL variation (Table 2.1). Body depth and gut length were negatively correlated with MTL (Figure 2.2a and 2.2e, respectively), whereas mouth width had a positive association (Table 2.2, Figure 2.2c). MTL varied according to tooth shape, whereby species without teeth had the lowest MTL, fishes with unicuspid and multicuspid teeth had intermediate values, fishes with conical teeth had high values, and final species with triangular serrated teeth had highest MTL (Figure 2.3a, 2.3d). MTL also varied among fishes with different mouth orientations. Fishes with superior mouths tend to have higher MTL compared to fishes with inferior, sub-terminal and terminal mouths (Figure 2.3c, 2.3e).

MTL was not associated with the shape of gill rakers (Table 2.2; Table A.5, Figure A.1). Similarly, no correlations were observed between relative maximum width and MTL (Table 2.2; Figure A.2). In all models (FULL, SUB and NULL), the H^2 and the conditional R^2 were high (H^2= 0.96 to 0.98, conditional R^2= 0.77 to 0.84; Table 2.1), indicating that MTL has a strong phylogenetic component, independent of the phylogenetic tree used.

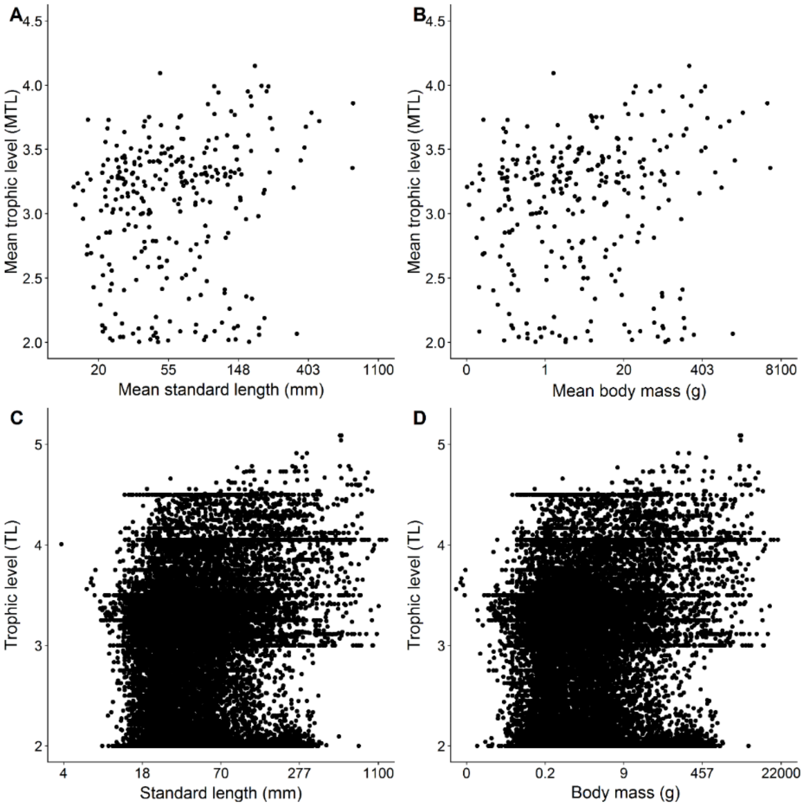

Figure 2.1 Relationship between body size and trophic level (TL or MTL) for freshwater and estuarine fishes from Texas (USA), Costa Rica, Venezuela, and Zambia. Mean trophic level (MTL) and mean standard length (A) and MTL and mean body mass (B) are presented for fish species with > 5 specimens dissected for dietary analysis. Data for individual trophic level (TL) and SL (C) and TL and body mass (D) are shown for species with at least 30 specimens. Parameter estimation and credible intervals for each one of these relationships can be found in Table 2.2 and 2.3.

These results did not appear to change when mean SL was replaced with mean body mass (Table 2.2, Figure 2.1b). Despite having slightly higher DIC than the NULL model, mean body mass alone was not strongly associated with MTL (FULL: slope of the MTL-body mass relationship= 0.02 [Lower CI= 0.00, Upper CI= 0.05]; SUB: slope of the MTL-body mass relationship= 0.01 [Lower CI= -0.02, Upper CI= 0.04]; Figure 2.1b, 2.2b), and mean body mass explained less than 1% of the variation in MTL (Table 2.1). The addition of other functional traits in the model (FULL) improved the model predicting variation in MTL (Table 2.1). Again, body depth, mouth orientation, mouth width, tooth shape, and gut length were consistent predictors of MTL, and their effects were similar to the models based on SL as the measure of body size (Table A.6, Figure A.3, A.4). H^2 and the conditional R^2 values were high in all models (H^2= 0.96 to 0.98, conditional R = 0.77 to 0.84; Table 2.1), indicating a role for phylogenetic constraint and/or niche conservatism in explaining interspecific variation in MTL.

Table 2.1 Comparisons between Bayesian phylogenetic linear mixed models aiming to explain mean trophic level (MTL) and the slope of the trophic level (TL)-body size relationship with body size and 7 other traits (FULL models), with only mean body size (SUB models) and without any explanatory variables (NULL). MTL was analyzed in three different ways: all fishes combined (Overall), carnivorous fishes only (MTL >2.5), and non-carnivorous fishes only (MTL < 2.5). MTL was also used alone as a predictor of the slope of TL-body size variation (SUB-MTL models). Standard length (SL) and body mass were used as two different estimates of body size. Numbers in parentheses are 2.5% and 97.5% quantiles based on the variation associated with phylogeny uncertainty. Marginal R^2 represent the variance explained only by the fixed factors, and Conditional R^2 represents the variance explained by both fixed and random factors. Marginal R^2 is zero for NULL models due to the absence of fixed factors. For SUB-models, marginal R^2 were lower than 0.01 in some cases (e.g., MTL [Overall]) and therefore were rounded to zero. H^2 indicates Lynch's phylogenetic heritability index and varies from 0, when the trait is evolving independently of the phylogeny, to 1, when the trait is evolving according to Brownian motion.

Model	**DIC**	**Delta**	**Weight**	**Marginal R^2**	**Conditional R^2**	**H^2**
MTL (Overall) / SL						
FULL	201.9(176.7,217.7)	0.0(0.0,0.0)	1.0(1.0,1.0)	0.35(0.31,0.38)	0.77(0.73,0.82)	0.96(0.94,0.97)
NULL	288.5(246.9,321.0)	86.7(56.0,127.6)	0.0(0.0,0.0)	0.00(0.00,0.00)	0.84(0.81,0.86)	0.98(0.97,0.98)
SUB	290.4(247.6,323.3)	89.5(54.4,130.9)	0.0(0.0,0.0)	0.00(0.00,0.00)	0.78(0.84,0.88)	0.98(0.97,0.98)
MTL(Overall)/Bodymass						
FULL	203.8(177.6,219.8)	0.0(0.0,0.0)	1.0(1.0,1.0)	0.35(0.31,0.39)	0.77(0.72,0.82)	0.96(0.94,0.97)
SUB	285.5(243.8,319.6)	81.9(48.7,124.9)	0.0(0.0,0.0)	0.00(0.00,0.00)	0.84(0.81,0.86)	0.98(0.97,0.98)
NULL	288.5(246.9,321.0)	84.3(54.7,126.5)	0.0(0.0,0.0)	0.00(0.00,0.00)	0.84(0.81,0.86)	0.98(0.97,0.98)
MTL(Carniv.)/SL						
FULL	93.3(70.1,100.4)	0.0(0.0,0.0)	1.0(1.0,1.0)	0.23(0.19,0.26)	0.52(0.43,0.68)	0.92(0.88,0.95)
NULL	120.9(96.7,137.3)	28.0(17.7,38.7)	0.0(0.0,0.0)	0.00(0.00,0.00)	0.61(0.54,0.68)	0.94(0.92,0.96)
SUB	122.4(103.3,125.8)	28.9(24.3,38.6)	0.0(0.0,0.0)	0.11(0.09,0.12)	0.32(0.26,0.47)	0.87(0.73,0.93)

Table 2.1 Continued.

Model	DIC	Delta	Weight	Marginal R^2	Conditional R^2	H^2
MTL(Carniv.)/Bodymass						
FULL	93.6(67.5,100.4)	0.0(0.0,0.0)	1.0(1.0,1.0)	0.23(0.18,0.26)	0.51(0.42,0.69)	0.92(0.86,0.95)
NULL	120.9(96.7,137.3)	28.3(18.9,39.8)	0.0(0.0,0.0)	0.00(0.00,0.00)	0.61(0.54,0.68)	0.94(0.92,0.96)
SUB	121.4(96.3,126.6)	28.6(22.7,36.2)	0.0(0.0,0.0)	0.10(0.08,0.11)	0.35(0.27,0.51)	0.89(0.76,0.94)
MTL(Non-Carniv.)/SL						
FULL	-75.5(-100.6,-50.9)	0.0(0.0,0.0)	1.0(1.0,1.0)	0.18(0.16,0.20)	0.80(0.66,0.87)	0.96(0.94,0.96)
NULL	-45.2(-50.6,-43.1)	30.2(7.2,53.3)	0.0(0.0,0.0)	0.00(0.00,0.00)	0.36(0.32,0.46)	0.86(0.78,0.93)
SUB	-43.6(-49.0,-41.6)	31.8(8.8,55.2)	0.0(0.0,0.0)	0.01(0.00,0.01)	0.36(0.32,0.44)	0.85(0.77,0.93)
MTL(Non-Carniv.)/Bodymass						
FULL	-75.2(-101.6,-50.1)	0.0(0.0,0.0)	1.0(0.9,1.0)	0.18(0.16,0.20)	0.79(0.65,0.87)	0.96(0.94,0.97)
NULL	-45.2(-50.6,-43.1)	29.3(6.8,51.9)	0.0(0.0,0.0)	0.00(0.00,0.00)	0.36(0.32,0.46)	0.85(0.78,0.93)
SUB	-43.7(-48.9,-41.7)	31.0(8.1,53.8)	0.0(0.0,0.0)	0.01(0.01,0.01)	0.36(0.33,0.45)	0.84(0.76,0.93)
Slope/SL						
FULL	56.1(53.5,56.7)	0.0(0.0,0.0)	1.0(1.0,1.0)	0.31(0.30,0.32)	0.37(0.36,0.42)	0.60(0.39,0.83)
SUB-MTL	73.8(68.9,74.3)	17.6(13.6,19.5)	0.0(0.0,0.0)	0.14(0.14,0.15)	0.22(0.20,0.27)	0.55(0.35,0.84)
NULL	100.6(96.9,101.2)	44.4(41.9,46.0)	0.0(0.0,0.0)	0.00(0.00,0.00)	0.10(0.07,0.15)	0.59(0.43,0.83)
Slope/Bodymass						
FULL	-246.0(-250.5,-244.5)	0.0(0.0,0.0)	1.0(1.0,1.0)	0.28(0.26,0.29)	0.39(0.36,0.47)	0.72(0.49,0.88)
SUB-MTL	-224.2(-231.7,-223.1)	21.5(17.1,24.0)	0.0(0.0,0.0)	0.09(0.08,0.09)	0.21(0.19,0.27)	0.63(0.45,0.88)
NULL	100.6(96.9,101.2)	346.3(344.5,350.4)	0.0(0.0,0.0)	0.00(0.00,0.00)	0.10(0.07,0.15)	0.59(0.43,0.83)

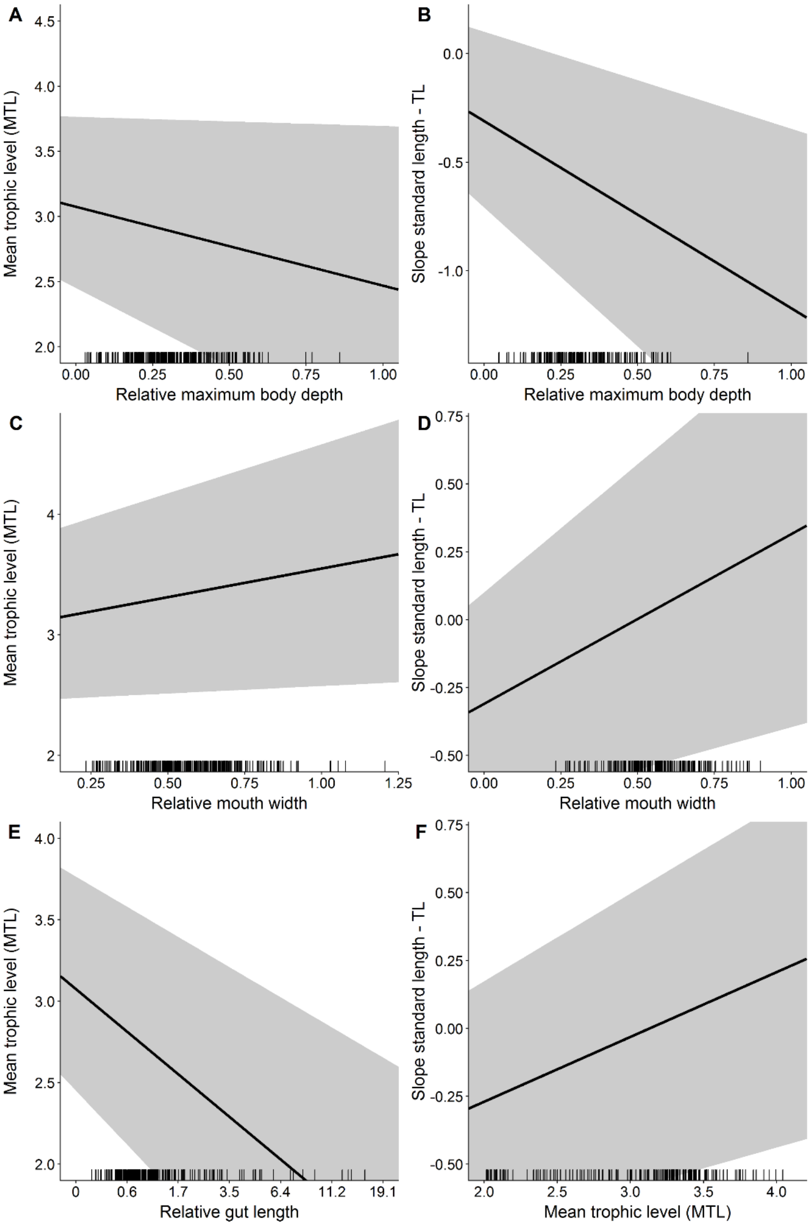

Figure 2.2 Marginal effects of relative maximum body depth (A and B), relative mouth width (C and D), relative gut length (E) and mean trophic level (MTL) (F) on MTL and/or the slope of standard length – trophic level (TL) relationship according to Bayesian phylogenetic linear mixed models performed on 100 different trees. Both carnivorous and non-carnivorous species are included in these analyses. Tick marks represent the position of the species according to the x variable. 95% credible intervals of slopes are shown as gray ribbons. Statistically nonsignificant results (i.e., credible intervals encompassing 0) and results based on body mass rather than SL can be found in Figure A.4 and A.17.

Both mean SL and mean body mass were positively associated with MTL only when carnivorous fishes were analyzed separately (Table 2.2; Figure A.6, A.8). The FULL models were still the most relevant as gut length, tooth shape and mouth gape influenced MTL (Table 2.1, 2.2; Table A.7, A.8, Figure A.5, A.6, A.7, A.8). The SUB models had lower DIC values than NULL models, which indicate that even being a consistent predictor, body size is redundant given its strong phylogenetic component. Mean body size (either SL or body mass) was not a good predictor of MTL when only non-carnivorous fishes were analyzed (Table 2.2). The only functional trait that significatively influenced MTL was gut length (Table 2.1, 2.2; Table A.9, A.10, Figure A.9, A.10, A.11, A.12). Overall, the division of MTL into carnivorous and non-carnivorous groups reduced the R^2 of the models (Table 2.1). H^2 values were also reduced, but remained high, especially when compared to the slope of TL-body size relationship (Table 2.1; see below).

Table 2.2 Coefficient estimates generated by Bayesian phylogenetic linear mixed models performed on 100 different trees aiming to explain the variation in the mean trophic level (MTL) of freshwater and estuarine fishes. MTL was analyzed in three different ways: all fishes combined (Overall), carnivorous fishes only (MTL >2.5), and non-carnivorous fishes only (MTL < 2.5). Coefficient estimation was based on FULL models containing the explanatory variables: mean body size (either SL or body mass), body depth, body width, mouth width, mouth position, tooth shape, gill raker length and number, and gut length. Numbers in bold indicate that the coefficient estimate was consistent (i.e., credible intervals not encompassing zero). The coefficients associated with levels of categorical variables (presented in parenthesis) represent their difference to a fixed baseline level (Tooth shape: Absence of teeth, Gill raker: Absence of gill rakers, Mouth orientation: Superior mouth). For pairwise comparisons between all levels of categorical variables, see Figure 2.3, A.3, A.5, A.7, A.9, and A.11, and Table A.6, A.7, A.8, A.9, and A.10.

Coefficients	**Overall**		**Carnivorous**		**Non-carnivorous**	
	Model with SL	Model with body mass	Model with SL	Model with body mass	Model with SL	Model with body mass
	Estimates	Estimates	Estimates	Estimates	Estimates	Estimates
Intercept	3.11(2.46/3.78)	3.38(2.82/3.94)	2.79(2.34/3.29)	3.34(2.97/3.71)	2.41(1.80/3.01)	2.42(1.87/2.95)
Size	0.06(-0.01/0.13)	0.02(0.00/0.05)	**0.12(0.05/0.18)**	**0.04(0.02/0.06)**	0.00(-0.06/0.07)	0.00(-0.02/0.02)
Max. body depth	**-0.63(-1.21/-0.07)**	**-0.62(-1.19/-0.06)**	-0.23(-0.78/0.29)	-0.27(-0.80/0.22)	0.08(-0.41/0.62)	0.07(-0.43/0.61)
Max. body width	0.17(-1.25/1.57)	0.10(-1.30/1.50)	0.15(-1.00/1.27)	-0.06(-1.20/1.07)	-0.33(-2.03/1.35)	-0.32(-2.02/1.37)
Gut length	**-0.52(-0.66/-0.37)**	**-0.53(-0.68/-0.38)**	**-0.31(-0.54/-0.08)**	**-0.32(-0.55/-0.09)**	**-0.13(-0.25/-0.01)**	**-0.13(-0.25/-0.02)**
Mouth width	**0.47(0.12/0.81)**	**0.43(0.08/0.77)**	**0.37(0.08/0.66)**	**0.31(0.02/0.61)**	0.01(-0.42/0.44)	0.02(-0.41/0.44)
Tooth shape (Unicuspid)	0.15(-0.08/0.37)	0.14(-0.08/0.37)	0.14(-0.07/0.36)	0.12(-0.10/0.33)	0.08(-0.12/0.28)	0.08(-0.11/0.28)
Tooth shape (Multicuspid)	0.16(-0.05/0.38)	0.16(-0.06/0.38)	0.08(-0.12/0.29)	0.06(-0.14/0.26)	-0.02(-0.26/0.22)	-0.01(-0.25/0.22)
Tooth shape (Conical)	**0.29(0.08/0.51)**	**0.30(0.08/0.51)**	0.15(-0.06/0.35)	0.13(-0.07/0.33)	0.00(-0.20/0.19)	0.00(-0.19/0.19)
Tooth shape (Triangular serrated)	**0.63(0.27/0.99)**	**0.60(0.24/0.97)**	**0.54(0.19/0.92)**	**0.49(0.14/0.87)**	0.02(-0.28/0.30)	0.02(-0.27/0.30)
Gill raker (Short)	-0.02(-0.20/0.17)	-0.04(-0.23/0.15)	-0.05(-0.23/0.12)	-0.08(-0.26/0.09)	0.00(-0.18/0.17)	0.00(-0.18/0.18)

Table 2.2 Continued.

Coefficients	**Overall**		**Carnivorous**		**Non-carnivorous**	
	Model with SL	Model with body mass	Model with SL	Model with body mass	Model with SL	Model with body mass
Gill raker (Intermediate)	-0.07(-0.27/0.12)	-0.10(-0.29/0.10)	-0.01(-0.20/0.17)	-0.04(-0.23/0.14)	-0.06(-0.22/0.10)	-0.06(-0.23/0.10)
Gill raker (Comb-like)	-0.12(-0.34/0.10)	-0.15(-0.36/0.07)	-0.07(-0.29/0.15)	-0.10(-0.32/0.12)	0.00(-0.17/0.16)	0.00(-0.17/0.16)
Mouth orientation (Terminal)	**-0.21(-0.33/-0.09)**	**-0.20(-0.32/-0.08)**	**-0.12(-0.23/-0.02)**	**-0.12(-0.22/-0.02)**	-0.10(-0.27/0.07)	-0.10(-0.27/0.07)
Mouth orientation (Subterminal)	**-0.23(-0.39/-0.06)**	**-0.23(-0.39/-0.06)**	-0.12(-0.26/0.02)	-0.13(-0.27/0.01)	0.03(-0.18/0.23)	0.03(-0.18/0.23)
Mouth orientation (Inferior)	-0.30(-0.63/0.03)	-0.29(-0.62/0.03)	-0.25(-0.55/0.04)	-0.27(-0.57/0.02)	-0.02(-0.32/0.29)	-0.03(-0.33/0.28)
Phylogenetic variance	0.18(0.05/0.36)	0.17(0.04/0.36)	0.05(0.00/0.16)	0.05(0.00/0.17)	0.04(0.00/0.13)	0.04(0.00/0.13)
Residual variance	0.09(0.06/0.13)	0.09(0.06/0.13)	0.07(0.05/0.10)	0.07(0.05/0.10)	0.01(0.00/0.03)	0.01(0.00/0.03)

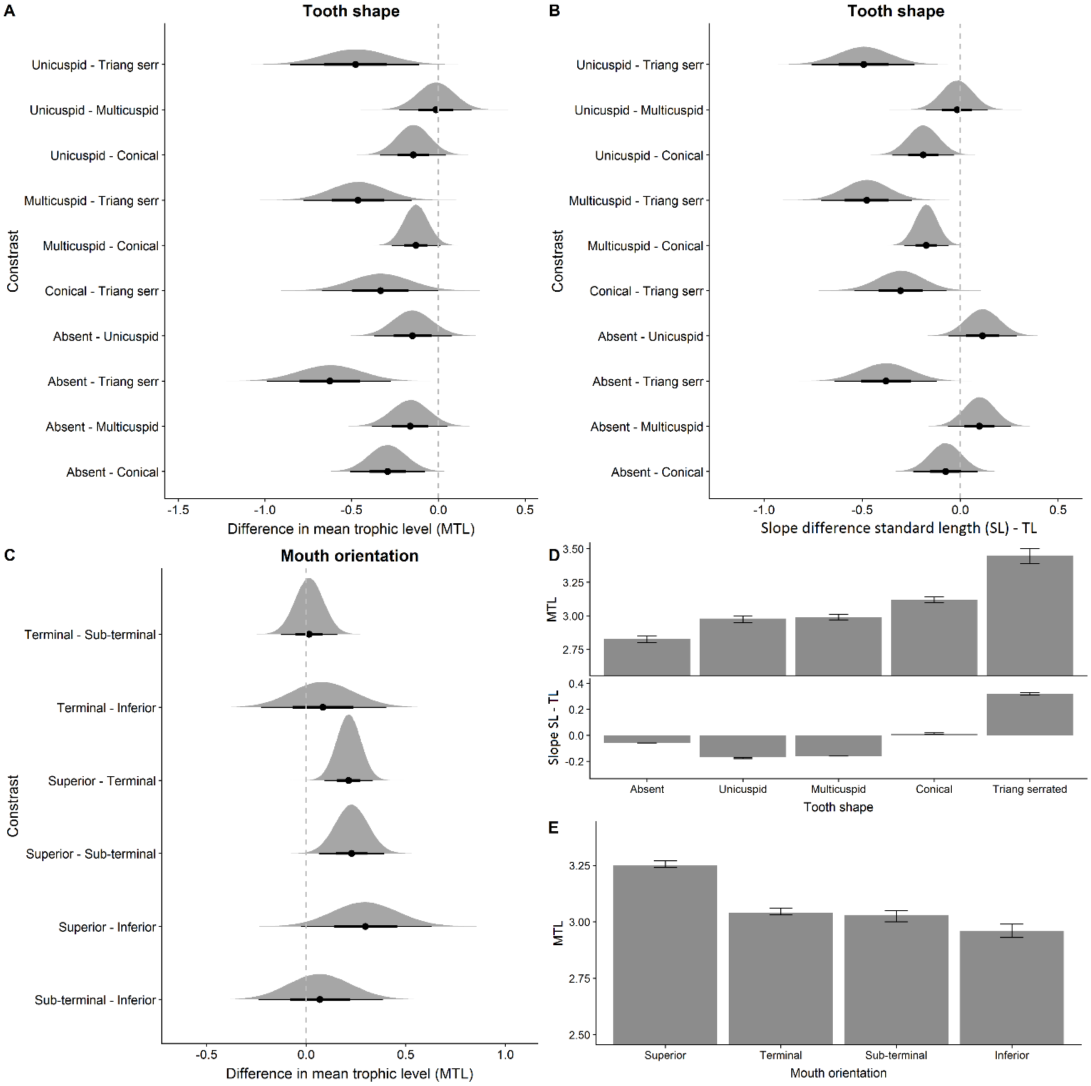

Figure 2.3 Posterior distributions of estimated marginal mean differences of mean trophic level (MTL) and/or the slope of the standard length (SL)–trophic level (TL) relationship among different types of tooth shape (A and B, respectively) and mouth orientation (just for MTL; C) according to Bayesian phylogenetic linear mixed models performed on 100 different trees. Estimated marginal means of MTL are presented for different types of tooth shape (D) and mouth orientation (E). Estimated marginal means of the SL-TL slopes are showed for different types of tooth shape (D). Both carnivorous and non-carnivorous species are included in these analyses. Statistically nonsignificant results (i.e., credible intervals encompassing 0) and results based on body mass rather than SL can be found in Table A.5, A.6, A.12, and A.13, and Figure A.1, A.3, A.16, and A.18.

Table 2.3 Coefficient estimates generated by Bayesian phylogenetic linear mixed models performed on 100 different trees aiming to explain the variation in the relationship between trophic level (TL) and body size (either standard length [SL] or body mass) of freshwater and estuarine fishes. Coefficient estimation was based on FULL models containing the explanatory variables: mean body size (either SL or body mass), body depth, body width, mouth width, mouth position, tooth shape, gill raker length and number, and gut length. Numbers in bold indicate that the coefficient estimate was consistent (i.e., credible intervals not encompassing zero). The coefficients associated with levels of categorical variables (presented in parenthesis) represent their difference to a fixed baseline level (baselines were as follows: Tooth shape– Absence of teeth, Gill raker– Absence of gill rakers, Mouth orientation– Superior mouth). For pairwise comparison between all levels of categorical variables, see Figure 2.3, and Table A.12 and A.13, and Figure A.16 and A.18.

Coefficients	**Model with SL**	**Model with body mass**
Intercept	-0.30(-0.71/0.10)	-0.13(-0.27/0.01)
Size	0.04(-0.10/0.18)	0.01(-0.01/0.03)
Maximum body depth	**-0.87(-1.28/-0.45)**	**-0.36(-0.54/-0.18)**
Maximum body width	0.11(-0.93/1.16)	0.10(-0.35/0.56)
Gut length	0.01(-0.09/0.12)	0.02(-0.03/0.06)
Mouth width	**0.63(0.31/0.94)**	**0.25(0.12/0.39)**
Tooth shape (Unicuspid)	-0.11(-0.29/0.06)	-0.03(-0.11/0.04)
Tooth shape (Multicuspid)	-0.10(-0.26/0.06)	-0.03(-0.10/0.04)
Tooth shape (Conical)	0.07(-0.09/0.24)	0.05(-0.03/0.12)
Tooth shape (Triangular serrated)	**0.38(0.12/0.64)**	**0.15(0.04/0.27)**
Gill raker (Short)	0.12(-0.03/0.28)	0.05(-0.01/0.12)
Gill raker (Intermediate)	0.08(-0.09/0.24)	0.02(-0.05/0.10)
Gill raker (Comb-like)	0.04(-0.15/0.23)	0.01(-0.07/0.09)
Mouth orientation (Terminal)	0.01(-0.10/0.12)	0.01(-0.04/0.06)
Mouth orientation (Subterminal)	-0.01(-0.15/0.13)	0.01(-0.05/0.07)
Mouth orientation (Inferior)	0.01(-0.23/0.24)	0.01(-0.10/0.11)
Phylogenetic variance	0.01(0.00/0.04)	0.00(0.00/0.01)
Residual variance	0.07(0.06/0.09)	0.01(0.01/0.02)

2.3.2. Raw data

The Bayesian semi-parametric generalized mixed model using TL for individual specimens rather than species MTL indicated that SL alone was not a good predictor of

TL (slope of the TL-SL relationship= -0.04 [Lower CI: -0.13, Upper CI: 0.04]). However, TL varied consistently with SL for 56 out of 179 species (31%) as indicated by the values of the random slopes of the model (Figure 2.4; Table A.11, Figure A.13). From those species with consistent relationships, 34 (61%) had negative relationship between SL and TL, whereas 22 (39%) had positive relationships. The correlation between individual fish body mass and TL also was weak and inconsistent (slope of the TL-body mass relationship =-0.02 [Lower CI=-0.08, Upper CI=0.04]). Random slope estimates generated by the model using body mass were convergent with the estimates generated using SL (Figure 2.4). In eight cases (4.5%), the models did not converge regarding the direction of the relationship (negative vs positive, or vice versa; Figure 2.4). However, the credible intervals of the slopes encompassed zero in all eight cases, indicating that the TL-body size (either measured as SL or body mass) relationship was not consistent. The number of species with consistent relationships between body size (SL or body mass) and TL could have been underestimated given that sample size had a small influence on the likelihood of finding consistent relationships (SL: $z= 4.60$, $p< 0.001$, $R^2= 0.13$; Body mass: $z= 3.71$, $p< 0.001$, $R^2= 0.07$; Figure A.15). Overall, there was no evidence that the range of body size affected the chance of finding consistent relationships between body size and TL (SL: $z=0.63$, $p= 0.53$, $R^2< 0.01$; Body mass: $z= -0.71$, $p= 0.48$, $R^2< 0.01$).

FULL models performed better than NULL models (Table 2.1), with the former explaining an average of 31.5% of total variation of the TL-body size relationships (CI marginal $R^2= 0.30$ to 0.32). The relationship between SL and TL was mainly influenced by three functional traits: body depth, mouth width and tooth shape (Figure 2.4). Fishes with laterally compressed bodies had more negative relationships between SL and TL than fishes with elongate and fusiform bodies (Figure 2.2b). Positive relationships were more likely to occur in fishes with relatively large mouths (Figure 2.2d). Fishes with unicuspid or multicuspid teeth tended to have negative slopes, fishes without teeth tended to have flat slopes, and those with conical and triangular serrated teeth had positive slopes (Figure 2.3b, 2.3d). Inconsistent patterns were found for body width, mouth orientation, gill raker shape, and gut length (Figure A.17). H^2 values and conditional R^2 were lower on average for analyses with TL-SL as response variable compared to values generated from analyses using species MTL ($H^2 = 0.55$ to 0.72, Conditional $R^2 = 0.10$ to 0.39; Table 2.1), indicating only a moderate influence of phylogenetic relationships on TL-SL relationships.

FULL models performed better than NULL models in explaining the variation of TL-body mass relationship (Table 2.1). Body depth, mouth width and tooth shape consistently influenced TL-body mass relationships, and their effects were similar to those observed with models using SL (Table 2.2; Figure A.19). Body width, mouth orientation, gill rakers, and gut length did not influence TL-body mass relationships (Table A.13, Figure A.18, A.19). Marginal and conditional R^2 and H^2 values were virtually the same as those obtained from models using SL (Table 2.1).

Despite the fact that the SUB-MTL models (containing only MTL as explanatory variable) performed poorly when compared to FULL models, MTL influenced both the TL-SL and TL-body mass relationships, explaining 14% and 9% of their variation, respectively (Table 2.1, Figure 2.2f; Figure A.17, A.19). In both cases, the slopes of the TL-body size relationships tended to be positive for species with higher MTL (Figure 2.2f).

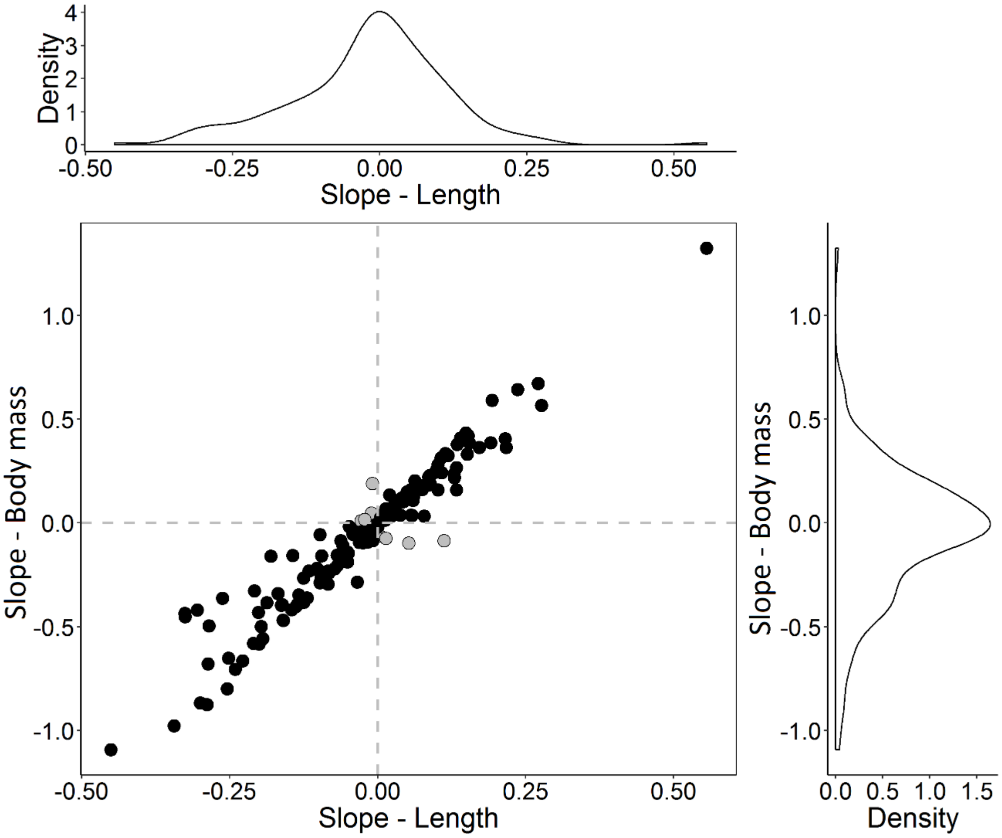

Figure 2.4 Comparison of the slopes of the trophic level (TL)–standard length (SL) relationship (x axis) and the slopes of the TL–body mass relationship (y axis) for 179 freshwater and estuarine fish species. Slopes were generated using Bayesian semi-parametric generalized mixed models, where species were treated as a random variable (random intercept and slope). All species analyzed contained at least 30 specimens dissected for dietary analysis. Gray dots represent cases (N=8) where the models did not converge regarding the direction of the relationship (negative vs positive, or vice-versa). Kernel-density estimation plots show the distribution of the slopes generated using both SL and body mass.

2.4. Discussion

My analysis of freshwater and estuarine fishes revealed a wasp-waist distribution between trophic level (either TL or MTL) and body size, which is not consistent with the general positive linear relationship for fishes reported by Romanuk, Hayward, and Hutchings (2011) and others. However, MTL increased with mean body size when carnivorous fishes were analyzed separately, a finding in agreement with several previous studies (e.g., Riede *et al*., 2011). Similar results were obtained using either body mass or standard length as the estimate of body size. The TL-body size relationship varied considerably among species, and patterns were associated with certain functional traits, especially body depth, mouth width, and tooth shape. This finding supports my prediction that functional traits associated with feeding and food processing mediate the relationship between TL and body size.

The lack of evidence for a general positive relationship between trophic level (either TL or MTL) and body size contrast with other studies conducted in both aquatic (Jennings *et al*., 2001, 2002, 2007; Al-Habsi *et al*., 2008; Rooney *et al*., 2008; Arim *et al*., 2010; Barnes *et al*., 2010; Gilljam *et al*., 2011; Riede *et al*., 2011; Romanuk *et al.*, 2011; Reum & Marshall, 2013; Romero-Romero *et al*., 2016; Potapov *et al*., 2019) and terrestrial ecosystems (Rooney *et al*., 2008; Riede *et al*., 2011). Most of these studies involved communities that are strongly size structured (Jennings *et al*., 2001, 2002; Al-Habsi *et al*., 2008; Romero-Romero *et al*., 2016) and/or were strongly focused on carnivores (Jennings *et al*., 2007; Arim *et al*., 2010; Barnes *et al*., 2010; Riede *et al*., 2011; Reum & Marshall, 2013). However, exclusion of species at lower trophic levels neglects an important part of community trophic diversity, especially for highly diverse taxa, such as teleost fishes and faunas of species-rich tropical regions. In my study, carnivorous fishes that have higher MTL tended to have positive relationships between TL and body size. Furthermore, the relationship between MTL and mean body size was significantly positive only when the analysis was restricted to carnivorous fishes (MTL > 2.5). Therefore, it is possible that studies that failed to include omnivorous, herbivorous and detritivorous species in their analysis (e.g., Romanuk *et al.*, 2011) may have overestimated the strength and slope of the MTL-body size relationship. Consequently, studies that analyze regional faunas or phylogenetic lineages that mostly or exclusively include carnivorous fishes should discuss potential bias when using resultant MTL-body size relationships for food web modeling.

The lack of a general relationship between MTL and body size likely reflects differences in the morphology, physiology and behavior of carnivorous and non-carnivorous fishes. In my study, MTL of carnivorous species increased with mean body size, which corroborates findings from several studies that analyzed only predatory fishes (e.g., Jennings *et al.*, 2007; Arim *et al*., 2010; Gilljam *et al*., 2011). In order to meet energetic requirements, large predators may feed preferentially on the largest and most profitable prey that can be successfully subdued (Werner & Hall, 1974; Mittelbach, 1981). Interestingly, a study conducted in a Neotropical floodplain river found that the MTL of carnivorous fishes did not increase with mean body size (Layman *et al.*, 2005). A possible explanation is that low availability of prey fish at higher trophic positions during certain periods of the annual hydrologic cycle forces large piscivores to feed at lower trophic levels to meet metabolic demands (Arim *et al.*, 2007), especially at tropical regions where the temperatures tend to be high (Dantas *et al.*, 2019). Research that explores the relationship between MTL and mean body size across multiple species of non-carnivorous fishes appears to be lacking. My results indicated that the relationship is flat, but given my relatively small sample size for this guild (52 species), inferences should be made with caution.

Shallow freshwater and estuarine habitats are in some respects more similar to terrestrial habitats than the marine pelagic habitats for which a strong trophic level (both TL and MTL)-body size relationships are believed to influence food web dynamics (Jennings *et al.*, 2007; Al-Habsi *et al*., 2008; Riede *et al.*, 2011; Reum & Marshall, 2013; Romero-Romero *et al*., 2016; Potapov *et al*., 2019). Marine pelagic food webs are largely supported by unicellular phytoplankton that are relatively nutrient-rich and easy to digest (Tucker & Rogers, 2014). Consequently, these food webs are characterized by efficient transfer of energy and body mass, and long food chains (McGarvey *et al.*, 2016). Under these circumstances, it is difficult for large animals to exploit food resources at or near the bottom of food chains due to the difficulty of ingesting and handling small particles. The exceptions are large filter feeders, such as basking sharks and whale sharks that strain large volumes of water through comb-like gill rakers, and baleen whales that strain particles using the comb-like baleen. However, the great majority of marine phytoplankton feeders are zooplankton, and most zooplankton are consumed by larger zooplankton and small fishes that target individual food particles. Shallow freshwater and estuarine systems, on the other hand, have food webs supported by combinations of unicellular and multicellular autotrophs, including phytoplankton, periphyton, aquatic macrophytes, and allochthonous plant material (Correll, 1978; Vannote *et al*., 1980; Junk *et al.*, 1989; Winemiller, 1990; Roach *et al.*, 2014). Detritus, both of autochthonous and allochthonous origin, also is an important food resource that is directly exploited by fishes in shallow freshwater and estuarine ecosystems (Darnell, 1967; Mann, 1988; Winemiller, 1990; Zeug & Winemiller, 2008). Many medium- and large-sized fishes are well-adapted to exploit food resources at the base of aquatic food webs, e.g., frugivorous pacus of the Amazon (e.g., *Colossoma macropomum, Piaractus brachypomus*) and omnivorous and herbivorous carps of Asia (e.g., *Catlocarpio siamensis*, *Ctenopharyngodon idella*). Basal production sources in freshwater ecosystems are exploited by other kinds of large vertebrates, including manatees (*Trichechus* spp.), beavers (*Castor* spp.), turtles (e.g., *Peltocephalus dumerilianus*), geese (e.g., *Anser* spp., *Branta* spp. and *Chen* spp.) and ducks (e.g., *Anas* spp.). Conversely, many small freshwater and estuarine fishes that feed on aquatic and terrestrial invertebrates are positioned at high trophic levels. These small invertivores include many species of tetras (Alestidae, Characidae, Lebiasinidae), minnows (Cyprinidae), killifishes (Fundulidae, Rivulidae), ricefishes (Adrianichthyidae) and mosquito fishes (Poeciliidae). Carnivorous arthropods that are prey of these small fishes also feed at high trophic levels; examples include spiders (*Argyroneta aquatica*), beetles (e.g., Hydrophilidae), water bugs (e.g., Belostomatidae, Nepidae) and water mites (e.g., *Hydracarina* spp.). On land, the high diversity of plants provides a vast range of options for herbivores (e.g., granivores, frugivores, browsers, grazers) spanning a wide range of body sizes, including some of Earth's largest terrestrial animals (e.g., elephants, giraffes, hippopotamus, rhinoceros). Half of all insect species, the most diverse group of animals on earth, are estimated to feed primarily on plants (Grimaldi & Engel, 2005; Nakadai, 2017), which implies that consumers smaller than their food resource should be the rule rather than the exception in terrestrial food webs. Therefore, positive TL-body size relationships should not be expected to be the rule for the majority of consumers in many communities, and the relationship between MTL and body size across all consumers in terrestrial communities as well as freshwater and estuarine ecosystems, should be very weak or absent, a position argued previously by others (Layman *et al*., 2005; Tucker & Rogers, 2014; Ou *et al.*, 2017; Potapov *et al.*, 2019).

Mean body size was a weak predictor of MTL compared to other functional traits (e.g., gut length, tooth shape, mouth orientation, mouth width, and body depth) when the relationship was assessed across all consumers. These other functional variables directly influence foraging success, yet surprisingly, they have received little attention in empirical and theoretical food web studies. Tooth shape influences food acquisition and processing by both herbivorous and predatory fishes (McCollum & Sharpe, 2001). Fishes without teeth or having unicuspid or multicuspid teeth tended to have low MTL. Some of these fishes (e.g., Neotropical Curimatidae, Loricariidae and Prochilodontidae, African Citharinidae and Distichodontidae, many Asian carps, and the North American gizzard shad, *Dorossoma cepedianum*) feed on fine particulate organic matter (FPOM). Unicuspid teeth are common in fishes that scrape periphyton adhered to surfaces (e.g., loricariids), whereas many fishes with multicuspid teeth (e.g., alestids, characids, some serrasalmids) use them to crush fruits and seeds (Winemiller, 1991b). Conical and triangular serrated teeth are common among predators that use them to pierce or tear flesh (Winemiller, 1991b). Fish mouth orientation is a strong indicator of the position for feeding within the water column (Keast & Webb, 1966; Winemiller, 1991b). In my study, fishes with a superior mouth orientation had higher MTLs than much larger fishes with terminal, sub-terminal, and inferior mouth positions. Most fishes with upturned mouths, such as the Neotropical characiforms *Thoracocharax stellatus* and *Triportheus* spp., feed on small terrestrial arthropods that fall onto the water surface (Cushing & Allan, 2001). Fishes with terminal and sub-terminal mouths were commonly observed among midwater-dwelling and epibenthic fishes, many of which were omnivorous with broad diets. Fishes with an inferior mouth orientation usually fed on substrates, either scraping periphyton from rocks and logs or using suction to ingest small aquatic invertebrates or FPOM. Mouth gape, here indicated by relative mouth width, sets an upper limit on the size of food items that can be consumed by animals that ingest food items whole, and therefore influences predator-prey size ratios and trophic level (Montaña *et al.*, 2011; Mihalitsis & Bellwood, 2017). Carnivorous species, specially piscivores that ingest prey whole (e.g., largemouth bass [*Micropterus salmoides*], peacock bass [*Cichla* spp.] and many catfishes [Siluriformes]) tended to have large mouths when compared to omnivorous, algivorous and detritivorous fishes. This difference would be expected given that predator-prey body size ratios tend to decrease with trophic level (Riede *et al.*, 2011), when mouth gape is the major factor limiting the size of prey that can be ingested. Gut length was associated with a diet gradient ranging from herbivory/detritivory (long gut) to carnivory (short gut). Because gut length affects digestion and nutrient absorption, it may be the single trait that best predicts trophic level in fishes (Kapoor *et al.*, 1975; Horn, 1989; German & Horn, 2006; Wagner *et al*., 2009), as well as reptiles and amphibians (Stevens & Hume, 1995; O'Grady *et al*., 2005), birds (Ricklefs, 1996; Battley & Piersma, 2005), and mammals (Schieck & Millar, 1985). Body shape is highly variable among teleosts and can affect both swimming performance and susceptibility to gape-limited predators. The negative relationship between body depth and MTL indicated that carnivorous fishes tend to have fusiform or elongated bodies that enhance pursuit speed (Webb, 1984a, 1984b). However, some piscivorous fishes, such as snappers (*Lutjanus* spp.) and certain cichlids (*Serranochromis* spp.), have relatively deep bodies and use ambush as a foraging strategy within structurally complex habitats (Webb, 1984b). Among fishes that inhabit structurally complex habitats, a relatively deep body also may facilitate agile movements to avoid capture (Webb, 1984a, 1984b; Wood & Bain, 1995). Functional traits other than body size also significantly influenced statistical models predicting the MTL of both carnivorous and non-carnivorous fishes. This suggest that more than just disentangling carnivorous from non-carnivorous fishes, functional traits can help deepen our understanding of how MTL varies at more restricted compartments of food webs.

From my intraspecific analyses, negative TL-body size correlations were more common than positive correlations, a finding that contrasts with those from some earlier studies (e.g., Jennings *et al*., 2002, 2007; Reum & Marshall, 2013). Negative TL-body size relationships were observed for many species with low values for MTL, and those with deep bodies, small mouths, and unicuspid or multicuspid teeth. These are characteristic of herbivorous fishes, many of which undergo diet shifts during early ontogeny. Their early life stages generally feed on heterotrophic microfauna, such as protozoa and rotifers, and zooplankton, such as copepods and cladocerans, and later shift to consuming algae or macrophyte tissues that are less nutritious but often abundant in their environments (Horn, 1989; German & Horn, 2006). Less is documented about diets of early life stages of detritivorous fishes, especially those from tropical freshwaters. Most detritivores in my study had TL-body size relationships with slightly negative or flat slopes (e.g., *Ancistrus triradiatus, Loricariichthys brunneus, Cyphocharax spilurus*, *Prochilodus mariae*; Table A.11), suggesting a less abrupt diet change than seen in herbivorous fishes. In my study, detritivores had the longest relative gut lengths, which may have contributed to the lack of a significant linear relationship between gut length and the TL-body size relationship. In contrast, herbivores and some omnivorous species had shorter guts and negative TL-body size relationships. Detritus varies in quality and generally contains bacteria, fungi and other microorganisms that may supply nutrition sufficient for growth of early life stages of detritivorous fishes (Bowen, 1980, 1983; Mann, 1988). Species with high MTL, elongated or fusiform bodies, conical or triangular-serrated teeth, and large mouths tended to have positive TL-body size relationships, which likely was influenced by the fact that larger predators can ingest larger prey without necessarily eliminating small prey from their diets (Woodward and Hildrew 2002, Costa 2009). This leads to an increase in maximum TL of most predatory species while minimum TL stays flat, resulting in an increase in both the mean and variance of TL (Dalponti *et al.*, 2018).

Potential sources of bias are always a concern for empirical studies. Body size distributions and sample sizes varied among species. Exploratory analysis with a portion of my dataset indicated that TL-body size relationships were not sensitive to the range of body sizes in species datasets. However, sample size influenced the statistical significance of results (i.e., parameter estimation either encompassing or non-encompassing zero), with small sample sizes sometimes producing nonsignificant relationships. I therefore conclude that the number of species with significant relationships may be underestimated. However, because I analyzed parameter estimates rather than their credible intervals, my major inferences should be largely unaffected by sample size. Trophic levels of my non-fish prey categories were estimated based on literature information, a potential source of error. The same issue confronts studies that estimate trophic level based on isotopic analysis (e.g., assumptions about trophic fractionation values, assimilation of material from basal resources, tissue turnover, sample size, body size, and habitat; Hoeinghaus & Zeug, 2008; Layman *et al.*, 2012). The use of mean trait values based on measurements of adult specimens used in Approach 1 and step 2 of Approach 2 discount the potential for ontogenetic allometry (e.g., German & Horn, 2006). To minimize this issue, I measured adult specimens with SLs near the mode of the species distribution. Functional traits were measured primarily on adult specimens, whereas my diet data were obtained from a broader size range that included some immature size classes. This source of variation could have weakened relationships between functional traits (including body size) and TL, especially if intraspecific dietary and morphological variation increases with size (e.g., Keppeler *et al*., 2015). In a separate analysis (unpublished), I found that restricting the diet data to only adults versus including a broader range of sizes had minimal effect on correlations between functional traits and food web descriptors.

Body size is acknowledged as one of the most important traits affecting ecological performance (Woodward *et al.*, 2005), but sometimes, in the interest of simplifying complex systems, it has been emphasized to the exclusion of other traits that are equally or more influential. An increasing number of models and theories assume that food web structure and dynamics are strongly size-based (Cohen *et al.*, 1990; Otto *et al.*, 2007; Petchey *et al.*, 2008; Berlow *et al.*, 2009; Arim *et al.*, 2010; McCann, 2011; Schneider *et al.*, 2016). Furthermore, it has been proposed that additional traits should correlate with body size and trophic level, such as traits affecting locomotion (McCann *et al.*, 2005; Rooney *et al.*, 2008), brain size (as a surrogate for cognitive ability and behavioral complexity; McCann *et al.*, 2005; Rooney *et al.*, 2008), and mouth gape size (Arim *et al*., 2010), although exceptions are found in all these examples (Chittka & Niven, 2009; De Bie *et al.*, 2012; Dunic & Baum, 2017). Thus, while the importance of body size has been overemphasized in food-web studies, I consider that the importance of other influential traits has been overlooked. Recent advances in ecological modeling and computation power allow the creation of more complex and realistic food web models that incorporate multiple traits of individual organisms (individual-based models) or life stages classes (age or stage-structured models) (DeAngelis & Grimm, 2014; Fujiwara, 2016).

2.4.1. Conclusions

General rules that explain complex natural systems have been a major goal in ecology, and the use of functional traits has increasingly been promoted as an avenue for advancement (Winemiller *et al*., 2015; Funk *et al*., 2017). Body size has been seen as an important determinant of predator-prey interactions and, consequently, food web structure and dynamics (Woodward *et al*., 2005; Brose *et al*., 2006). Here, I found that the MTL was positively related with body size in fishes only when non-carnivorous species were excluded from the analysis. I did not find a general positive association between trophic level and body size in fishes as widely reported (e.g., Romanuk *et al.*, 2011), and this was true for both interspecific and intraspecific comparisons. I speculate that similar results may be found in other systems wherein higher plants and detritus are important food resources for animals. TL-body size relationships varied considerably among fish species and also were influenced by several functional traits. This was expected given the high trophic and morphological diversity observed among teleost fishes. Body size has a relationship with TL, more so for fish that are strict carnivores, and therefore may influence the structure of food webs dominated by predatory fishes (e.g., pelagic marine systems; Jennings *et al*., 2001, 2002; Al-Habsi *et al*., 2008). However, this relationship was not strong for any trophic group in my dataset for freshwater and estuarine fishes, and it was very weak for these fishes overall. Further exploration of relationships among key functional traits and trophic ecology likely will lead to improved predictions about food web patterns and dynamics of both carnivorous and non-carnivorous species.

2.5. References

Adams S.M., Kimmel B.L. & Ploskey G.R. (1983) Sources of organic matter for reservoir fish production: a trophic dynamics analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, 40, 1480–1495. https://doi.org/10.1139/f83-170

Akin S. & Winemiller K.O. (2006) Seasonal variation in food web composition and structure in a temperate tidal estuary. *Estuaries and Coasts*, 29, 552–567. https://doi.org/10.1007/BF02784282

Al-Habsi S.H., Sweeting C.J., Polunin N.V.C. & Graham N.A.J. (2008) δ15N and δ13C elucidation of size-structured food webs in a Western Arabian Sea demersal trawl assemblage. *Marine Ecology Progress Series*, 353, 55–63. https://doi.org/10.3354/meps07167

Albrecht G.H., Gelvin B.R. & Hartman S.E. (1993) Ratios as a size adjustment in morphometrics. *American Journal of Physical Anthropology*, 91, 441–468. https://doi.org/10.1002/ajpa.1330910404

Arim M., Abades S.R., Laufer G., Loureiro M. & Marquet P.A. (2010) Food web structure and body size: trophic position and resource acquisition. *Oikos*, 119, 147–153. https://doi.org/10.1111/j.1600-0706.2009.17768.x

Arim M., Bozinovic F. & Marquet P.A. (2007) On the relationship between trophic position, body mass and temperature: reformulating the energy limitation hypothesis. *Oikos*, 116, 1524–1530. https://doi.org/10.1111/j.0030-1299.2007.15768.x

Barnes C., Maxwell D., Reuman D.C. & Jennings S. (2010) Global patterns in predator-prey size relationships reveal size dependency of trophic transfer efficiency. *Ecology*, 91, 222–232. https://doi.org/10.1890/08-2061.1

Barton K. (2019) *MuMIn: multi-model inference*. Available at: https://CRAN.R-project.org/package=MuMIn (accessed 02 February 2019).

Battley P.F. & Piersma T. (2005) *Adaptive interplay between feeding and ecology and features of the digestive tract in birds*. In: Starck J.M. & Wang T. (eds) Physiological and ecological adaptations to feeding in vertebrates. Science Publishers Inc., Enfield, pp 201–228.

Berlow E.L., Dunne J.A., Martinez N.D., Stark P.B., Williams R.J. & Brose U. (2009) Simple prediction of interaction strengths in complex food webs. *Proceedings of the National Academy of Sciences*, 106, 187–191. https://doi.org/10.1073/pnas.0806823106

De Bie T., De Meester L., Brendonck L., Martens K., Goddeeris B., Ercken D., Hampel H., Denys L., Vanhecke L., Van der Gucht K., Van Wichelen J., Vyverman W. & Declerck S.A.J. (2012) Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. *Ecology Letters*, 15, 740–747. https://doi.org/10.1111/j.1461-0248.2012.01794.x

Boettiger C., Lang D.T. & Wainwright P.C. (2012) rfishbase: exploring, manipulating and visualizing FishBase data from R. *Journal of Fish Biology*, 81, 2030–2039. https://doi.org/10.1111/j.1095-8649.2012.03464.x

Bolnick D.I., Amarasekare P., Araújo M.S., Bürger R., Levine J.M., Novak M., Rudolf V.H.W., Schreiber S.J., Urban M.C. & Vasseur D. (2011) Why intraspecific trait variation matters in ecology. *Trends in Ecology and Evolution*, 26, 183–192. https://doi.org/10.1016/j.tree.2011.01.009

Bowen S.H. (1980) Detrital nonprotein amino acids are the key to rapid growth of Tilapia in Lake Valencia, Venezuela. *Science*, 207, 1216–1218. https://doi.org/10.1126/science.207.4436.1216

Bowen S.H. (1983) Detritivory in neotropical fish communities. *Environmental Biology of Fishes*, 9, 137–144. https://doi.org/10.1007/BF00690858

Brose U., Williams R.J. & Martinez N.D. (2006) Allometric scaling enhances stability in complex food webs. *Ecology Letters*, 9, 1228–1236. https://doi.org/10.1111/j.1461-0248.2006.00978.x

Brose U., Archambault P., Barnes A.D., Bersier L-F., Boy T., Canning-Clode J., Conti E., Dias M., Digel C., Dissanayake A., Flores A.A.V., Fussmann K., Gauzens B., Gray C., Häussler J., Hirt M.R., Jacob U., Jochum M., Kéfi S., McLaughlin O., MacPherson M.M., Latz E., Layer-Dobra K., Legagneux P., Li Y., Madeira C., Martinez N.D., Mendonça V., Mulder C., Navarrete S.A., O'Gorman E.J., Ott D., Paula J., Perkins D., Piechnik D., Pokrovsky I., Raffaelli D., Rall B.C., Rosenbaum B., Ryser R., Silva A., Sohlström E.H., Sokolova N., Thompson M.S.A., Thompson R.M., Vermandele F., Vinagre C., Wang S., Wefer J.M., Williams R.J., Wieters E., Woodward G. & Iles A.C. (2019) Predator traits determine food-web architecture across ecosystems. *Nature Ecology and Evolution*, 3, 919–927.

https://doi.org/10.1038/s41559-019-0899-x

Brown J.H., Gillooly J.F., Allen A.P., Savage V.M. & West G.B. (2004) Toward a metabolic theory of ecology. *Ecology*, 85, 1771–1789. https://doi.org/10.1890/03-9000

Bruno J.F. & O'Connor M.I. (2005) Cascading effects of predator diversity and omnivory in a marine food web. *Ecology Letters*, 8, 1048–1056. https://doi.org/10.1111/j.1461-0248.2005.00808.x

Burress E.D., Holcomb J.M., Bonato K.O. & Armbruster J.W. (2016) Body size is negatively correlated with trophic position among cyprinids. *Royal Society Open Science*, 3, 150652. https://doi.org/10.1098/rsos.150652

Caughlin T.T., Ferguson J.M., Lichstein J.W., Zuidema P.A., Bunyavejchewin S. & Levey D.J. (2014) Loss of animal seed dispersal increases extinction risk in a tropical tree species due to pervasive negative density dependence across life stages. *Proceedings of the Royal Society B*, 282, 20142095. https://doi.org/10.1098/rspb.2014.2095

Chittka L. & Niven J. (2009) Are bigger brains better? *Current Biology*, 19, R995–R1008. https://doi.org/10.1016/j.cub.2009.08.023

Cohen J.E., Briand F. & Newman C.M. (1990) *Community food webs: data and theory*. Springer, Berlin.

Cohen J.E., Pimm S.L., Yodzis P. & Saldaña J. (1993) Body sizes of animal predators and animal prey in food webs. *Journal of Animal Ecology*, 62, 67–78. https://doi.org/10.2307/5483

Cohen J.E., Jonsson T. & Carpenter S.R. (2003) Ecological community description using the food web, species abundance, and body size. *Proceedings of the National Academy of Sciences of the United States of America*, 100, 1781–1786. https://doi.org/10.1073/pnas.232715699

Correll D.L. (1978) Estuarine productivity. *BioScience*, 28, 646–650. https://doi.org/10.2307/1307395

Costa G.C. (2009) Predator size, prey size, and dietary niche breadth relationships in marine predators. *Ecology*, 90, 2014–2019. https://doi.org/10.1890/08-1150.1

Cushing C.E. & Allan J.D. (2001) *Streams: their ecology and life*. Academic Press, San Diego.

Dalponti G., Guariento R.D. & Caliman A. (2018) Hunting high or low: body size drives trophic position among and within marine predators. *Marine Ecology Progress Series*, 597, 39–46. https://doi.org/10.3354/meps12584

Dantas D.D.F., Caliman A., Guariento R.D., Angelini R., Carneiro L.S., Lima S.M.Q., Martinez P.A. & Attayde J.L. (2019) Climate effects on fish body size-trophic position relationship depend on ecosystem type. *Ecography*, 42, 1579–1586. https://doi.org/10.1111/ecog.04307

Darnell R.M. (1967) *Organic detritus in relation to the estuarine ecosystem*. In: G.H. Lauff (ed) Estuaries. American Association for the Advancement of Science, Washington D.C., pp 376–382.

DeAngelis D.L. & Grimm V. (2014) Individual-based models in ecology after four decades. *F1000Prime Reports*, 6, 39. https://doi.org/10.12703/P6-39

Dunic J.C. & Baum J.K. (2017) Size structuring and allometric scaling relationships in coral reef fishes. *Journal of Animal Ecology*, 86, 577–589. https://doi.org/10.1111/1365-2656.12637

Elton C.S. (1927) *Animal ecology*. Macmillan, New York.

Eklöf A., Jacob U., Kopp J., Bosch J., Castro-Urgal R., Chacoff N.P., Dalsgaard B., de Sassi C., Galetti M., Guimarães P.R., Lomáscolo S.B., González A.M.M., Pizo M.A., Rader R., Rodrigo A., Tylianakis J.M., Vázquez D.P. & Allesina S. (2013) The dimensionality of ecological networks. *Ecology Letters*, 16, 577–583. https://doi.org/10.1111/ele.12081

Escobar M.D. & West M. (1995) Bayesian density estimation and inference using mixtures. *Journal of the American Statistical Association*, 90, 577–588. https://doi.org/10.1080/01621459.1995.10476550

Froese R. & Pauly D. (2019) FishBase. www.fishbase.org.

Froese R., Thorson J.T. & Reyes Jr. R.B. (2014) A Bayesian approach for estimating length-weight relationships in fishes. *Journal of Applied Ichthyology*, 30, 78–85. https://doi.org/10.1111/jai.12299

Fujiwara M. (2016) Incorporating demographic diversity into food web models: effects on community structure and dynamics. *Ecological Modelling*, 322, 10–18. https://doi.org/10.1016/j.ecolmodel.2015.11.015

Funk J.L., Larson J.E., Ames G.M., Butterfield B.J., Cavender-Bares J., Firn J., Laughlin D.C., Sutton-Grier A.E., Williams L. & Wright J. (2017) Revisiting the Holy Grail: using plant functional traits to understand ecological processes. *Biological Reviews,* 92, 1156–1173. https://doi.org/10.1111/brv.12275

Gatz Jr A.J. (1979) Community organization in fishes as indicated by morphological features. *Ecology*, 60, 711–718. https://doi.org/10.2307/1936608

Gelman A. & Rubin D.B. (1992) Inference from iterative simulation using multiple sequences. *Statistical Science*, 7, 457–472. https://doi.org/10.1214/ss/1177011136

German D.P. & Horn M.H. (2006) Gut length and mass in herbivorous and carnivorous prickleback fishes (Teleostei: Stichaeidae): ontogenetic, dietary, and phylogenetic effects. *Marine Biology*, 148, 1123–1134. https://doi.org/10.1007/s00227-005-0149-4

Gilljam D., Thierry A., Edwards F.K., Figueroa D., Ibbotson A.T., Jones J.I., Lauridsen R.B., Petchey O.L., Woodward G. & Ebenman B. (2011) Seeing double: size-based versus taxonomic views of food web structure. *Advances in Ecological Research*, 45, 67–133. https://doi.org/10.1016/B978-0-12-386475-8.00003-4

Grimaldi D. & Engel M.S. (2005) *Evolution of the insects*. Cambridge University Press, New York.

Guillerme T. & Healy K. (2018*) mulTree: performs MCMCglmm on multiple phylogenetic trees*. R package version 1.3.4.

Hadfield J.D. (2010) MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software*, 33, 1–22. https://doi.org/10.18637/jss.v033.i02

Hansen T.F. & Orzack S.H. (2005) Assessing current adaptation and phylogenetic inertia as explanations of trait evolution: the need for controlled comparisons. *Evolution*, 59, 2063–2072. https://doi.org/10.1111/j.0014-3820.2005.tb00917.x

Helfman G.S., Collette B.B., Facey D.E. & Bowen B.W. (2009) *The diversity of fishes*. Willey-Blackwell, West Sussex.

Hoeinghaus D.J. & Zeug S.C. (2008) Can stable isotope ratios provide for community-wide measures of trophic structure? Comment. *Ecology*, 89, 2353–2357. https://doi.org/10.1890/07-1143.1

Horn M.H. (1989) Biology of marine herbivorous fishes. *Oceanography and Marine Biology, An Annual Review*, 27, 167–272.

Ilha P., Schiesari L., Yanagawa F.I., Jankowski K. & Navas C.A. (2018) Deforestation and stream warming affect body size of Amazonian fishes. *PLoS ONE*, 13, e0196560. https://doi.org/10.1371/journal.pone.0196560

Ingram T., Stutz W.E. & Bolnick D.I. (2011) Does intraspecific size variation in a predator affect its diet diversity and top-down control of prey? *PLoS ONE*, 6, e20782. https://doi.org/10.1371/journal.pone.0020782

Jara A., Hanson T.E., Quintana F.A., Müller P. & Rosner G.L. (2011) DPpackage: Bayesian semi- and nonparametric modeling in R. *Journal of Statistical Software*, 40, 1–30. https://doi.org/10.18637/jss.v040.i05

Jennings S., De Oliveira J.A.A. & Warr K.J. (2007) Measurement of body size and abundance in tests of macroecological and food web theory. *Journal of Animal Ecology*, 76, 72–82. https://doi.org/10.1111/j.1365-2656.2006.01180.x

Jennings S., Pinnegar J.K., Polunin N.V.C. & Boon T.W. (2001) Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. *Journal of Animal Ecology*, 70, 934–944.

https://doi.org/10.1046/j.0021-8790.2001.00552.x

Jennings S., Pinnegar J.K., Polunin N.V.C. & Warr K.J. (2002) Linking size-based and trophic analyses of benthic community structure. *Marine Ecology Progress Series*, 226, 77–85. https://doi.org/10.3354/meps226077

Jonsson T., Cohen J.E. & Carpenter S.R. (2005) Food webs, body size and species abundance in ecological community description. *Advances in Ecological Research*, 36, 1–83. https://doi.org/10.1016/S0065-2504(05)36001-6

Jonsson T., Kaartinen R., Jonsson M. & Bommarco R. (2018) Predictive power of food web models based on body size decreases with trophic complexity. *Ecology Letters*, 21, 702–712. https://doi.org/10.1111/ele.12938

Junk W.J., Bayley P.B. & Sparks R.E. (1989) The flood pulse concept in river-floodplain systems. *Canadian Special Publication in Fisheries and Aquatic Sciences*, 106, 110–127.

Kapoor B.G., Smit H. & Verighina I.A. (1975) The alimentary canal and digestion in teleosts. *Advances in Marine Biology*, 13, 109–239. https://doi.org/10.1016/S0065-2881(08)60281-3

Keast A. & Webb D. (1966) Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. *Journal of the Fisheries Research Board of Canada*, 23, 1845–1874. https://doi.org/10.1139/f66-175

Keppeler F.W., Lanés L.E.K., Rolon A.S., Stenert C., Lehmann P., Reichard M. & Maltchik L. (2015) The morphology – diet relationship and its role in the coexistence of two species of annual fishes. *Ecology of Freshwater Fish*, 24, 77–90.

https://doi.org/10.1111/eff.12127

Kéry M. (2010) *Introduction to WinBUGS for ecologists: a Bayesian approach to regression, ANOVA, mixed models, and related analyses*. Academic Press, Burlington.

Keys A.B. (1928) The weight-length relationship in fishes. *Proceedings of the National Academy of Science*, 14, 922–925. https://doi.org/10.1073/pnas.14.12.922

Klecka J. & Boukal D.S. (2013) Foraging and vulnerability traits modify predator-prey body mass allometry: freshwater macroinvertebrates as a case study. *Journal of Animal Ecology*, 82, 1031–1041. https://doi.org/10.1111/1365-2656.12078

Kleiber M. (1932) Body size and metabolism. *Hilgardia*, 6, 315–353. https://doi.org/10.3733/hilg.v06n11p315

Layman C.A., Araújo M.S., Boucek R., Hammerschlag-Peyer C.M., Harrison E., Jud Z.R., Matich P., Rosenblatt A.E., Vaudo J.J., Yeager L.A., Post D.M. & Bearhop S. (2012) Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biological Reviews*, 87, 545–562. https://doi.org/10.1111/j.1469-185X.2011.00208.x

Layman C.A., Winemiller K.O., Arrington D.A. & Jepsen D.B. (2005) Body size and trophic position in a diverse tropical food web. *Ecology*, 86, 2530–2535. https://doi.org/10.1890/04-1098

Lynch M. (1991) Methods for the analysis of comparative data in evolutionary biology. *Evolution*, 45, 1065–1080. https://doi.org/10.1111/j.1558-5646.1991.tb04375.x

Mann K.H. (1988) Production and use of detritus in various freshwater, estuarine, and coastal marine ecosystems. *Limnology and Oceanography*, 33, 910–930. https://doi.org/10.4319/lo.1988.33.4part2.0910

McCann K.S. (2011) *Food webs*. Princeton University Press, New Jersey.

McCann K.S., Rasmussen J.B. & Umbanhowar J. (2005) The dynamics of spatially coupled food webs. *Ecology Letters,* 8, 513–523. https://doi.org/10.1111/j.1461-0248.2005.00742.x

McCollum M. & Sharpe P.T. (2001) Evolution and development of teeth. *Journal of Anatomy*, 199, 153–159. https://doi.org/10.1046/j.1469-7580.2001.19910153.x

McGarvey R., Dowling N. & Cohen J.E. (2016) Longer food chains in pelagic ecosystems: trophic energetics of animal body size and metabolic efficiency. *The American Naturalist*, 188, 76–86. https://doi.org/10.1086/686880

McLaughlin O.B., Jonsson T. & Emmerson M.C. (2010) Temporal variability in predator–prey relationships of a forest floor food web. *Advances in Ecological Research*, 42, 171–264. https://doi.org/10.1016/B978-0-12-381363-3.00004-6

Mihalitsis M. & Bellwood D.R. (2017) A morphological and functional basis for maximum prey size in piscivorous fishes. *PLoS ONE*, 12, e0184679. https://doi.org/10.1371/journal.pone.0184679

Mittelbach G.G. (1981) Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology*, 62, 1370–1386. https://doi.org/10.2307/1937300

Montaña C.G., Layman C.A. & Winemiller K.O. (2011) Gape size influences seasonal patterns of piscivore diets in three Neotropical rivers. *Neotropical Ichthyology*, 9, 647–655. https://doi.org/10.1590/S1679-62252011005000028

Montaña C.G. & Winemiller K.O. (2013) Evolutionary convergence in Neotropical cichlids and Nearctic centrarchids: evidence from morphology, diet, and stable isotope analysis. *Biological Journal of the Linnean Society*, 109, 146–164. https://doi.org/10.1111/bij.12021

Müeller P., Quintana F.A. & Page G. (2018) Nonparametric Bayesian inference in applications. *Statistical Methods and Applications*, 27, 175–206. https://doi.org/10.1007/s10260-017-0405-z

Nakadai R. (2017) Species diversity of herbivorous insects: a brief review to bridge the gap between theories focusing on the generation and maintenance of diversity. *Ecological Research*, 32, 811–819. https://doi.org/10.1007/s11284-017-1500-1

Nakagawa S. & Schielzeth H. (2013) A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4, 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Nakazawa M. (2018) *fmsb: functions for medical statistics book with some demographic data*. Available at: https://CRAN.R-project.org/package=fmsb (accessed 02 February 2019).

Nakazawa T. (2015) Ontogenetic niche shifts matter in community ecology: a review and future perspectives. *Population Ecology*, 57, 347–354. https://doi.org/10.1007/s10144-014-0448-z

Nakazawa T. (2017) Individual interaction data are required in community ecology: a conceptual review of the predator–prey mass ratio and more. *Ecological Research*, 32, 5–12. https://doi.org/10.1007/s11284-016-1408-1

Nakazawa T., Ohba S. & Ushio M. (2013) Predator-prey body size relationships when predators can consume prey larger than themselves. *Biology Letters*, 9, 20121193. https://doi.org/10.1098/rsbl.2012.1193

Nilsson P.A. & Brönmark C. (2000) Prey vulnerability to a gape-size limited predator: behavioural and morphological impacts on northern pike piscivory. *Oikos*, 88, 539–546. https://doi.org/10.1034/j.1600-0706.2000.880310.x

O'Grady S.P., Morando M., Avila L. & Dearling M.D. (2005) Correlating diet and digestive tract specialization: examples from the lizard family Liolaemidae. *Zoology*, 108, 201–210. https://doi.org/10.1016/j.zool.2005.06.002

Otto S.B., Rall B.C. & Brose U. (2007) Allometric degree distributions facilitate food-web stability. *Nature,* 450, 1226–1229. https://doi.org/10.1038/nature06359

Ou C., Montaña C.G. & Winemiller K.O. (2017) Body size-trophic position relationships among fishes of the lower Mekong basin. *Royal Society Open Science,* 4, 160645. https://doi.org/10.1098/rsos.160645

Pagel M. (1999) Inferring the historical patterns of biological evolution. *Nature,* 401, 877–884. https://doi.org/10.1038/44766

Pauly D., Christensen V., Dalsgaard J., Froese R. & Torres Jr.F. (1998) Fishing down marine food webs. *Science*, 279, 860–863. https://doi.org/10.1126/science.279.5352.860

Petchey O.L., Beckerman A.P., Riede J.O. & Warren P.H. (2008) Size, foraging, and food web structure. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 4191–4196. https://doi.org/10.1073/pnas.0710672105

Peters R.H. (1983) *The ecological implications of body size*. Cambridge University Press, New York.

Peterson C.C., Keppeler F.W., Saenz D.E., Bower L.M. & Winemiller K.O. (2017) Seasonal variation in fish trophic networks in two clear-water streams in the Central Llanos region, Venezuela. *Neotropical Ichthyology*, 15, e160125. https://doi.org/10.1590/1982-0224-20160125

Potapov A.M., Brose U., Scheu S. & Tiunov A.V. (2019) Trophic position of consumers and size structure of food webs across aquatic and terrestrial ecosystems. *The American Naturalist*, 194, 823–839. https://doi.org/10.1086/705811

R Core Team (2019) *R: A language and environment for statistical computing*. Availalble at: http://www.rproject.org (accessed 02 February 2019).

Rabosky D.L., Chang J., Title P.O., Cowman P.F., Sallan L., Friedman M., Kaschner K., Garilao C., Near T.J., Coll M. & Alfaro M.E. (2018) An inverse latitudinal gradient in speciation rate for marine fishes. *Nature*, 559, 392–395. https://doi.org/10.1038/s41586-018-0273-1

Reiss M. (1988) Scaling of home range size: body size, metabolic needs and ecology. *Trends in Ecology and Evolution*, 3, 85–86. https://doi.org/10.1016/0169-5347(88)90025-0

Reum J.C.P. & Marshall K.N. (2013) Evaluating δ15N-body size relationships across taxonomic levels using hierarchical models. *Oecologia*, 173, 1159–1168. https://doi.org/10.1007/s00442-013-2715-7

Ricklefs R.E. (1996) Morphometry of the digestive tracts of some passerine birds. *The*

Condor, 98, 279–292. https://doi.org/10.2307/1369146

Riede J.O., Brose U., Ebenman B., Jacob U., Thompson R., Townsend C.R. & Jonsson T. (2011) Stepping in Elton’s footprints: a general scaling model for body masses and trophic levels across ecosystems. *Ecology Letters*, 14, 169–178. https://doi.org/10.1111/j.1461-0248.2010.01568.x

Ripple W.J., Wolf C., Newsome T.M., Hoffmann M., Wirsing A.J. & McCauley D.J. (2017) Extinction risk is most acute for the world’s largest and smallest vertebrates. *Proceedings of the National Academy of Sciences*, 114, 10678–10683. https://doi.org/10.1073/pnas.1702078114

Roach K.A., Winemiller K.O. & Davis III S.E. (2014) Autochthonous production in shallow littoral zones of five floodplain rivers: effects of flow, turbidity and nutrients. *Freshwater Biology*, 59, 1278–1293. https://doi.org/10.1111/fwb.12347

Robertson C.R., Zeug S.C. & Winemiller K.O. (2008) Associations between hydrological connectivity and resource partitioning among sympatric gar species (Lepisosteidae) in a Texas river and associated oxbows. *Ecology of Freshwater Fish*, 17, 119–129. https://doi.org/10.1111/j.1600-0633.2007.00265.x

Roff D.A. (1992) *The evolution of life histories*. Chapman and Hall, New York.

Romanuk T.N., Hayward A. & Hutchings J.A. (2011) Trophic level scales positively with body size in fishes. *Global Ecology and Biogeography*, 20, 231–240. https://doi.org/10.1111/j.1466-8238.2010.00579.x

Romero-Romero S., Molina-Ramírez A., Höfer J. & Acuña J.L. (2016) Body size-based trophic structure of a deep marine ecosystem. *Ecology*, 97, 171–181.

https://doi.org/10.1890/15-0234.1

Rooney N., McCann K.S. & Moore J.C. (2008) A landscape theory for food web architecture. *Ecology Letters*, 11, 867–881. https://doi.org/10.1111/j.1461-0248.2008.01193.x

Rudolf V.H.W. (2008) Consequences of size structure in the prey for predator-prey dynamics: the composite functional response. *Journal of Animal Ecology*, 77, 520–528. https://doi.org/10.1111/j.1365-2656.2008.01368.x

Rudolf V.H.W., Rasmussen N.L., Dibble C.J. & Allen B.G.V. (2014) Resolving the roles of body size and species identity in driving functional diversity. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20133203. https://doi.org/10.1098/rspb.2013.3203

Sánchez-Hernández J., Nunn A.D., Adams C.E. & Amundsen P-A. (2019) Causes and consequences of ontogenetic dietary shifts: a global synthesis using fish models. *Biological Reviews*, 94, 539–554. https://doi.org/10.1111/brv.12468

Schieck J.O. & Millar J.S. (1985) Alimentary tract measurements as indicators of diets of small mammal. *Mammalia*, 49, 93–104. https://doi.org/10.1515/mamm.1985.49.1.93

Schneider F.D., Brose U., Rall B.C. & Guill C. (2016) Animal diversity and ecosystem functioning in dynamic food webs. *Nature Communications*, 7, 12718. https://doi.org/10.1038/ncomms12718

Segura A.M., Franco-Trecu V., Franco-Fraguas P. & Arim M. (2015) Gape and energy limitation determine a humped relationship between trophic position and body size.

Canadian Journal of Fisheries and Aquatic Sciences, 72, 198–205. https://doi.org/10.1139/cjfas-2014-0093

Speakman J.R. (2005) Body size, energy metabolism and lifespan. *Journal of Experimental Biology*, 208, 1717–1730. https://doi.org/10.1242/jeb.01556

Spiegelhalter D.J., Best N.G., Carlin B.P. & van der Linde A. (2002) Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society*, 64, 583–639. https://doi.org/10.1111/1467-9868.00353

Stevens C.E. & Hume I.D. (1995) *Comparative physiology of the vertebrate digestive system*. Cambridge University Press, Cambridge.

Su G., Villéger S. & Brosse S. (2019) Morphological diversity of freshwater fishes differs between realms, but morphologically extreme species are widespread. *Global Ecology and Biogeography*, 28, 211–221. https://doi.org/10.1111/geb.12843

Tarim S. (2002) *Relationships among fish populations, species assemblages, and environmental factors on a heterogeneous floodplain landscape*. Doctoral dissertation, Texas A&M University, College Station.

Toussaint A., Charpin N., Beauchard O., Grenouillet G., Oberdorff T., Tedesco P.A., Brosse S. & Villéger S. (2018) Non-native species led to marked shifts in functional diversity of the world freshwater fish faunas. *Ecology Letters*, 21, 1649–1659. https://doi.org/10.1111/ele.13141

Tseng M., Kaur K.M., Pari S.S., Sarai K., Chan D., Yao C.H., Porto P., Toor A., Toor H.S. & Fograscher K. (2018) Decreases in beetle body size linked to climate change and warming temperatures. *Journal of Animal Ecology*, 87, 647–659.

https://doi.org/10.1111/1365-2656.12789

Tucker M.A. & Rogers T.L. (2014) Examining predator-prey body size , trophic level and body mass across marine and terrestrial mammals. *Proceedings of the Royal Society B*, 281, 20142103. https://doi.org/10.1098/rspb.2014.2103

Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushing C.E. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, 37, 130–137. https://doi.org/10.1139/f80-017

Villéger S., Brosse S., Mouchet M., Mouillot D. & Vanni M.J. (2017) Functional ecology of fish: current approaches and future challenges. *Aquatic Sciences*, 79, 783–801. https://doi.org/10.1007/s00027-017-0546-z

Violle C., Navas M-L., Vile D., Kazakou E., Fortunel C., Hummel I. & Garnier E. (2007) Let the concept of trait be functional! *Oikos*, 116, 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Wagner C.E., McIntyre P.B., Buels K.S., Gilbert D.M. & Michel E. (2009) Diet predicts intestine length in Lake Tanganyika's cichlid fishes. *Functional Ecology*, 23, 1122–1131. https://doi.org/10.1111/j.1365-2435.2009.01589.x

Warren P.H. & Lawton J.H. (1987) Invertebrate predator-prey body size relationships: an explanation for upper triangular food webs and patterns in food web structure? *Oecologia*, 74, 231–235. https://doi.org/10.1007/BF00379364

Webb P.W. (1984a) Body form, locomotion and foraging in aquatic vertebrates. *American Zoologist*, 24, 107–120. https://doi.org/10.1093/icb/24.1.107

Webb P.W (1984b) Form and function in fish swimming. *Scientific American*, 251, 72–

83. https://doi.org/10.1038/scientificamerican0784-72

Werner E.E. & Gilliam J.F. (1984) The ontogenetic niche and species interactions in size-structured populations. *Annual Review in Ecology and Systematics*, 15, 393–425. https://doi.org/10.1146/annurev.es.15.110184.002141

Werner E.E. & Hall D.J. (1974) Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology*, 55, 1042–1052. https://doi.org/10.2307/1940354

Winemiller K.O. (1989) Patterns of variation in life history among South American fishes in seasonal environments. *Oecologia*, 81, 225–241. https://doi.org/10.1007/BF00379810

Winemiller K.O. (1990) Spatial and temporal variation in tropical fish trophic networks. *Ecological Monographs*, 60, 331–367. https://doi.org/10.2307/1943061

Winemiller K.O. (1991a) Comparative ecology of *Serranochromis* species (Teleostei: Cichlidae) in the Upper Zambezi River floodplain. *Journal of Fish Biology*, 39, 617–639. https://doi.org/10.1111/j.1095-8649.1991.tb04393.x

Winemiller K.O. (1991b) Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. *Ecological Monographs*, 61, 343–365. https://doi.org/10.2307/2937046

Winemiller K.O., Fitzgerald D.B., Bower L.M. & Pianka E.R. (2015) Functional traits, convergent evolution, and periodic tables of niches. *Ecology Letters*, 18, 737–751. https://doi.org/10.1111/ele.12462

Winemiller K.O. & Kelso-Winemiller L.C. (1994) Comparative ecology of the African pike, *Hepsetus odoe*, and tigerfish, *Hydrocynus forskahlii*, in the Zambezi River floodplain. *Journal of Fish Biology*, 45, 211–225. https://doi.org/10.1111/j.1095-8649.1994.tb01301.x

Winemiller K.O. & Kelso-Winemiller L.C. (1996) Comparative ecology of catfishes of the Upper Zambezi River floodplain. *Journal of Fish Biology*, 49, 1043–1061. https://doi.org/10.1111/j.1095-8649.1996.tb01777.x

Winemiller K.O. & Kelso-Winemiller L.C. (2003) Food habits of tilapiine cichlids of the Upper Zambezi River and floodplain during the descending phase of the hydrologic cycle. *Journal of Fish Biology*, 63, 120–128. https://doi.org/10.1046/j.1095-8649.2003.00134.x

Winemiller K.O., Montaña C.G., Roelke D.L., Cotner J.B., Montoya J.V., Sanchez L., Castillo M.M. & Layman C.A. (2014) Pulsing hydrology determines top-down control of basal resources in a tropical river–floodplain ecosystem. *Ecological Monographs*, 84, 621–635. https://doi.org/10.1890/13-1822.1

Wood B.M. & Bain M.B. (1995) Morphology and microhabitat use in stream fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 52, 1487–1498. https://doi.org/10.1139/f95-143

Woodward G., Ebenman B., Emmerson M., Montoya J.M., Olesen J.M., Valido A. & Warren P.H. (2005) Body size in ecological networks. *Trends in Ecology & Evolution*, 20, 402–409. https://doi.org/10.1016/j.tree.2005.04.005

Woodward G. & Hildrew A.G. (2002) Body-size determinants of niche overlap and intraguild predation within a complex food web. *Journal of Animal Ecology*, 71, 1063–1074. https://doi.org/10.1046/j.1365-2656.2002.00669.x

Zeug, S.C. & Winemiller K.O. (2007) Ecological correlates of fish reproductive activity in floodplain rivers: A life history-based approach. Canadian Journal of Fisheries and Aquatic Sciences, 64, 1291–1301. https://doi.org/10.1139/f07-094

Zeug S.C. & Winemiller K.O. (2008) Evidence supporting the importance of terrestrial carbon in a large-river food web. *Ecology*, 89, 1733–1743. https://doi.org/10.1890/07-1064.1

3. INCORPORATING INDIRECT PATHWAYS IN BODY SIZE-TROPHIC POSITION RELATIONSHIPS

3.1. Introduction

Given the importance of food web structure to the flow of energy and matter within and across ecosystems, a major goal of ecology is to understand factors that mediate consumer-resource interactions. Predator size, prey size, trophic position and trophic niche width are the variables most often examined by food web studies, including those focused on energy and nutrient dynamics (Lindemann, 1942; DeAngelis, 2012) and have been linked with food web stability and dynamics (Brose *et al.*, 2006; Arim *et al.*, 2010; McCann, 2011). In recent decades, much effort has been devoted to understanding the relationship between body size and trophic position; however, empirical data for trophic position are limited, which potentially biases inferences (Paine, 1988; Winemiller, 1990; Woodward *et al.*, 2005b).

Prey size and predator size often are positively correlated (Warren & Lawton, 1987; Cohen *et al.*, 1993; Jennings *et al.*, 2002; Barnes *et al.*, 2010). Larger predators have a higher energy demand and therefore may preferentially consume larger prey that are more profitable, whereas small predators generally are incapable of capturing and handling large prey (Werner & Hall, 1974; Mittelbach, 1981). In contrast, animals that consume small particles near the base of the food web, such as algivores and detritivores, may show little variation in the size of consumed food items as they grow (Brooks & Dodson, 1965; Tonin *et al*., 2018). Trophic niche width is expected to be broader for larger predators (Warren & Lawton, 1987; Barclay & Brigham, 1991; Costa, 2009). As the size of a mouth gape-limited predator (i.e., those that ingest food items whole) increases, large prey are added to the diet faster than small ones are eliminated (Barclay & Brigham, 1991; Costa, 2009). Also, larger animals tend to have larger home ranges (Reiss 1988) and may encounter more diverse prey (Costa, 2009). Few studies have assessed the correlation between body size and diet breadth in primary consumers, although it has been widely assumed that food selectivity decreases with body size given that larger herbivores generally have longer food retention times and higher digestive efficiencies than small herbivores (Clauss *et al.*, 2013).

Positive relationships between predator size and prey size and between predator size and diet diversity imply that predator size also should correlate positively with trophic position, TP (Elton, 1927; Dalponti *et al.*, 2018). Indeed, positive relationships between TP and body size have been reported for both terrestrial (Riede *et al.*, 2011) and aquatic carnivores (Jennings *et al.*, 2007; Arim *et al.*, 2010; Barnes *et al.*, 2010; Gilljam *et al.*, 2011; Riede *et al.*, 2011; Reum & Marshall, 2013). Available evidence indicates that a positive TP–body size relationship also occurs across multiple consumer types in aquatic ecosystems, especially within the marine realm, but not in terrestrial ecosystems (Jennings *et al.*, 2002; Al-Habsi *et al.*, 2008; Romero-Romero *et al.*, 2016; Potapov *et al.*, 2019). Weak or absent relationships between TP and body size are expected in freshwater and terrestrial ecosystems given that herbivores of many sizes, from small insects to large vertebrates, have evolved to explore abundant plants (Tucker & Rogers, 2014; Potapov *et al.*, 2019). Moreover, large animals may be forced to feed at lower trophic positions due to a conflict between the energy available at the top of food webs and the high metabolic demand associated with a large body size, weakening the expected positive relationship between TP and body size (Arim *et al.*, 2007; Segura *et al.*, 2015; Dantas *et al.*, 2019).

Relationships between predator size, prey size, diet breadth, and trophic position have been analyzed using bivariate methods (Scharf *et al.*, 2000; Layman *et al.*, 2005; Costa, 2009; Barnes *et al.*, 2010; Riede *et al.*, 2011; Tucker & Rogers, 2014) that fail to assess the potential for indirect effects, interactions, and collinearity among the variables, thus hindering inferences about cause-effect relationships (Fan *et al.*, 2016). Furthermore, most studies have not incorporated phylogenetic influences into their statistical analyses, although some evidence has demonstrated a strong phylogenetic signal for both TP and body size (Naisbit *et al.*, 2011; Keppeler et al. unpublished data). Failure to consider species ancestry can bias conclusions about the drivers of certain ecological patterns (e.g., Hultgren *et al.*, 2018). Another common issue is that several studies omitted non-carnivorous species from their analysis (e.g., Barnes *et al.*, 2010; Riede *et al.*, 2011; Romanuk *et al.*, 2011). TP-body size relationships involving non-carnivorous organisms should be more complex, and models may require inclusion of additional predictor variables associated with morphology and physiology. Non-carnivorous organisms are important components of ecosystems, and this is especially the case for fish assemblages in tropical freshwater and marine systems (Wootton & Oemeke, 1992; Floeter *et al.*, 2005). Exclusion of non-carnivorous species from food web analyses and models hamper our ability to understand ecological patterns and dynamics and understanding of ecosystem functions, such as nutrient cyclings.

Here, using a large, well-resolved dataset for diets of Neotropical freshwater fishes, I analyze patterns of intercorrelation among consumer body size, food item size, food size variation (a proxy for trophic niche width), and consumer TP (trophic position). The diet dataset includes both carnivorous and non-carnivorous species. In order to accommodate diverse feeding strategies, I also analyzed the influence of two additional consumer traits: mouth gape size and gut length. Mouth gape sets a maximum limit for the size of food items that can be ingested by consumers that ingest food items whole (Nilsson & Bronmark, 2000; Mihalitsis & Bellwood, 2017). Gut length affects digestion and nutrient absorption and is generally known to reflect a dietary gradient, ranging from herbivory/detritivory (food with relatively low nutritional quality requiring a long gut for digestion and absorption) to carnivory (food with high protein and lipid content requiring only a relatively short gut) (Schieck & Millar, 1985; Battley & Piersma, 2005; Wagner *et al.*, 2009). I hypothesized that: 1) consumer body size indirectly determines food item size (herein referred as food size), the coefficient of variation of food size (herein referred as food size variation), and TP; 2) food size and food size variation have a direct positive effect on TP; 3) a larger mouth gape allows fish to ingest larger and more diverse food items, and consequently has an indirect influence on TP; and 4) gut length has a strong negative relationship with TP, food size, and food size variation, with longer guts being associated with herbivorous and detritivorous feeding strategies. I tested these hypotheses using piecewise (or directed acyclic) confirmatory path analyses (CPA), a multivariate technique that facilitates inference of cause–effect relationships. Because it has a flexible mathematical structure, piecewise CPA can extend traditional path analyses and structural equation models (SEM), allowing the incorporation of different model structures, assumptions and variable distributions (Shipley, 2009; Lefcheck, 2016). Using this approach, I also examined the influence of shared ancestry on the consistency of models predicting the relationship between consumer body size and TP.

3.2. Methods

3.2.1. Fish sampling and dietary analysis

I used fish diet data collected by Dr. Kirk O. Winemiller in 1984 and 1985 from four lowland streams, two in Venezuela (Caño Maraca and Caño Volcán) and two in Costa Rica (Caño Agua Fría Viejo and Quebrada). At each location, fishes were collected monthly over one year using multiple gears (dip nets, gillnets, seine nets; for details see Winemiller 1990). Fishes were preserved and then each specimen was identified to species and measured for standard length (SL) to the nearest 0.1 mm.

When available, 30 specimens of each species from each monthly collection were dissected for gut contents analysis. Given that piscivorous fishes usually have higher incidence of empty stomachs, all available specimens of piscivores were dissected for gut contents analysis. Given the low intraspecific dietary variation and greater amount of effort and time required to estimate dietary proportions for detritivorous and algivorous species, the number of dissected individuals for these fishes was reduced to 20 specimens from each monthly sample (Winemiller, 1990).

The volumetric contribution of each food item recovered from guts was estimated, and sizes of food items were recorded based on 10-mm intervals (Winemiller, 1990). Non-fish food items were assigned trophic positions based on information in literature sources (Table B.1). The trophic position of each fish specimen was calculated using the formula:

$$Trophic\ position_i = 1.0 + \sum_{j=0}^{n} (T_j * p_{ij}),$$

where, T_j is the trophic level of a prey taxon *j* and p_{ij} is the fraction of prey taxon *j* ingested by predator *i*. Additional details about habitat characteristics, surveys, and dietary analysis can be found in Winemiller (1990).

3.2.2. Consumer body size, gut length, and mouth gape

Fish SL was converted to weight (g) using the allometric formula:

$$W_i = aL_i^b,$$

where W_i is the predicted weight of individual *i*, L_i is the length of individual *i*, and *a* and *b* are the intercept and slope, respectively, of the logarithmic form of the length-weight relationship of individual *i*’s population. Values of the parameters *a* and *b* for each species were estimated by posterior modes (i.e., kernel density estimation) generated by the Bayesian hierarchical approach proposed by Froese, Thorson, and Reyes (2014). I used body mass (g) rather than standard length as my index of body size due to the diverse body shapes represented in the fish assemblages.

I measured SL, gut length and mouth gape width of three to five large (most of them adult size classes) preserved specimens (formalin-fixed, EtOH-preserved) of specimens housed in the ichthyology collections at Texas A&M University (Biodiversity Research and Teaching Collections - BRTC) and The University of Texas at Austin (Texas Natural History Collections - THNC). Measurements were based on the protocol described by Winemiller (1991). For each measured specimen, I divided the value of each trait by its body mass, resulting in a body ratio that was subsequently used to calculate a species average. Although I tried to match the size of fishes that were measured for gut length and mouth gape to those of conspecific specimens dissected for dietary analysis, there were differences in some cases due to limited availability of preserved specimens (Table B.2). Given that body mass increases approximately as the cube of body length (Cube Law), trait ratios (e.g., mouth gape/body weight) decrease with body weight (Figure B.1). To account for this relationship, I corrected the trait ratios when there was a size mismatch between diet and morphometric datasets using the formula:

$R_c = R_m - D * b$,

where R_c is the corrected trait ratio, R_m is the trait ratio measured, D is the body size difference between the species measured for morphological traits and those species dissected for diet analysis, and b is the slope of the linear relationship between the trait ratio and body mass (see Figure B.1). Trait ratios, body mass and size differences were all log-transformed prior the correction and the regressions. The corrected ratio (R_c) was then multiplied by the body mass of the dissected fishes to generate actual estimates of gut length and mouth gape length (mm). These estimates of mouth gape and gut length were very similar to what would be expected for estimates based on standard length ratios (Figure B.2). For the purpose of my comparative study, I assumed that intraspecific variation in these two traits had minimal influence on patterns derived from interspecific analyses. Although gut length and mouth gape proportions may vary to some degree during ontogeny as shown in previous studies (e.g., Wagner *et al.*, 2009; Dunic & Baum, 2017), this variation was assumed to be minor compared to interspecific variation within and among the four fish assemblages (Winemiller, 1991; Montaña & Winemiller, 2013).

3.2.3. Data processing

Body size distributions varied among fish species, and some species had multiple body size modes. To reduce intraspecific dietary variation associated with ontogeny, I filtered the dataset. For each species dataset, I excluded outliers and only retained specimens comprising the main mode of the body size distribution. This was done visually using kernel density plots. I also removed any species with less than 5 total specimens, reducing the original dataset from 17305 to 14359 specimens and from 122 species to 117 species. Since nearly all of my measurements of gut length and mouth gape were made on adult size classes, a second dataset was created by retaining only specimens larger than the 90th percentile of the size distribution for each species (i.e., largest 10% of specimens dissected for dietary analysis). I made exceptions for a few species with low number of specimens, for which I slightly increased this threshold to ensure a minimum number of five specimens per species. This filtering approach reduced the original dataset to 2,117 specimens and 119 species, thereby trading off larger sample sizes in order to achieve a more conservative criterion for the range of body sizes included for analysis. Both approaches for filtering the dataset (main mode vs. largest 10%) produced very similar and qualitatively identical results, and therefore I report here only results based on the main mode approach. Results from the largest 10% approach appear in the Appendix B (Table B.3, Figure B.3).

After dataset filtering, the number of specimens and body size range still varied greatly among species. To reduce bias caused by sample size differences, I calculated the mean fish size, maximum food size, coefficient of variance of food size (standard deviation of food size / mean food size) and mean trophic position as the average of 1,000 sub-samples consisting of five randomly drawn specimens for each species. I decided to use maximum value for food size rather than the mean value due to the former's lower correlation with the coefficient of variation of food size (mean food size is the denominator of this index), and also because it better reflects the physical limitation of consumers to ingest larger food items. Either way, maximum food size (herein referred only as food size) was strongly correlated with mean food size (Pearson correlation > 0.9), and, therefore, both descriptors reflect similar diet patterns. This rarefaction technique effectively removed the tendency for species with large samples sizes to have greater diet variability (Figure B.4.a). After performing this bootstrapping procedure, I found no evidence that intraspecific variation in body size influenced variation in the size of ingested food items (Figure B.4.b).

To test the reliability of values for fish size, food size, food size variation, and trophic position generated based on sub-samples of five specimens, I compared them with values generated based on sub-samples of 10 and 30 specimens. In all cases, the correlation was strong and positive ($r > 0.9$; Figure B.5, B.6). Exploratory analyses also indicated that CPA (confirmatory path analyses) using variables based on sub-samples of five specimens generated similar results with CPA using sub-samples of 10 and 30 specimens. In addition, sub-samples of five specimens allowed me to include more species in the model, increasing the statistical power of my interspecific analyses. Consumer body size, gut length, and mouth gape data were log-transformed prior to analysis.

3.2.4. Data analysis

Relationships between consumer body size, mouth gape, gut length, maximum food size, food size variation, and trophic position were analyzed using piecewise confirmatory path analyses (CPA) (Lefcheck, 2016). Piecewise CPA are equivalent to structural equation modeling (SEM), but with some important distinctions (Shipley, 2000a, 2009; Lefcheck, 2016). First, it does not incorporate latent variables (i.e., variables that are not directly observed but are rather inferred from other variables that were observed). Second, each set of linear structured equations is estimated independently and then combined to generate inferences about the path model. Therefore, piecewise confirmatory path analysis does not rely on the simultaneous estimation of the relationships in a single variance-covariance matrix, such as done in traditional SEM. Consequently, piecewise CPA require smaller sample sizes than SEM and also permit the incorporation of more complex models that can handle different variable distributions and lack of independence among sampling units. Given that piecewise CPA does not provide a valid global covariance matrix, the goodness-of-fit needs to be assessed through the test of directed separation (d-separation). D-separation tests the assumption of independent relationships between the variables in each path model (Shipley, 2000a) and is carried out by three main steps: 1) obtainment of the minimum set of conditional independence claims linked with the theorized path model (basis set); 2) calculation of *P* values associated with each independence claim; and 3) combination of all *P* values associated with the independence claims in a Fisher's C test. The theoretical model is considered in agreement with the data (i.e., the model is valid) when Fisher's C test is non-significant ($P > 0.05$).

For my theoretical model, I considered consumer body size to be positively associated with food size, food size variation, and TP. Food size and food size variation were considered to be correlated, and these two variables were assumed to have a positive relationship with TP (Figure 3.1). Gut length was considered to have a negative influence on food size, food size variation, and TP, whereas mouth width was considered to affect positively these three variables (Figure 3.1). All relationships were considered to be linear, which is a reasonable assumption given the distribution of partial residuals (Figure 3.2; Figure B.7, B.8, B.9; Breheny & Burchett, 2017). In a few cases, mainly those involving gut length, I tested the addition of polynomial terms. However, in all cases, the simplest models had the lowest AIC value. I also tested the level of multicollinearity among my predictor variables in each component of the path model using the variance inflation factor (VIF). All VIF values were lower than 2.6, indicating acceptable levels of multicollinearity (values > 10 are often considered problematic).

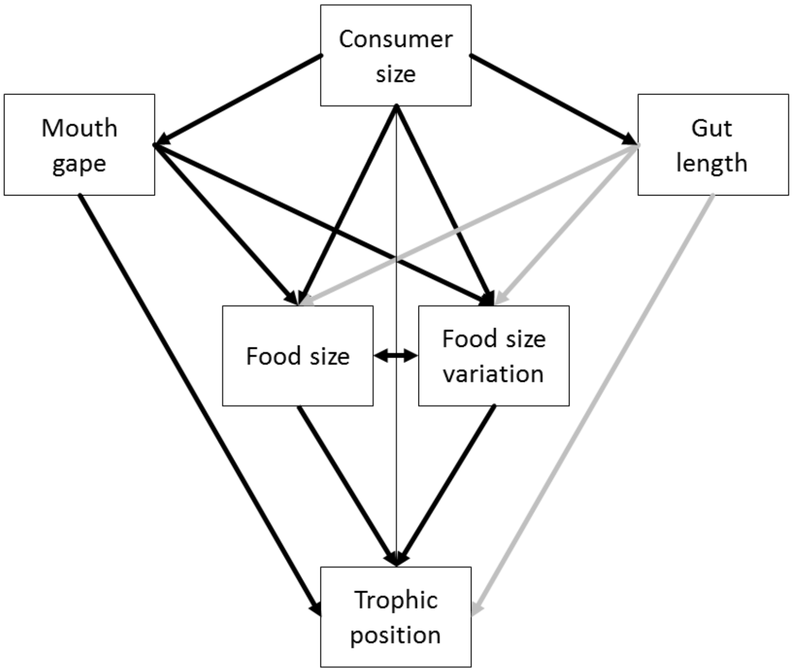

Figure 3.1 Theoretical model showing causal effects and correlations assumed between consumer size, consumer mouth gape, consumer gut length, maximum food item size (Food size), coefficient of variation of food item size (Food size variation), and trophic position. Solid arrows represent unidirectional relationships among variables. Black and gray arrows represent positive and negative relationships, respectively. Double-headed arrows with dash lines indicate correlated errors between the variables.

Path models were implemented with linear regression models. Given that species are not independent sample units due to degrees of shared ancestry (Table B.4), each relationship in the SEMs was also analyzed using Phylogenetic Generalized Least Squares (PGLS). The phylogenetic component of the PGLS models was based on a super tree derived from analysis of molecular data from ca. 15,000 fish species and timecalibration using fossil records (Rabosky *et al.*, 2018). The tree lacks information for 37% of the species analyzed in the current study. I placed those species in positions on the tree based on the positions of species or genera that are considered most closely related (Table B.5, Figure B.10).

Direct path coefficients were calculated using standard slope coefficients. Piecewise CPA allows one to calculate indirect and total net effects of predictor variables. Following the protocol proposed by Shipley (2000b), I obtained estimates of indirect effects by multiplying the parameters associated with the sequence of arrows that connects one variable to next. For cases in which there was more than one indirect path connecting the variable of interest, I calculated the overall indirect effect by summing all indirect effects (Shipley, 2000b). Finally, the net effect of a given variable was calculated by summing its direct and overall indirect effects (Shipley, 2000b).

All analyses and bootstrap procedures were conducted in R (R Core Team, 2019). Piecewise CPA and PGLS were conducted using the R packages piecewiseSEM (Lefcheck, 2016) and nlme (Pinheiro *et al.*, 2008), respectively.

3.3. Results

Shipley's test of direct separation indicated that independence claims made by my CPA models were supported ($P > 0.05$; Figure 3.3). Overall, CPA models based on linear regressions and phylogenetic generalized least squares (PGLS) generated equivalent results with only slight changes in path coefficients (Figure 3.3; Table B.6). The coefficients of determination (R^2) generated by the models were typically high (R^2

varying from 0.22 to 0.77), indicating that a large percentage of the variance was explained by the set of descriptor variables. Food size variation was the variable that had the lowest amount of variance explained (Path model constructed with linear regressions: $R^2 = 0.23$, Path model constructed with PGLS: $R^2 = 0.22$), followed by TP ($R^2 = 0.50$, $R^2 = 0.53$) and maximum food size ($R^2 = 0.54$, $R^2 = 0.53$). High R^2 values were associated with mouth gape ($R^2 = 0.76$, $R^2 = 0.77$) and gut length ($R^2 = 0.61$, $R^2 = 0.56$) due to their strong dependence on consumer body mass.

Consumer body mass positively and significatively influenced gut length (Figure 3.2a), mouth gape (Figure 3.2b), food size (Figure 3.2c), and food size variation (Figure 3.2d, 3.3). Consumer body mass had no effect on TP (Figure 3.2e, 3.3). The net effect of consumer size on food size, food size variation, and TP was lower than its direct effect due to strong negative indirect effects via gut length (Figure 3.3; Table B.6).

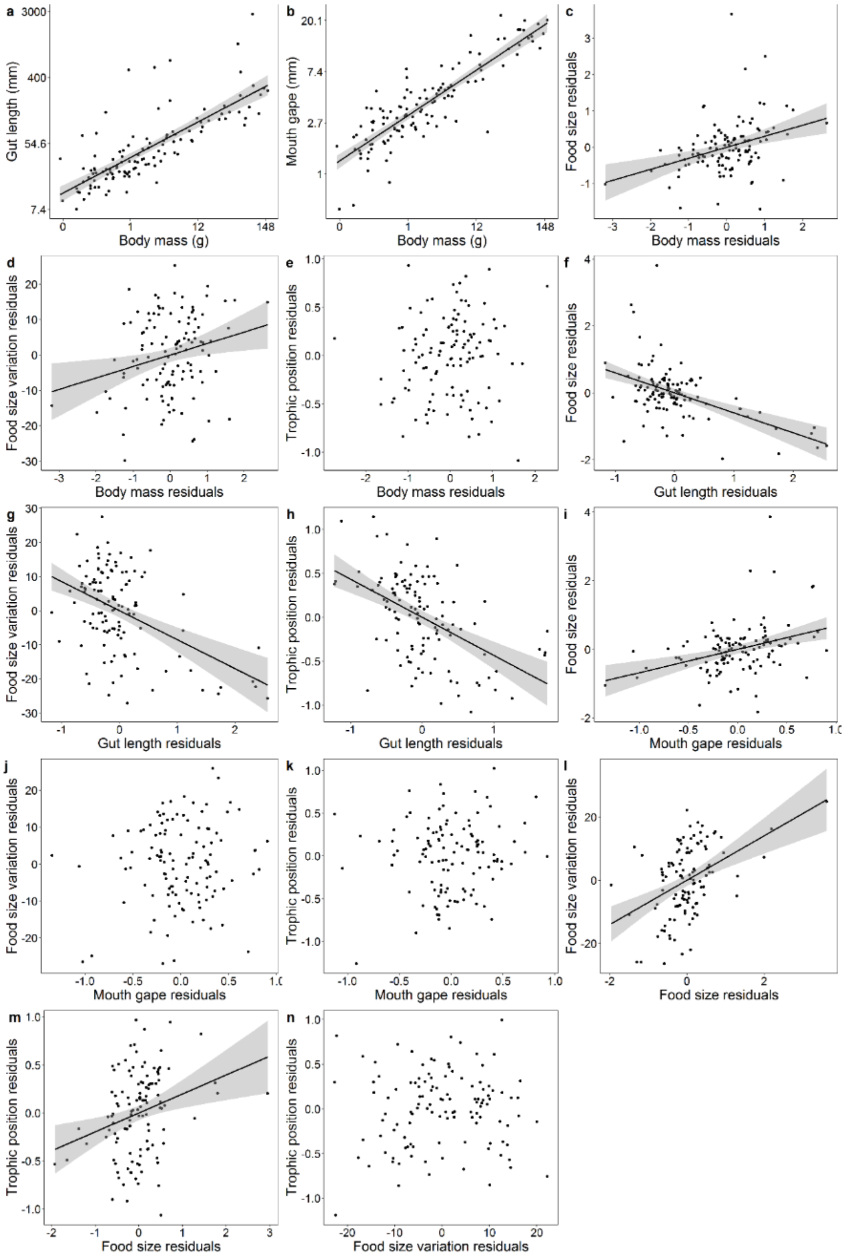

Figure 3.2 Estimated relationships between body mass and gut length (a), body mass and mouth gape (b), body mass and food size (c), body mass and food size variation (d), body size and trophic position (e), gut length and food size (f), gut length and food size variation (g), gut length and trophic position (h), mouth gape and food size (i), mouth gape and food size variation (j), mouth gape and trophic position (k), food size and food size variation (l), food size and trophic position (m), and food size variation and trophic position (n). Excepting panels “a” and “b” that are based on the original values of the variables (single explanatory variable), the estimated relationships are based on partial residuals. Trend lines are provided for significant relationships (P<0.05).

Gut length had strong and significant negative relationships with maximum food size (Figure 3.2f), food size variation (Figure 3.2g), and TP (Figure 3.2h, 3.3). Mouth gape positively influenced maximum food size (Figure 3.2i) but did not affect food size variation (Figure 3.2j) and TP (Figure 3.2k, 3.3). Maximum food size and food size variation were positively correlated (Figure 3.2l, 3.3). Maximum food size had a significant positive effect on TP (Figure 3.2m), and the food size variation had a weak non-significant effect on TP (Figure 3.2n, 3.3).

3.4. Discussion

Consumer body size, mouth gape, gut length, food size, and food size variation formed a network of direct and indirect pathways that statistically modeled fish vertical trophic position (TP). Consumer size indirectly influenced maximum food size, food size variation, and TP, thus corroborating my first hypothesis. My second hypothesis was partially corroborated given that food size, but not the food size variation, directly influenced TP. Mouth gape was directly linked with food size but was not related with food size variation and TP, partially corroborating my third hypothesis. Gut length directly influenced food item size and variation as well as TP, supporting my fourth hypothesis. Despite the strong phylogenetical signal associated with most of the variables I measured (mouth gape, gut length) and estimated (TP), results from CPA were essentially the same whether or not I controlled for phylogeny. These findings highlight the importance of incorporating functional traits in studies seeking to describe the trophic structure of communities with diverse feeding strategies.

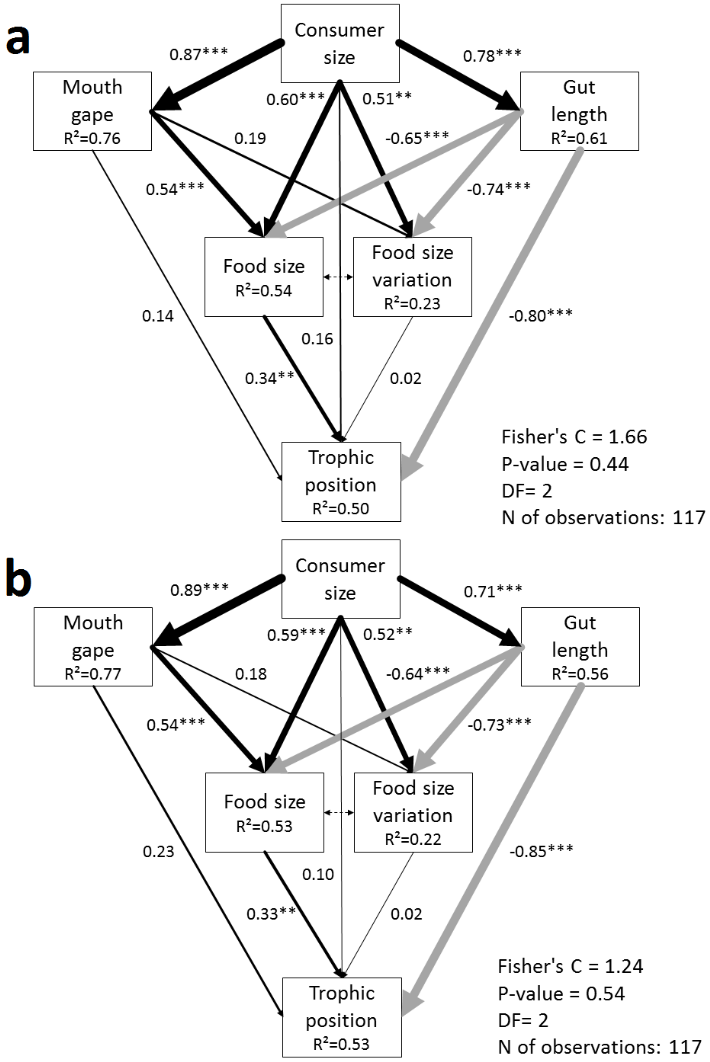

Figure 3.3 Piecewise confirmatory path analyses (CPA) models for the variables consumer body size, consumer mouth gape, consumer gut length, maximum food item size (Food size), coefficient of variation of food item size (Food size variation), and trophic position. The dataset used for these models was based on the main mode approach. Compartments of the Piecewise CPA consist either of linear regressions (a) or phylogenetic generalized least squared models (PGLS) (b) that account for shared species ancestry. Black and gray arrows represent positive and negative relationships, respectively. Arrow size is proportional to the strength of the relationship. Double-headed arrows with dash lines indicate correlated errors between the variables. Direct path coefficients are shown next to their respective arrows. Asterisks indicate significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Coefficients of determination (R^2) are shown for each response variable. P-values associated with Fisher's C score that are larger than 0.05 indicate consistent CPA models.

The finding that fish TP is only indirectly correlated with body size contrasts with a large literature reporting results from bivariate analyses (e.g., Jennings *et al.*, 2002; Barnes *et al*., 2010; Riede *et al.*, 2011; Romero-Romero *et al.*, 2016; Ou *et al.*, 2017). Most researchers implicitly assume that body size influences traits, such as mouth gape, metabolic rate and feeding interval, that in turn affect trophic ecology (Woodward *et al.*, 2005a). However, bivariate analysis of the relationship between TP and body size normally yields a weak relationship, and few studies have employed multivatiate methods to examine the influence of underlying drivers (e.g., Ou *et al.*, 2017). Most comparative studies have analyzed TP–body size relationships only among predatory species (e.g., Barnes *et al.*, 2010; Riede *et al.*, 2011; Romanuk *et al.*, 2011). This has resulted in advancement of food web models founded on size-based assumptions (e.g., Cohen *et al.*, 2003; Rooney *et al.*, 2008). In my study, food size was a better descriptor of consumer trophic position than was consumer body size. Food size is usually seen as a response variable and not a predictor. The influence of food size on trophic position is well-illustrated by the many large herbivorous and detritivorous fishes that feed on tiny food particles (e.g., unicellular algae, fine organic matter; Bowen, 1983; Winemiller, 1990).

The absence of a direct effect of consumer body size on trophic position may also reflect greater energy demands for animals with larger bodies (Arim *et al.*, 2007). In systems with low availability of food resources at higher trophic positions, there may be selection on large consumers to feed at lower trophic positions in order to meet metabolic demands (Arim *et al.*, 2007). This selection process is expected to be stronger in tropical regions due to the positive relationship between energetic demand and temperature (Dantas *et al.*, 2019). Exceptions may include endotherms in cold environments that must feed on energy-rich food resources at higher trophic positions to meet their high energy demands, as well as ectotherms that feed on large prey and then reduce their active metabolism to reduce energy demand. The diverse trophic niches represented in tropical fish assemblages also was likely responsible for lack a significant TP–body size relationship in my dataset. There tend to be many more herbivorous, detritivorous and omnivorous fishes in the tropics than temperate and polar regions (Wootton & Oemeke, 1992; Floeter *et al.*, 2005; Behrens & Lafferty, 2007), a trend that should weaken the TP–body size relationship in tropical faunas (Dantas *et al.*, 2019). Stoichiometry and temperature dependency of digestive physiology of fishes and other ectothermic vertebrates may account for latitudinal and altitudinal trends in herbivory (Behrens & Lafferty, 2007; Moody *et al.*, 2019).

My study corroborated the general positive relationship between consumer body size and food size observed for gape-limited predators (Warren & Lawton, 1987; Cohen *et al.*, 1993; Jennings *et al.*, 2002; Barnes *et al.*, 2010). Consumer body size explained maximum food size even after accounting for the effect of mouth gape. Larger fish often possess better visual acuity and greater burst and sustained swimming speeds (Keast & Webb, 1966; Beamish, 1978) and therefore may encounter, pursue, subdue and ingest large profitable prey more efficiently than can smaller predators. At the same time, large prey usually have greater reaction distance, better swimming performance, and more robust defenses than small prey (Folkvord & Hunter, 1986; Blaxter & Fuiman, 1990), all of which impose additional challenges for small predators (Scharf *et al.*, 2000).

Food size variation, which should reflect food item diversity (although exceptions are not uncommon, e.g., Costa, 2009), tended to increase with consumer body size. Several studies have found that larger predators can ingest larger items without removing small food items from the diet even though the latter may be less profitable, and this leads to high variance in the size of ingested food items (Scharf *et al.*, 2000; Woodward & Warren, 2007; Costa, 2009). Mouth gape is one the main determinants of the positive relationship observed between body size and size range of consumed food items (Pimm, 1982). However, in my study, mouth gape was a weak predictor of food size variation when body size was included in my analysis, indicating that other factors are involved in the positive relationship between prey size variation and body size. Given that numeric ecological pyramids tend to be bottom heavy (Elton, 1927; Hatton *et al.*, 2015), predators may be more likely to encounter small prey more often than large prey. If small prey are frequently encountered and easily ingested and digested, it seems logical to expect that they should be retained in the diet of large predators even when large prey are more profitable (Schoener, 1971). For example, tiny midge larvae (Diptera, Chironomidae) typically are abundant and constitute an important food resource for fishes of many different sizes inhabiting streams worldwide (Armitage *et al.*, 1995). Most predators can complement their diet with smaller less profitable prey when availability of preferred larger prey declines (Murdoch, 1969). Moreover, given the positive relationship between body size and home range in freshwater fish

(Woolnough *et al.*, 2009) and the positive relationship between species richness and area for most organisms, larger fish are more likely to encounter and consume a larger variety of prey than smaller fish.

As expected, mouth gape was strongly correlated with food size in fish diets. Mouth gape limitation does not only restrict food ingestion for animals that consume food items whole (e.g., most fishes, frogs and snakes), but also for animals, such as frugivorous fishes, birds and mammals, that consume certain portions of plants or animals (Wheelwright, 1985). On the other hand, several species in my dataset (e.g., detritivorous fishes of the families Curimatidae, Loricariidae, and Prochilodontidae) fed on fine particulate organic matter, including detritus and microalgae. Diets of these fishes should not be limited by mouth gape, and consequently these species usually were outliers in correlations among body size, mouth gape and food size. Detritivorous and herbivorous fishes tend to have relatively long guts compared to carnivorous fishes (Kapoor *et al.*, 1975). A longer alimentary canal increases the efficiency of digestion and absorption of nutrients from plant material and detritus by fishes (Kapoor *et al.*, 1975; Wagner *et al.*, 2009) and many other animals (e.g., Schieck & Millar, 1985; Battley & Piersma, 2005). In my study, gut length had strong negative relationships with food size, food size variation, and TP. Inclusion of gut length in the path model allowed us to analyze variation associated with detritivory and herbivory, trophic niches that are common in tropical freshwater fish assemblages.

Most species in my dataset ingested discrete food particles of various sizes, such as unicellular algae, seeds, rotifers, zooplankton, aquatic insects and fish. Estimation of the size of food items in these cases is fairly straightforward; however, estimation of food size is sometimes problematic for specialized grazers, including macrophyte feeders (*Schizodon scotorhabdotus*), scale feeders (*Roeboides* spp.), fin nippers (*Serrasalmus* spp.), and mucus scrapers (*Ochmacanthus alternus*). The body size of an individual macrophytes is sometimes a challenge to estimate due to vegetative reproduction through clonal growth and presence of semi-autonomous modules (Ottaviani *et al.*, 2017). I recorded food size based on the size of the ingested particle, which has been shown to influence the fitness of both the plant (Zvereva & Kozlov, 2014) and herbivore (Clauss & Hummel, 2005). Ultimately, the size of ingested food items depends on the behavioral means (e.g., engulfing, sucking, biting, scraping, piercing, sifting, mastication) and structures (e.g., mouth parts, auxiliary appendices) used to harvest and process material with different properties.

The testing of causal-relationships from a theoretical foundation is one the main purposes of CPA and SEM (Shipley, 2000b). However, inference of causation from correlation can be a challenge for complex systems such as food webs (Rosenberg, 1999). For instance, consumer body size is often assumed to determine the size of ingested food items. As I have inferred here for fishes, this body size influence is indirect via pathways involving mouth gape, gut length and perhaps other functional traits (e.g., tooth shape). One could propose that food supply determines consumer body size (i.e., availability of larger and more profitable prey leads to more rapid growth of the consumer). A similar argument has been invoked to explain plasticity of gut length in response to diets of different nutritional qualities (Wagner *et al.*, 2009). My assumptions of cause-effect were primarily based on proximal causes (larger fish eat larger prey) and not distal causes (fish growth is a response to food intake). Moreover, certain functional relationships were assumed; e.g., fishes with long guts are adapted to exploit foods with relatively low nutritional value when compared to carnivorous fishes that have short guts. Although my model structures were robust, inclusion of additional functional traits or the removal of weak links (e.g., food size variation –> TP) might strengthen predictive power. Future research should expand the model presented here to include additional consumer traits (e.g., tooth shape, home range) and food web descriptors (e.g., functional diversity of food items).

Although I attempted to control for potential sources of bias, some unresolved issues remain. First, I assumed that ratios of gut length/ body size and mouth gape/ body size were constant within species; however, at fine scales of resolution this probably is not the case. Nonetheless, the allometry of these ratios is likely to be much less than the magnitude of interspecific differences in my dataset (Winemiller, 1991; Montaña & Winemiller, 2013). Second, consumer body size distributions and the number of individuals analyzed varied according to species. I tried to minimize these potential sources of error by filtering the data and also by comparing average and maximum values of food item descriptors calculated from a thousand fixed sub-sample sizes of each species. In addition, trophic positions of food items were estimated based on literature information which could have introduced error. Similar concerns confront other commonly used methods for estimating TP, such as stable isotopic analysis (e.g., assumptions about trophic fractionation values, tissue turnover, inclusion of relevant sources; Layman *et al.*, 2012). Finally, the resolution of food size (10-mm intervals) could have affected my analysis of food size variation. Size variation among large food items may influence feeding to a greater extent than comparable units of variation among smaller food items. However, the use of coefficient of variation rather than variance *per se* to estimate food size variation should have mitigated potential biases since it takes into account the sample average (i.e., food size).

My study revealed how consumer body size, mouth gape, gut length, food size, and food size variation interact to influence the trophic position of tropical freshwater fishes. To date, most studies have analyzed these variables in a bivariate manner (e.g., Costa, 2009; Riede *et al.*, 2011), which limits the ability to test cause-effect relationships involving multiple interacting factors (Fan *et al.*, 2016). I further expanded analysis of the TP-body size relationship by also considering the potential influence of species shared ancestry. Future research on trophic relationships among species comprising higher taxa or ecological communities using CPA or SEM should compile data for additional predictor and response variables. Inclusion of more predictor variables will improve understanding functional relationships when investigating organisms, such as fish, that have diverse feeding strategies. Such studies should advance understanding of both trophic autecology and food web ecology and pave the way for development of more predictive models.

3.5. References

Al-Habsi S.H., Sweeting C.J., Polunin N.V.C. & Graham N.A.J (2008) δ15N and δ13C elucidation of size-structured food webs in a Western Arabian Sea demersal trawl assemblage. *Marine Ecology Progress Series*, 353, 55–63. https://doi.org/10.3354/meps07167

Arim M., Bozinovic F. & Marquet P.A. (2007) On the relationship between trophic position, body mass and temperature: reformulating the energy limitation hypothesis. *Oikos*, 116, 1524–1530. https://doi.org/10.1111/j.0030-1299.2007.15768.x

Arim M., Abades S.R., Laufer G., Loureiro M. & Marquet P.A. (2010) Food web structure and body size: trophic position and resource acquisition. *Oikos*, 119, 147–153. https://doi.org/10.1111/j.1600-0706.2009.17768.x

Armitage P.D., Cranston P.S. & Pinder L.C.V. (1995) *Biology and ecology of non-biting midges*. Chapman & Hall, London.

Barclay R.M.R. & Brigham R. (1991) Prey detection, dietary niche breadth, and body size in bats: why are aerial insectivorous bats so small? *The American Naturalist*, 137, 693–703. https://doi.org/10.1086/285188

Barnes C., Maxwell D., Reuman D.C. & Jennings S. (2010) Global patterns in predator-prey size relationships reveal size dependency of trophic transfer efficiency. *Ecology*, 91, 222–232. https://doi.org/10.1890/08-2061.1

Battley P.F. & Piersma T. (2005) *Adaptive interplay between feeding and ecology and features of the digestive tract in birds*. In: Starck J.M. & Wang T. (eds) Physiological and ecological adaptations to feeding in vertebrates. Science Publishers Inc., Enfield, pp 201–228.

Beamish F. (1978) *Swimming capacity*. In: Hoar W.S. & Randall D.J. (eds) Fish physiology. Academic Press, New York, pp 101–187.

Behrens M.D. & Lafferty K.D. (2007) Temperature and diet effects on omnivorous fish performance: implications for the latitudinal diversity gradient in herbivorous fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, 64, 867–873. https://doi.org/10.1139/f07-063

Blaxter J. & Fuiman L. (1990) The role of the sensory systems of herring larvae in evading predatory fishes. *Journal of the Marine Biological Association of the United Kingdom*, 70, 413–427. https://doi.org/10.1017/S0025315400035505

Bowen S.H. (1983) Detritivory in neotropical fish communities. *Environmental Biology of Fishes*, 9, 137–144. https://doi.org/10.1007/BF00690858

Breheny P. & Burchett W. (2017) Visualization of regression models using visreg. *The R Journal*, 9, 56–71. https://doi.org/10.32614/RJ-2017-046

Brooks J.L. & Dodson S.I. (1965) Predation, body size and composition of plankton. *Science*, 150, 28–35. https://doi.org/10.1126/science.150.3692.28

Brose U., Williams R.J. & Martinez N.D. (2006) Allometric scaling enhances stability in complex food webs. *Ecology Letters*, 9, 1228–1236. https://doi.org/10.1111/j.1461-0248.2006.00978.x

Clauss M. & Hummel J. (2005) The digestive performance of mammalian herbivores: why big may not be that much better. *Mammal Review*, 35, 174–187. https://doi.org/10.1111/j.1365-2907.2005.00062.x

Clauss M., Steuer P., Müller D.W.H., Codron D. & Hummel J. (2013) Herbivory and body size: allometries of diet quality and gastrointestinal physiology, and implications for herbivore ecology and dinosaur gigantism. *Plos One*, 8, e68714. https://doi.org/10.1371/journal.pone.0068714

Cohen J.E., Jonsson T. & Carpenter S.R. (2003) Ecological community description using the food web, species abundance, and body size. *Proceedings of the National Academy of Sciences of the United States of America*, 100, 1781–1786. https://doi.org/10.1073/pnas.232715699

Cohen J.E., Pimm S.L., Yodzis P. & Saldaña J. (1993) Body sizes of animal predators and animal prey in food webs. *Journal of Animal Ecology*, 62, 67–78. https://doi.org/10.2307/5483

Costa G.C. (2009) Predator size, prey size, and dietary niche breadth relationships in marine predators. *Ecology*, 90, 2014–2019. https://doi.org/10.1890/08-1150.1

Dalponti G., Guariento R.D. & Caliman A. (2018) Hunting high or low: body size drives trophic position among and within marine predators. *Marine Ecology Progress Series*, 597, 39–46. https://doi.org/10.3354/meps12584

Dantas D.D.F., Caliman A., Guariento R.D., Angelini R., Carneiro L.S., Lima S.M.Q., Martinez P.A. & Attayde J.L. (2019) Climate effects on fish body size-trophic position relationship depend on ecosystem type. *Ecography*, 42, 1579-1586. https://doi.org/10.1111/ecog.04307

DeAngelis D.L. (2012) *Dynamics of nutrient cycling and food webs*. Springer Science & Business Media, New York.

Dunic J.C. & Baum J.K. (2017) Size structuring and allometric scaling relationships in coral reef fishes. *Journal of Animal Ecology*, 86, 577-589. https://doi.org/10.1111/1365-2656.12637

Elton C. (1927) *Animal ecology*. Macmillan, New York.

Fan Y., Chen J., Shirkey G., John R., Wu S.R., Park H. & Shao C. (2016) Applications of structural equation modeling (SEM) in ecological studies: an updated review. *Ecological Processes*, 5, 19. https://doi.org/10.1186/s13717-016-0063-3

Floeter S.R., Behrens M.D., Ferreira C.E.L., Paddack M.J. & Horn M.H. (2005) Geographical gradients of marine herbivorous fishes: patterns and processes. *Marine Biology*, 147, 1435–1447. https://doi.org/10.1007/s00227-005-0027-0

Folkvord A. & Hunter J.R. (1986) Size-specific vulnerability of northern anchovy, Engraulis mordax, larvae to predation by fishes. *Fishery Bulletin- National Oceanic and Atmospheric Administration*, 84, 859–869.

Froese R., Thorson J.T. & Reyes R.B. (2014) A Bayesian approach for estimating length-weight relationships in fishes. *Journal of Applied Ichthyology*, 30, 78–85. https://www.doi.org/10.1111/jai.12299

Gilljam D., Thierry A., Edwards F.K., Figueroa D., Ibbotson A.T., Jones J.I., Lauridsen R.B., Petchey O.L., Woodward G. & Ebenman B. (2011) Seeing double: size-based versus taxonomic views of food web structure. *Advances in Ecological Research*, 45, 67–133. https://doi.org/10.1016/B978-0-12-386475-8.00003-4

Hatton I.A., McCann K.S., Fryxell J.M., Davies T.J., Smerlak M., Sinclair A.R.E. & Loreau M. (2015) The predator-prey power law: biomass scaling across terrestrial and aquatic biomes. *Science*, 349, aac6284.

https://www.doi.org/1126/science.aac6284

Hultgren K.M., Jeffery N.W., Moran A. & Gregory T.R. (2018) Latitudinal variation in genome size in crustaceans. *Biological Journal of the Linnean Society*, 123, 348–359. https://doi.org/10.1093/biolinnean/blx153

Jennings S., Pinnegar J., Polunin N. & Warr K. (2002) Linking size-based and trophic analyses of benthic community structure. *Marine Ecology Progress Series*, 226, 77–85. https://www.doi.org/10.3354/meps226077

Jennings S., Oliveira J.A.A.D. & Warr K.J. (2007) Measurement of body size and abundance in tests of macroecological and food web theory. *Journal of Animal Ecology*, 76, 72–82. https://doi.org/10.1111/j.1365-2656.2006.01180.x

Kapoor B.C., Smith H. & Verighina I.A. (1975) The alimentary canal and digestion in teleosts. *Advances in Marine Biology*, 13, 109–239. https://doi.org/10.1016/S0065-2881(08)60281-3

Keast A. & Webb D. (1966) Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. *Journal of the Fisheries Research Board of Canada*, 23, 1845–1874. https://www.doi.org/10.1139/f66-175

Layman C.A., Araujo M.S., Boucek R., Hammerschlag-Peyer C.M., Harrison E., Jud Z.R., Matich P., Rosenblatt A.E., Vaudo J.J., Yeager L.A., Post D.M. & Bearhop S. (2012) Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biological Reviews*, 87, 545–562. https://doi.org/10.1111/j.1469-185X.2011.00208.x

Layman C.A., Winemiller K.O., Arrington D.A. & Jepsen D.B. (2005) Body size and trophic position in a diverse tropical food web. *Ecology,* 86, 2530–2535. https://doi.org/10.1111/10.1890/04-1098

Lefcheck J. (2016) piecewiseSEM: piecewise structural equation modeling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution,* 7, 573–579. https://doi.org/10.1111/2041-210X.12512

Lindemann R.L. (1942) The trophic dynamics aspect of ecology. *Ecology*, 23, 399–413. https://doi.org/10.2307/1930126

McCann K.S. (2011) *Food webs*. Princeton University Press, New Jersey.

Mihalitsis M. & Bellwood D.R. (2017) A morphological and functional basis for maximum prey size in piscivorous fishes. *Plos One*, 12, e0184679. https://doi.org/10.1371/journal.pone.0184679

Mittelbach G.G. (1981) Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology*, 62, 1370–1386. https://doi.org/10.2307/1937300

Montaña C.G. & Winemiller K.O. (2013) Evolutionary convergence in Neotropical cichlids and Neartic centrarchids: evidence from morphology, diet and stable isotope analysis. *Biological Journal of the Linnean Society*, 109, 146-164. https://doi.org/10.1111/bij.12021

Moody E.K., Lujan N.K., Roach K.A. & Winemiller K.O. (2019) Threshold elemental ratios and the temperature dependence of herbivory in fishes. *Functional Ecology*, 33, 913-923. https://doi.org/10.1111/1365-2435.13301

Murdoch W.W. (1969) Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecological Monographs*, 39, 335–354.

https://doi.org/10.2307/1942352

Naisbit R.E., Kehrli P., Rohr R.P. & Bersier L-F. (2011) Phylogenetic signal in predator-prey body-size relationships. *Ecology*, 92, 2183–2189. https://doi.org/10.1890/10-2234.1

Nilsson P.A. & Bronmark C. (2000) Prey vulnerability to a gape-size limited predator: behavioural and morphological impacts on northern pike piscivory. *Oikos*, 88, 539–546. https://doi.org/10.1034/j.1600-0706.2000.880310.x

Ou C., Montaña C.G. & Winemiller K.O. (2017) Body size-trophic position relationships among fishes of the lower Mekong basin. *Royal Society Open Science*, 4, 160645. doi: https://doi.org/10.1098/rsos.160645

Ottaviani G., Martínková J., Herben T., Pausas J.G. & Klimešová J. (2017) On plant modularity traits: functions and challenges. *Trends in Plant Science*, 22, 648–651. https://doi.org/10.1016/j.tplants.2017.05.010

Paine R.T. (1988) On food webs: road maps of interactions or the grist for theoretical development? *Ecology*, 69, 1648–1654. https://doi.org/10.2307/1941141

Pimm S. (1982) *Food webs*. Chapman & Hall, London.

Pinheiro J., Bates D., DebRoy S., Sarkar D. & R Core Team (2018) *nlme: linear and nonlinear mixed effects models*. Available at: https://cran.r-project.org/package=nlme (accessed 15 June 2019).

Potapov A.M., Brose U., Scheu S. & Tiunov A.V. (2019) Trophic position of consumers and size structure of food webs across aquatic and terrestrial ecosystems. *The American Naturalist*, 194, 823–839. https://doi.org/10.1086/705811

R Core Team (2019) *R: a language and environment for statistical computing*. Availalble at: http://www.rproject.org (accessed 20 June 2019).

Rabosky D.L., Chang J., Title P.O., Cowman P.F., Sallan L., Friedman M., Kaschner K., Garilao C., Near T.J., Coll M. & Alfaro M.E. (2018) An inverse latitudinal gradient in speciation rate for marine fishes. *Nature*, 559, 392–395. https://doi.org/10.1038/s41586-018-0273-1

Reiss M. (1988) Scaling of home range size: body size, metabolic needs and ecology. *Trends in Ecology and Evolution*, 3, 85–86. https://doi.org/10.1016/0169-5347(88)90025-0

Reum J.C.P. & Marshall K.N. (2013) Evaluating δ15N-body size relationships across taxonomic levels using hierarchical models. *Oecologia*, 173, 1159–1168. https://doi.org/10.1007/s00442-013-2715-7

Riede J.O., Brose U., Ebenman B., Jacob U., Thompson R., Townsend C.R. & Jonsson T. (2011) Stepping in Elton's footprints: a general scaling model for body masses and trophic levels across ecosystems. *Ecology Letters*, 14, 169–178. https://doi.org/10.1111/j.1461-0248.2010.01568.x

Romanuk T.N., Hayward A. & Hutchings J.A. (2011) Trophic level scales positively with body size in fishes. *Global Ecology and Biogeography*, 20, 231–240. https://doi.org/10.1111/j.1466-8238.2010.00579.x

Romero-Romero S., Molina-Ramírez A., Höfer J. & Acuña J.L. (2016) Body size-based trophic structure of a deep marine ecosystem. *Ecology*, 97, 171–181. https://doi.org/10.1890/15-0234.1

Rooney N., McCann K.S. & Moore J.C. (2008) A landscape theory for food web architecture. *Ecology Letters*, 11, 867–881. doi: https://doi.org/10.1111/j.1461-0248.2008.01193.x

Rosenberg A. (1999) *Instrumental biology, or the disunity of science*. The University of Chicago Press, Chicago.

Scharf F.S., Juanes F. & Rountree R.A. (2000) Predator size - prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Marine Ecology Progress Series*, 208, 229–248. https://doi.org/10.3354/meps208229

Schieck J.O. & Millar J.S. (1985) Alimentary tract measurements as indicators of diets of small mammal. *Mammalia*, 49, 93–104. https://doi.org/10.1515/mamm.1985.49.1.93

Schoener T.W. (1971) Theory of feeding strategies. *Annual Review of Ecology, Evolution, and Systematics*, 2, 369–404. https://doi.org/10.1146/annurev.es.02.110171.002101

Segura A.M., Franco-Trecu V., Franco-Fraguas P. & Arim M. (2015) Gape and energy limitation determine a humped relationship between trophic position and body size. *Canadian Journal of Fisheries and Aquatic Sciences*, 72, 198–205. https://doi.org/10.1139/cjfas-2014-0093

Shipley B. (2000a) A new inferential test for path models based on directed acyclic graphs. *Structural Equation Modeling*, 7, 206–218. https://doi.org/10.1207/S15328007SEM0702_4

Shipley B. (2000b) *Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference*. Cambridge University Press, Cambridge.

Shipley B. (2009) Confirmatory path analysis in a generalized multilevel context. *Ecology*, 90, 363-368. https://doi.org/10.1890/08-1034.1

Tonin A.M., Pozo J., Monroy S., Basaguren A., Pérez J., Gonçalves J.F., Pearson R., Cardinale B.J. & Boyero L. (2018) Interactions between large and small detritivores influence how biodiversity impacts litter decomposition. *Journal of Animal Ecology*, 87, 1465–1474. https://doi.org/10.1111/1365-2656.12876

Tucker M.A. & Rogers T.L. (2014) Examining predator-prey body size, trophic level and body mass across marine and terrestrial mammals. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20142103. https://doi.org/10.1098/rspb.2014.2103

Wagner C.E., McIntyre P.B., Buels K.S., Gilbert D.M. & Michel E. (2009) Diet predicts intestine length in Lake Tanganyika's cichlid fishes. *Functional Ecology*, 23, 1122–1131. https://doi.org/10.1111/j.1365-2435.2009.01589.x

Warren P.H. & Lawton J.H. (1987) Invertebrate predator-prey body size relationships: an explanation for upper triangular food webs and patterns in food web structure. *Oecologia*, 74, 231–235. https://doi.org/10.1007/BF00379364

Werner E.E. & Hall D.J. (1974) Optimal foraging and the size selection of prey by the bluegill sunfish (Lepomis macrochirus). *Ecology*, 55, 1042–1052. https://doi.org/10.2307/1940354

Wheelwright N.T. (1985) Fruit size, gape width, and the diet of fruit-eating birds.

Ecology, 66, 808–818. https://doi.org/10.2307/1940542

Winemiller K.O. (1990) Spatial and temporal variation in tropical fish trophic networks. *Ecological Monographs*, 60, 331–367. https://doi.org/10.2307/1943061

Winemiller K.O. (1991) Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. *Ecological Monographs*, 61, 343–365. https://doi.org/10.2307/2937046

Woodward G., Ebenman B., Emmerson M., Montoya J., Olesen J., Valido A. & Warren P. (2005a) Body size in ecological networks. *Trends in Ecology and Evolution*, 20, 402–409. https://doi.org/10.1016/j.tree.2005.04.005

Woodward G., Speirs D.C. & Hildrew A.G. (2005b) Quantification and resolution of a complex, size structured food web. *Advances in Ecological Research*, 36, 85–135. https://doi.org/10.1016/S0065-2504(05)36002-8

Woodward G. & Warren P. (2007) *Body size and predatory interactions in freshwaters: scaling from individuals to communities*. In: Hildrew A.G., Raffaelli D. & Edmonds-Brown R. (eds) Body size: the structure and function of aquatic ecosystems. Cambridge University Press, Cambridge, pp 98–117. https://doi.org/10.1017/cbo9780511611223.007

Woolnough D.A., Downing J.A. & Newton T.J. (2009) Fish movement and habitat use depends on water body size and shape. *Ecology of Freshwater Fish*, 18, 83–91. https://doi.org/10.1111/j.1600-0633.2008.00326.x

Wootton J.T. & Oemke M.P. (1992) Latitudinal differences in fish community trophic structure, and the role of fish herbivory in a Costa Rican stream. *Environmental*

Biology of Fishes, 35, 311-319. https://doi.org/10.1007/BF00001899

Zvereva E.L. & Kozlov M.V. (2014) Effects of herbivory on leaf life span in woody plants: a meta-analysis. *Journal of Ecology*, 102, 873-881. https://doi.org/10.1111/1365-2745.12252

4. CAN ANCESTRY AND MORPHOLOGY BE USED AS SURROGATES FOR SPECIES NICHE RELATIONSHIPS?[†]

4.1. Introduction

Species interactions are an important mechanism structuring ecological communities (HilleRisLambers *et al.*, 2012) with the potential to influence ecosystems processes and services (Traill *et al.*, 2010). A fundamental challenge in ecology is to quantify these interactions and understand their implications for community assembly (Xu *et al.*, 2018) and ecosystem dynamics (Jordano, 2016). In a broader context, a better understanding about species functional traits may improve understanding of evolutionary processes, such as adaptive radiation and convergence (Takahashi & Koblmüller, 2011; Bower & Winemiller, 2019). When analyses integrate functional, phylogenetic and species interaction data, diversity patterns can be elucidated and community assembly mechanisms can be inferred at multiple scales (Nanthavong *et al.*, 2015; Peralta, 2016).

Direct and indirect metrics have been used to access species interaction strength (Berlow *et al.*, 1999; Wootton & Emmerson, 2005). From a food web perspective,

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stomach contents analysis (hereafter, referred to as dietary analysis) has been used to estimate predator-prey interactions (e.g., Rosi-Marshall & Wallace, 2002) and infer the potential strength of interspecific competition (e.g., Jung *et al.*, 2015). Despite providing fairly direct documentation of consumer-resource interactions, dietary analysis has some well-known limitations, including 1) sample size dependency (i.e., a sample merely represents a snapshot in time and space, and may not reflect long-term patterns of consumption); 2) difficulty to identify fragmented or partially digested food items; and 3) short retention time of ingested items (Votier *et al.*, 2003; Araújo *et al.*, 2007). In recent decades, several studies have analyzed stable isotope ratios, especially of nitrogen (N) and carbon (C), as an alternative method for making inferences about trophic ecology (Fry, 2006). The ratio of ^{15}N to ^{14}N ($\delta^{15}N$) is positively correlated with trophic level given its natural enrichment of 2-3‰ during assimilation of ingested material into consumer tissue (Peterson & Fry, 1987; Post, 2002). The ratio of ^{13}C to ^{12}C ($\delta^{13}C$) varies among primary producers at the base of food chains and largely reflects differences in photosynthetic pathways (C3, C4, CAM) as well as inorganic sources of carbon assimilated by plants (Peterson & Fry, 1987). Consequently, variation in $\delta^{13}C$ and $\delta^{15}N$ of animals has been proposed as an indicator of trophic niche differences (Layman *et al.*, 2012). A potential advantage of stables isotopes over diet analysis is its capability of integrating assimilation of consumed items over time (Layman *et al.*, 2012), allowing the assessment of important ecological properties, such as individual specialization (Araújo *et al.*, 2007; Harrison *et al.*, 2017). Stable isotope ratios provide an indirect estimate of the trophic niche; however, isotopic ratios are influenced by other factors (Zanden, Cabana, & Rasmussen, 1997; Davis *et al*., 2012; Bastos *et al*., 2017; Villamarín *et al*., 2018). For example, tissue isotopic turnover and trophic enrichment (Δ^{13}C and Δ^{15}N) can vary according to consumer body size, age, metabolism and environmental conditions, which increases the uncertainty of estimates and inferences about trophic ecology based on stable isotopic analysis (Caut *et al.*, 2009). In some cases, isotopic ratios may be more strongly associated with physiology linked to variation in morphological traits, such as body size, than with feeding history per se (Villamarín *et al*., 2018).

Morphologically similar species are generally expected to have similar niches (McGill *et al*., 2006; Rocha *et al.*, 2011), resulting in relatively high dietary overlap (Gatz, 1979) and similar isotopic ratios provided that environmental conditions are similar (Layman *et al*., 2007; Hopkins III & Kurle, 2016). Morphological traits often have a strong phylogenetic signal (Losos, 2008), and, therefore, one might expect a certain level of correlation between phylogenetic distance, diet, and isotopic ratios (Lind *et al*., 2015; Fraser *et al.*, 2018). However, if there is rapid adaptive divergence or strong evolutionary convergence, some species may be more or less similar ecologically than would be expected based on phylogenetic relationships (Kamilar & Cooper, 2013; Cachera & Le Loc'h, 2017). Indicators of recent ecological performance, such as diet composition, would be expected to reveal weaker phylogenetic signals than morphological traits that have higher heritability, therefore less strongly influenced by environmental variation, and also are less subject to measurement error (Freckleton *et al.*, 2002; Blomberg *et al.*, 2003).

Trait-diet relationships may be weak because species that appear to be specialists based on their morphology sometimes perform as ecological generalists under certain conditions (Liem, 1978); this incongruity has been called Liem’s paradox (Mayr, 1984; Greenwood, 1989). A possible explanation for this paradox is that a given phenotype can perform multiple ecological functions, and different phenotypes sometimes can perform the same ecological function (Wainwright *et al*., 2005; Zelditch *et al*., 2017). For example, species that are trophic specialists during times of resource scarcity may switch to feed on profitable food resources when these are temporarily abundant (Robinson & Wilson, 1998). Similarly, functionally versatile phenotypes may allow consumers to specialize on certain resources when preferred resources become scarce (Murdoch, 1969). Examples of weak links between morphological specialization and diet have been found in several ecosystems, including highly diverse coral reefs where most lineages of wrasses and parrotfishes have shown high levels of trophic versatility (Bellwood *et al*., 2006). This challenges the traditional view that local community structure derives mainly from niche-partitioning and opens the possibility for alternative hypotheses that metapopulational dynamics (e.g., mass effects) and regional species extinction probabilities (e.g., Lottery Competition and Neutral Theory) are strong determinants of the structure and diversity of local communities (Sale, 1977; Chesson & Warner, 1981; Bell, 2001; Hubbell, 2001). Either way, the relationships between phylogeny, morphological similarity and indicators of ecological performance (e.g., diet) remain poorly documented, this in spite of the fact that numerous studies have assumed morphological traits and/or phylogeny are effective surrogates for species niches when analyzing patterns of community structure (e.g., Cooper *et al.*, 2008; Kraft *et al*., 2008; Côte *et al.*, 2019).

Here, I investigated species similarity with respect to morphological traits, diet, isotopic ratios, phylogeny, and patterns of intercorrelation among these variables using datasets for freshwater fishes from streams in Central and South America. Fish assemblages in these streams have high taxonomic, morphological and ecological diversity (Winemiller, 1990). Streams in both regions have seasonal hydrology that causes changes in food resource availability and fish diets (Winemiller, 1989, 1990; Peterson *et al*., 2017). Previous research revealed significant food resource partitioning throughout the year (Winemiller, 1989; Winemiller & Pianka, 1990; Peterson *et al*., 2017). What remains unclear is the degree to which morphological traits and phylogeny are associated with patterns of resource partitioning in these diverse fish assemblages. Earlier studies evaluated trophic ecology based on dietary analysis, and here I analyze those data in conjunction with stable isotope data obtained from some of the same specimens that were preserved and archived in natural history collections. Analysis were restricted to the dry periods and potential differences between sites were considered. Four hypotheses (Figure 4.1) were tested: i) Morphological traits have a significant phylogenetic signal; ii) species with similar morphological traits have high dietary overlap and similar isotopic ratios; iii) phylogeny affects diet and isotopic ratios only indirectly and therefore has a weaker association with diet and isotopic ratios than morphological traits; and iv) species with similar isotopic ratios have higher dietary overlap.

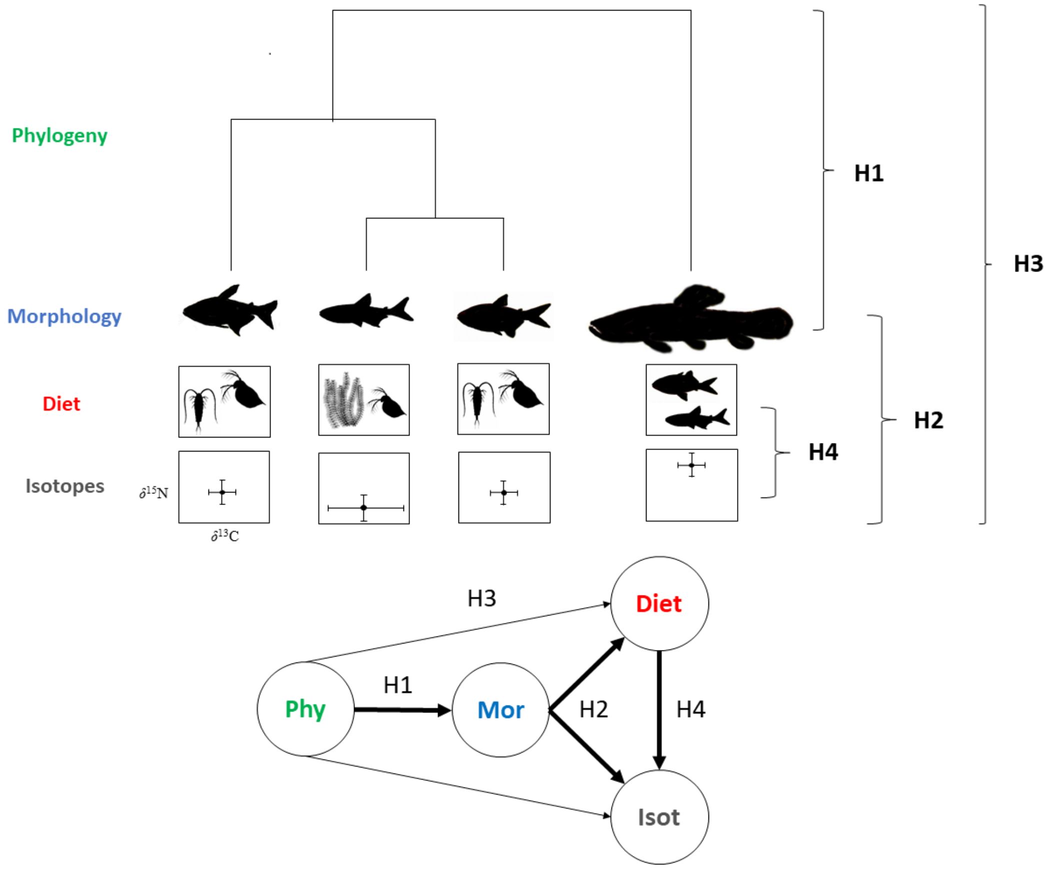

Figure 4.1 Theoretical model for interrelationships among phylogeny, morphological traits, diet, and isotopic ratios. I hypothesized that: i) morphological trait variation has a strong phylogenetic signal (H1); ii) species with similar morphological traits have high diet overlap and similar isotopic ratios (H2); iii) phylogeny influences dietary and isotopic ratios only indirectly and therefore has a weaker relationship with dietary and isotopic patterns than morphological traits (H3); and iv) species with similar isotopic ratios have higher diet overlap (H4).

4.2. Methods

4.2.1. Fish samples

Fishes were sampled in 1983 and 1984 from Caño Maraca, a swamp creek located in the Western Llanos of Venezuela, and Caño Agua Fría Viejo, a coastal stream located approximately 10 km upstream from the confluence of the Río Tortuguero with the Caribbean Sea in Costa Rica (Figure 4.2; Winemiller, 1990). At each site, fishes were collected monthly during an entire year using dip nets, gillnets, and seine nets to obtain a reasonably complete sample of the local fish assemblage during each month (Winemiller, 1990). Sampled fish were identified, measured for standard length (SL, mm), and several specimens of the most abundant species were placed in 10% formalin solution for up to 10 months, rinsed, transferred to 70% ethanol solution, and deposited in the Texas Natural History Collection (TNHC) at The University of Texas at Austin.

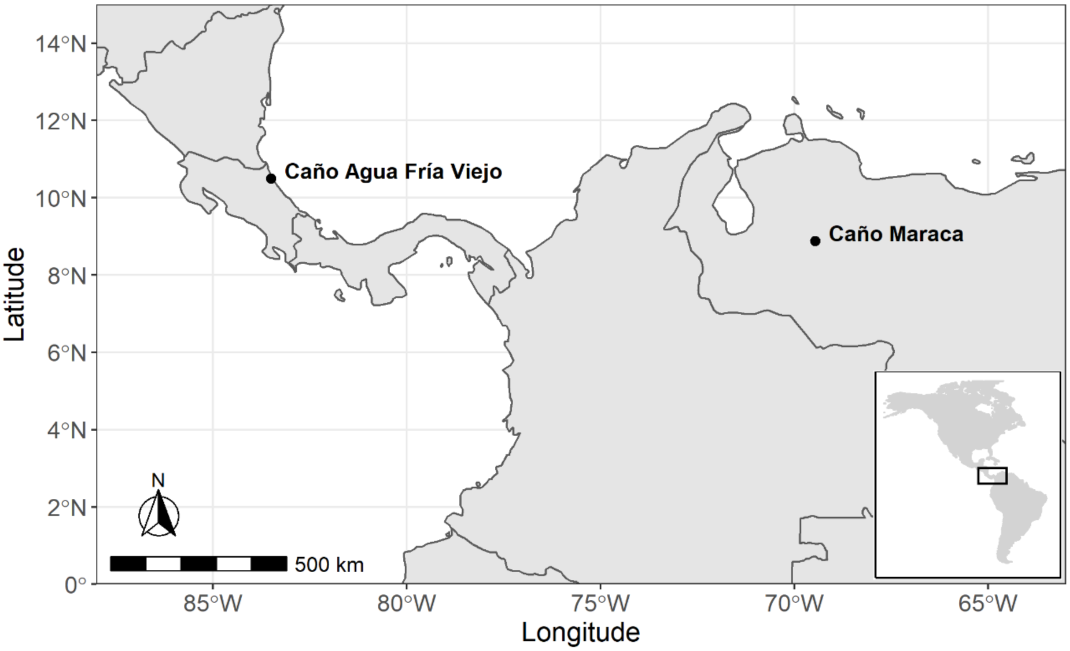

Figure 4.2 Location of the two streams analyzed in this study. Caño Maraca is a swamp creek situated in the Western Llanos of Venezuela, whereas Caño Agua Fría Viejo is a coastal stream located near the confluence of the Río Tortuguero with the Caribbean Sea in Costa Rica.

Here, I restricted my analysis to the most abundant fish species (45 species from Caño Maraca and 24 from Caño Agua Fría Viejo; Table C.1) collected only during the dry and transition periods (September to April in Caño Maraca, and March to May and September to October in Caño Agua Fria Viejo). This restriction was necessary to standardize environmental conditions and facilitate comparisons between isotopic ratios and diet data. Moreover, the majority of preserved specimens deposited in the TNHC and available for isotopic analysis (see below) were collected during the dry and transition periods. The number of species included in this study compressed ~54% of the total number of species collected in Caño Maraca (~86% of the total abundance) and ~41 % of the species in Caño Agua Fría Viejo (~90% of the total abundance) during an entire annual cycle (Winemiller, 1990). There were not any shared species between Caño Maraca and Caño Agua Fría Viejo in the database analyzed in this study (Table C.1).

4.2.2. Phylogenetic data

Phylogenetic relationships were based on a supertree created from analysis of molecular data (multiple genes) from ca. 11,000 fish species (marine and freshwater species) and time-calibrated using fossil records (Rabosky *et al*., 2018; Chang *et al*., 2019). For 21 out of 68 species in my dataset (~31%), genetic information was not available, and those species were not present in the published supertree. I placed those species in positions on the tree occupied by their most closely related taxon, usually a congeneric species (Table C.3). I then created a similarity matrix whereby the phylogenetic relationship of each pair of species was expressed as cophenetic distances.

4.2.3. Morphological data

Twenty-six morphological traits related to feeding, locomotion, and habitat preference (Gatz, 1979; Winemiller, 1991) were measured: standard length, body depth, body width, caudal peduncle length, caudal peduncle height, caudal peduncle width, body depth below midline, head length, head depth, eye position, eye diameter, mouth width, snout length (shut), dorsal fin height, dorsal fin length, pectoral fin length, pectoral fin height, caudal fin length, caudal fin height, pelvic fin length, anal fin length, anal fin height, gut length, mouth orientation (superior, terminal, sub-terminal, inferior), tooth shape (absent, unicuspid, multicuspid, conical, triangular serrated), and gill raker shape (absent, short/blunt/toothlike, intermediate/long and sparse, long and comb-like). Measures were taken from 3 to 9 preserved specimens of each species according to methods reported by Winemiller (1991; Table C.1). To reduce variation associated with ontogeny, I restricted measurements to the largest specimens available, most of which were classified as adults based on reported sizes at maturation (Winemiller, 1989; Fishbase https://www.fishbase.in/search.php). Following the protocol described by Winemiller (1991), linear measurements of various body and fin dimensions were converted to proportions to to remove the effect of body size differences, and then specimen proportions were averaged for each species. Body size ratios can introduce allometric biases in morphometric analyses (Albrecht *et al.*, 1993), however, this source of potential bias should have little influence for broad interspecific comparisons (Winemiller, 1991). Besides, body size ratios have straightforward ecological and functional interpretations (Winemiller, 1991; Montaña & Winemiller, 2013; Villéger *et* *al*., 2017) and have been widely used in functional ecology studies (e.g., Toussaint *et al*., 2018; Su *et al.*, 2019). Finally, I constructed a similarity matrix based on Gower distance; this approach was used because the dataset contained three morphological traits (tooth shape, gill raker shape, mouth position) that were categorical.

4.2.4. Isotopic data

Isotopic analysis of $\delta^{13}C$ and $\delta^{15}N$ were conducted on large preserved specimens (composed mainly of adults) deposited in the TNHC (see Fish Data section). For most species, I sampled 3 individuals, although in a few cases this number was higher (max=7) or lower (min=2) depending on availability of preserved specimens from the field studies (Table C.1). Although not uncommon in community ecology studies (e.g., Montaña *et al*., 2020), small isotopic sample sizes may provide poor representation of species/population isotopic signatures when there is high variation associated with isotopic samples. This could ultimately weaken the association between isotopic ratios and other datasets (e.g., diet, morphological traits). I decided to retain species with small samples for isotopic analysis for two main reasons: 1) standard deviation around the average values of $\delta^{13}C$ and $\delta^{15}N$ was relatively small compared to the average of each species (Figure C.1); and 2) removing species with small samples size would reduce the number of species analyzed and, consequently, reduce the representativeness of each community.

At the time of tissue sampling, the deposited species had been preserved for the past 34-35 years. Studies have indicated that the preservation method can affect values of $\delta^{15}N$ and $\delta^{13}C$, but changes seem to be small when compared to natural fractionation processes and are directionally uniform (Arrington & Winemiller, 2002; Edwards *et al.*, 2002; Sarakinos *et al.*, 2002). Several studies have performed stable isotope analysis using material from preserved specimens to reconstruct feeding interactions (e.g., Araújo *et al*., 2009; Kishe-Machumu *et al*., 2017), including some stored as long as the ones used in my study (e.g., English *et al*., 2018).

Fish muscle tissue samples were removed from the ventrum just anterior to the anus (the exception was gymnotiforms, for which tissue was taken anywhere from the abdominal region because the anus is located just posterior to the head). Tissue samples were rinsed in distilled water, dried in an oven for 48 h at 60°C, and then ground to a fine pounder using pestle and mortar. Subsamples weighing 10 to 30 mg were packed into Ultra-Pure tin capsules (Costech Analytical, Valencia, California, USA). The encapsulated samples were sent to the Analytical Chemistry Laboratory of the Institute of Ecology at the University of Georgia (USA) for analysis of stable-isotope ratios of $\delta^{13}C$ and $\delta^{15}N$. Samples were dry combusted (microDumas technique) using a Carlo Erba CHN elemental analyzer, and the purified gases released from the process were introduced into a Finnigan Delta C mass spectrometer. Stable isotope ratios were quantified as deviations relative to standard materials (atmospheric nitrogen for $\delta^{15}N$ and Pee Dee Belemnite for $\delta^{13}C$). Isotopic ratios had a precision of $\leq 1.5\%$ for $\delta\ ^{15}N$ and $\leq 1\%$ for $\delta^{13}C$, measured as the maximum deviation to the mean of bovine (Standard Reference Material [SRM] 1577c) reference samples (measured after every 12 fish tissue samples).

A similarity matrix based on raw isotopic data (without any corrections) was constructed to compare the isotopic ratios of each pair of species. Distance between species was calculated using Euclidean distance after the data were standardized (zero mean and unit variance).

4.2.5. Diet data

Diet analysis was conducted by Winemiller (1990), who dissected 30 specimens of each species from each monthly sample when available. For herbivores and detritivores, the number of dissected specimens was reduced to 20 due to low intraspecific diet variation and the much greater time and effort required to analyze gut contents of these fishes (Winemiller, 1990). Because piscivores typically have a high incidence of empty stomachs (Arrington *et al.*, 2002) and their gut contents are processed rapidly when compared to omnivores, herbivores, and detritivores, all available specimens of piscivorous species were dissected. I did not restrict my diet analysis to just the largest specimens that were used for isotopic and morphological analysis because this would have compromised the accuracy of the diet estimates. All else being equal, estimates of diet composition are much more sensitive to sample size than are estimates of morphological dimensions and isotopic composition. Consequently, although average values were similar, the variation in the size of fish examined for diet analysis was a little higher than the variation of those used for isotopic and morphological analysis (Table C.1). This source of variation could weaken relationships between morphological traits/isotopic ratios and diet especially if intraspecific dietary and morphological variation increases with size (e.g., Keppeler *et al.*, 2015). However, in a previous study (unpublished), I found that restricting the diet data to only adults versus including a broader range of sizes had minimal effect on correlations between morphological traits and diet data. In this sense, the higher body size variation in the diet dataset likely has minimum influence on the correlations between diet and the other datasets, especially in interspecific comparisons like mine.

The volume of each identifiable food category within the material recovered from each fish stomach was estimated either by water displacement in appropriate-sized graduated cylinders or, for microscopic items, by estimating the area covered on a slide when viewed under a compound microscope and then scaling the percent coverage estimate according to the total volume of the food mass recovered from the gut (Winemiller, 1990). The volumetric method has been widely applied in diet studies of medium-small size fishes (e.g. Silva *et al.*, 2010; Peterson *et al*., 2017) and is considered an efficient and practical way to estimate food item importance (Hyslop, 1980). Prey were identified to the lowest taxonomic level that was feasible based on the degree of decomposition and observable characters. In most cases, invertebrates were identified to the family or order level, whereas fish prey varied from species-level to order or even class due to faster digestion rates. Detritus was classified according to particle size as either fine, coarse or vegetative detritus (i.e., fragments of dead plant material). Algae were classified according to size (unicellular vs. filamentous) and type (diatoms vs. green and cyanobacteria). Plants were classified according to origin (terrestrial vs. aquatic), tissue (e.g., fruit, seed, leaf) and, in some cases, taxon (e.g., *Wolffia* sp., *Lemna* sp.). Later, food item volumes were transformed into relative abundances (i.e., standardize to vary from 0 to 1) for each fish individual. For more details about the protocol used for diet analysis, see Winemiller (1990).

Pairwise dietary similarity is strongly influenced by data resolution (Yodzis & Winemiller, 1999). In addition, some kinds of food items are functionally more similar than others, and consequently, some fish trophic guilds (e.g., detritivores) tend to reveal higher dietary overlap than others that display greater niche diversification (e.g., piscivores). I developed a simple new approach that takes into account the nested structure of diet data and generates a single distance value for each pair of species. First, I identified the degree of similarity among food items and created a hierarchical scheme that best describes the data structure (Table C.2, Figure C.2). The hierarchical structure was organized in 7 different vertical levels forming a pyramid-like structure (Table C.2, Figure C.2). Food categories were broad at the top of the pyramid and categories were defined more narrowly at the bottom (Figure C.2). There is an inherent tradeoff. As food items are combined into broader categories, resolution becomes poorer but the amount of data available increases; conversely, as the taxonomic resolution increases, some food items are eliminated due to limitations of identification caused by digestion and/or difficulty of identifying diagnostic features of organisms. To avoid major data loss at the bottom of the pyramid, I defined some food categories according to functional categories that were easily identifiable (e.g., detritus, vegetation, seeds; Table C.2). However, I removed data for food items that were badly fragmented or digested even though they could be recognized as belonging to a broad category, such as macroinvertebrates or fish (Table C.2).

Second, I created a diet matrix for each hierarchical level of the pyramid-like structure described above (Table C.2, Figure C.2). The number of specimens dissected varied greatly among species, from 16 to 396 (Table C.1; Total N=7,720). I accounted for these differences by rarefying the number of individuals per species based on the value for the smallest sample (N= 16) for each hierarchical level. Then, I averaged the food item ingested among all individuals of each species for each hierarchical level. These matrices with species averaged data were then transformed into similarity matrices (Bray-Curtis dissimilarity; Figure C.2). This procedure was conducted 1,000 times and the information documenting each computer loop interaction was saved. For each hierarchical level, the 1,000 similarity matrices were averaged. Finally, I averaged the similarity matrices associated with each hierarchical level, forming a unified similarity matrix that summarizes food overlap between species (Figure C.2).

4.2.6. Data analysis

For all datasets, species from all sites were combined into the same similarity matrix as exploratory analysis indicated a low statistical power caused by the small sample size for Caño Agua Fria Viejo (N=24 species). In order to account for potential site differences, I created a binary similarity matrix (herein referred to as site similarity matrix), where 0 and 1 indicate species from the same and different sites, respectively. Then, I conducted partial Mantels to test the correlation between all possible pairings of four similarity matrices that based on different types of data (diet, isotopic ratios, morphological traits, and phylogeny) using the site similarity matrix as a covariable. I also used the Mantel test to investigate the influence of the site similarity matrix on the phylogenetic, morphological, dietary, and isotopic similarity matrices. Mantel and partial Mantels were based on the Spearman correlation statistic which relaxes the assumption of linear relationship assumed by the Pearson statistic (Mantel, 1967; Dietz, 1983). Significance was assessed by permuting the rows and columns of the similarity matrix 10,000 times and comparing the observed value.

To explore the structure of the similarity matrices, dendrograms were created using the UPGMA (unweighted pair group method with arithmetic mean) algorithm. UPGMA method was chosen after comparing results from other cluster methods (Ward D, Ward D2, Single, Complete, WPGMA, WPGMC, UPGMC). This was done by comparing correlation values between the cophenetic distance generated from the dendrogram and the initial distance between the data, i.e. the highest correlation indicates the most representative cladogram of the original similarity matrix (Mouchet & Mason, 2008; Cachera & Le Loc'h, 2017). I created pairwise tanglegrams to compare the similarity between dendrograms of different datasets (e.g., phylogeny, morphological traits). To improve the visualization of the tanglegrams, I used the untangle function (algorithm step2side) of the R package dendextend and colored connecting lines according to taxonomic order and trophic groups. Trophic groups were based on diet data and classified into five groups: Herbivorous/Detritivores (> 70% of plant/detritus ingested), omnivores 1 (> 30% of plants/detritus and > 30% of invertebrates ingested), invertivorous (>70% of invertebrates ingested), omnivores 2 (>30% of invertebrates and >30% of fish ingested), and piscivores (>70% of fish ingested). I also calculated the topological similarity between dendrograms using the score proposed by Nye, Liò, and

Gilks (2006). The algorithm proposed by Nye, Liò, and Gilks (2006) finds the best one-to-one mapping of branches among a pair of dendrograms by comparing a calculated similarity score for the clades separated by each branch; the similarity score of the best mapping represents the degree of association between the dendrograms (Nye, Liò, and Gilks, 2006). The similarity score generated by the algorithm is a measure of the percentage of matched branches between two compared trees and varies from 0 (branches completely unmatched) to 1 (branches completely matched) and is insensitive to the number of terminal nodes. This algorithm has been shown to be superior to other topological similarity metrics, including the ones that take branch length into account, when dendrogram topology is not highly similar (Kuhner & Yamato, 2015). Finally, I calculated the phylogenetic signal associated with each dendrogram (diet, isotopic ratios, morphological traits) using a method similar to the one described by Cachera and Le Loc'h (2017). More specifically, I generated a quantitative state for each tip of each dendrogram using Brownian simulations (value for ancestral state= 0, instantaneous variance= 0.1). I then tested the phylogenetic signal of these quantitative states using Abouheif's C_{mean} index (Abouheif, 1999), which performs better than other indexes under the Brownian motion (BM) model of evolution (Münkemüller *et al*., 2012). This procedure was repeated 10,000 times, generating a distribution of Abouheif's C_{mean} index values for each dendrogram. Abouheif's C_{mean} varies from -1, when no phylogenetic signal is detected, to 1, when the signal is complete. Because topological similarity and phylogenetic signal of tanglegrams do not control for potential effects of site-specificity, I also conducted these analyses for each site individually. Besides that, I standardized isotopic ratios (zero mean and unit variance) per site to account for potential differences in $\delta^{13}C$ and $\delta^{15}N$ enrichment between sites.

Concerns have been raised regarding the power of distance-based tests, such as (partial) Mantel, to detect correlations between datasets (Legendre & Fortin, 2010; Legendre *et al.*, 2015). I, therefore, conducted a complementary approach using canonical analyses to confirm results generated by partial Mantels. Canonical analysis has far greater statistical power than distance-based tests (Legendre & Fortin, 2010), but it requires a reasonable number of sampling units per variable to avoid data overfitting. In my dataset, the number of variables (e.g., 26 morphological traits) was high compared to the number of sampling units (i.e., 65 species). To overcome this limitation, I reduced the dimensionality of the predictor datasets using Principal Coordinates Analysis (PCoA). Phylogeny was considered a predictor of all datasets. Morphological trait data were set as a predictor of both dietary and isotopic data, and dietary data were set as the predictor of the isotopic data. I then selected the most relevant PCoA axes using scree plots. After evaluating scree plots for gradients produced from PCoA performed separately for phylogenetic, morphological and dietary similarity matrices, I selected 4 axes to describe phylogenetic relationships (cumulative variation explained = 94%), 14 axes for morphological traits (78%), and 10 axes for diet (63.4%).

Axes of each dataset were then correlated with the response data using Redundancy Analysis (RDA; isotopic ratios modeled by morphological traits, phylogeny, and diet) and Distance-Based Redundancy Analysis (db-RDA; diet modeled by morphological traits and phylogeny, and morphological traits modeled by phylogeny). In each case, I simplified the canonical models via forward selection based on permutation tests (10,000 randomizations) to include only significant explanatory variables (i.e., PCoA axes) in the models. Forward selection retained all four of the dominant phylogenetic axes for the phylogeny-morphological traits comparison; three phylogenetic axes for the phylogeny-diet comparison; the first two phylogenetic axes for the comparison of the phylogeny-isotopic ratios; six PCoA axes for the morphological traits-diet comparison; three PCoA axes for the morphological traits-isotopic ratios comparison; and five PCoA axes for the diet-isotopic ratios comparison.

After defining the best model for each comparison, I assessed the unique contribution of the explanatory dataset to a given response dataset by conditioning its effect by site (Caño Maraca or Caño Agua Fría Viejo; for more details about the method used, see Peres-Neto *et al.*, 2006). The significance of these contributions was assessed using an ANOVA-like permutation test for canonical analysis (Legendre & Legendre, 2012). Finally, I used the first two PCoA axes from the morphological data and the phylogenetic tree to construct a phylomorphospace plot, which is a projection of the phylogenetic tree into morphospace (represented by the first two PcoA axes). The tips of the tree were colored according to the species trophic groups, δ^{15}N, and δ^{13}C values to better visualize the link between phylogeny, morphology, and trophic ecology.

All analyses were conducted in R (R Core Team, 2019). Canonical analysis and (partial) Mantel tests were carried out in vegan (Oksanen *et al.*, 2019). Dendrograms, tanglegrams, and Nye’s topological comparisons were conducted in the packages stats (R Core Team, 2019), dendextend (Galili, 2015) and TreeSearch (Smith, 2018), respectively. Brownian motion simulations and phylomorphospace plots were carried in the package phytools (Revell, 2012), and the Abouheif's C_{mean} index was calculated in the package adephylo (Jombart *et al.*, 2010). Fish phylogeny was retrieved from the fishtree package (Chang *et al.*, 2019).

4.3. Results

4.3.1. Morphology-phylogeny association

Partial Mantel results indicated that the phylogenic similarity matrix was significantly associated with the morphological similarity matrix ($r= 0.19$, $p< 0.001$; Figure 4.3). Dendrograms based on phylogenetic and morphological data had the highest levels of topological similarity and phylogenetic signal (Table 4.1, 4.2). The partial db-RDA (conditioned by sites) also confirmed that phylogeny significantly influenced fish morphological traits ($F_{4,60}= 6.07$, $P< 0.001$, Adj. $R^2= 0.30$; Figure 4.3). Tanglagrams and phylomorphospace plots indicated that morphological traits are particularly conserved in Gymnotiformes (knifefishes) and Pleuronectiformes (flatfish) (Figure 4.4) with species presenting a distinct eel-like body shape with a long anal fin in the former and a flat body with strong asymmetry in the latter (Figure 4.5). A large proportion of Siluriformes (catfishes), Perciformes (perch-like fishes) and Characiformes (characins and their allies) also had relevant conservation of traits. Siluriformes, particularly loricariids and callichthyids (armored catfishes), were mainly associated with morphological adaptations to inhabit benthic environments (e.g., inferior mouths, depressed body shape) and feed on attached algae and detritus (long guts, unicuspid teeth) (Figure 4.4, 4.5). Perciformes, particularly cichlids, were characterized by deep body shapes with conspicuous fins (Figure 4.5). Characiformes, particularly the family Characidae, were mainly associated with fusiform body shapes and terminal mouths, typical of pelagic fishes, and multicuspid teeth (Figure 4.5).

Table 4.1 Topological similarity of the phylogenetic, morphological, dietary, and isotopic dendrograms. Dendrograms were created for all species combined (ALL), and also for species in each site individually (Caño Maraca and Caño Agua Fria Viejo). Topological similarity was calculated according to the algorithm proposed by Nye, Liò, and Gilks (2006) and each value is given in percentage (higher values indicate higher similarity). Phy= Phylogeny, Traits= Morphological traits, Iso= Stable isotope ratios. A comparison between the results of topological similarity, partial Mantel tests, and constrained ordination methods can be found in Figure 4.3.

Comparison	**All**	**Maraca**	**Agua Fria**
Phy vs Traits	0.33	0.24	0.11
Phy vs Diet	0.22	0.13	0.09
Phy vs Iso	0.18	0.12	0.07
Traits vs Diet	0.23	0.15	0.10
Traits vs Iso	0.17	0.13	0.09
Diet vs Iso	0.20	0.13	0.09

4.3.2. Association of phylogeny with diet and isotopes

According to partial Mantel analysis, the phylogenetic similarity matrix was not associated with neither the diet (r= 0.03, p= 0.12, Figure 4.3) nor isotopic similarity matrix (r= -0.03, p= 0.84, Figure 4.3). Phylogenetic dendrograms had intermediate scores for topological similarity with diet dendrograms and only low scores with isotopic dendrograms (Table 4.1). Despite some degree of overlap, the phylogenetic signal of the diet dendrogram was also weaker than the phylogenic signal of morphology, but stronger than the isotopic dendrogram (Table 4.2). The constrained ordinations also indicated that despite being significant (Phylogeny vs Diet: F2,62= 6.07, P= 0.002, Adj. R^2= 0.08; Phylogeny vs Isotopes: F2,62= 4.63, P= 0.005, Adj. R^2= 0.10), the association of phylogeny with diet and isotopic ratios were weaker than the association between phylogeny and morphological traits (Figure 4.3). Although some clades were consistently composed of the same trophic groups (for example, loricariids [Siluriformes] were mainly herbivores/detritivorous), most clades had species with multiple feeding strategies (Figure 4.4, 4.5). No strong gradient of neither δ13C nor δ15N were found along fish phylogeny, indicating that these elements are not effective to distinguished between different phylogenetic clades (Figure 4.6).

Table 4.2 Average phylogenetic signal associated with dendrograms created from morphological (traits), dietary, and isotopic datasets. Dendrograms were created for all species combined (ALL) and for species from a single site (Caño Maraca, Caño Agua Fria Viejo). The procedure used here is similar to the one described by Cachera and Le Loc'h (2017), where a quantitative state for each tip of each dendrogram is created using Brownian simulations (value for ancestral state= 0, instantaneous variance=0.1). I used the Abouheif's C_{mean} index (Abouheif, 1999) as my measured of phylogenetic signal. Abouheif's C_{mean} varies from -1, when no phylogenetic signal is detected, to 1, when the signal is complete. Values in parentheses are the 2.5% and 97.5% quantiles based on the variation associated with the Brownian simulations (10,000 times for each dendrogram). The distribution of Abouheif's C_{mean} values can be found in Figure C.4.

Dendrogram	**All**	**Maraca**	**Agua Fria**
Morphological traits	0.22 (-0.02, 0.47)	0.25 (-0.05, 0.56)	0.11 (-0.20, 0.45)
Diet	0.13 (-0.09, 0.38)	0.11 (-0.15, 0.43)	0.02 (-0.25, 0.33)
Isotopic ratios	0.04 (-0.14, 0.24)	0.03 (-0.18, 0.28)	-0.05 (-0.28, 0.22)

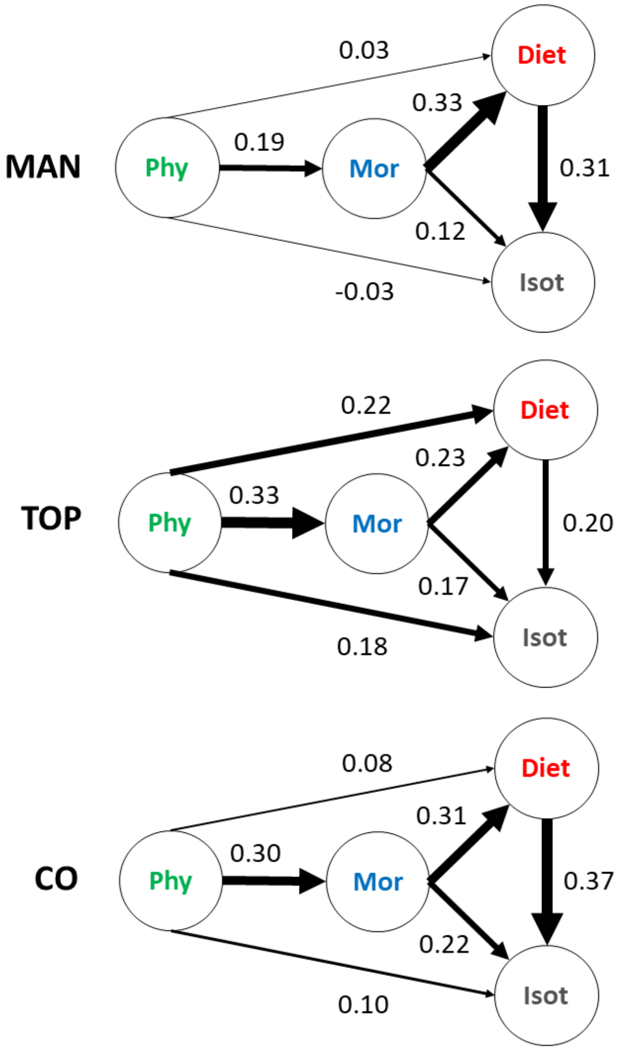

Figure 4.3 Pairwise relationships between phylogeny (Phy), morphological traits (Morpho), isotopic ratios (Isot) and diet based on three different approaches: partial Mantel (MAN), topological similarity (TOPO), and constrained ordinations (CO). Sites were used as co-variables for partial Mantel and constrained ordinations, but not for topological similarities (topological similarities calculated for each site individually can be found in Table 4.1). Arrows thickness are proportional to the association among datasets, which was assessed using Spearman's statistic in the partial Mantels, topological similarity based on the algorithm proposed by Nye, Liò, and Gilks (2006), and partial R^2 for constrained ordinations (RDA). The actual values of these statistics are also presented associated with each connecting arrow.

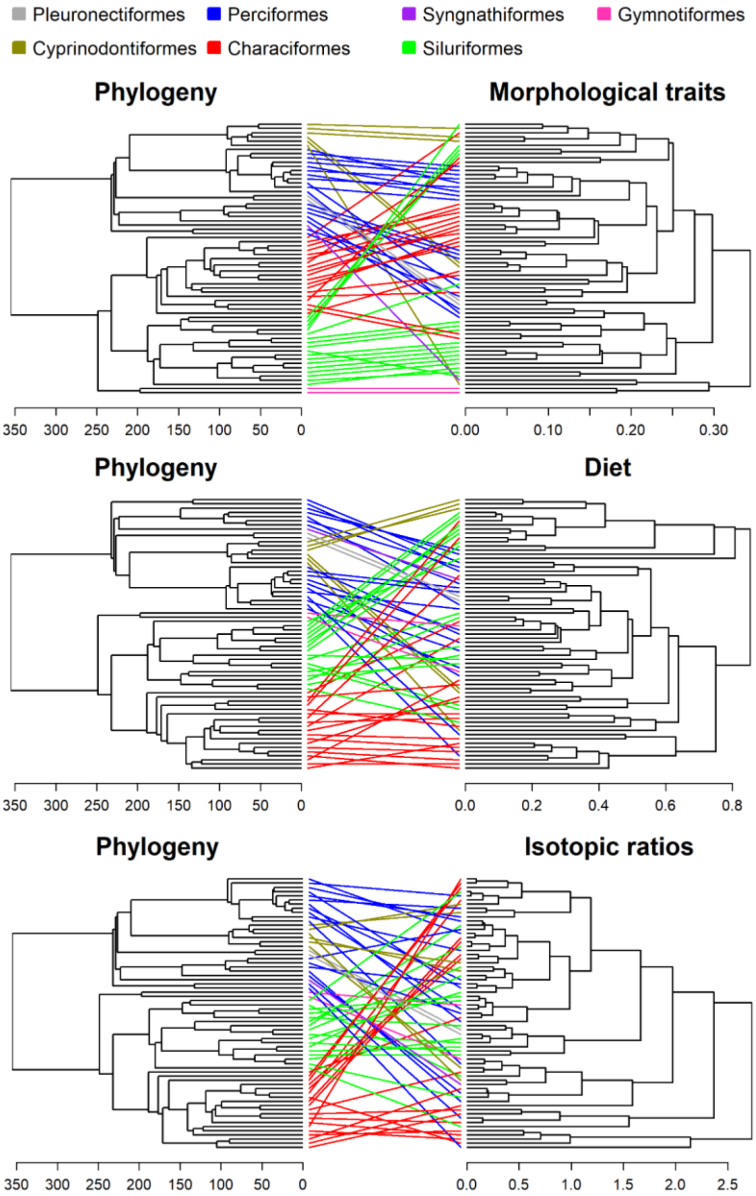

Figure 4.4 Pairwise relationships between phylogeny (Phy), morphological traits (Morpho), isotopic ratios (Isot) and diet based on three different approaches: partial Mantel (MAN), topological similarity (TOPO), and constrained ordinations (CO). Sites were used as co-variables for partial Mantel and constrained ordinations, but not for topological similarities (topological similarities calculated for each site individually can be found in Table 4.1). Arrows thickness are proportional to the association among datasets, which was assessed using Spearman’s statistic in the partial Mantels, topological similarity based on the algorithm proposed by Nye, Liò, and Gilks (2006), and partial R^2 for constrained ordinations (RDA). The actual values of these statistics are also presented associated with each connecting arrow.

4.3.3. Association of morphology with diet and isotopes

The partial Mantel results indicate that morphological similarity matrix was significantly associated with both diet ($r= 0.33$, $p= 0.001$; Figure 4.3) and isotopic similarity matrices ($r= 0.12$, $p= 0.03$; Figure 4.3), although the relationship was weaker for the latter. The morphological dendrogram had an intermediate score (0.22) for topological similarity with diet dendrograms (Table 4.1, Figure 4.3). This similarity score was a little stronger than the similarity score found between the morphological dendrogram and isotopic dendrograms (0.17; Table 4.1, Figure 4.3). Constrained ordinations also confirmed a significance association of morphological traits with diet ($F_{6,58}= 5.72$, $P< 0.001$, Adj. $R^2= 0.31$) and isotopic signatures ($F_{3,61}= 7.04$, $P< 0.001$, Adj. $R^2=0 .22$); the latter being stronger than the former (Figure 4.3). Associations between morphology and diet varied between trophic groups, being typically stronger for herbivores/detritivores (Figure 4.5, 4.7). However, the same pattern did not hold for the relationship between morphology and isotopic ratios, which was noisier (Fig 4.6 and 4.7).

4.3.4. Diet and isotopes association

According to the partial Mantel, diet and isotopic similarity matrices were significantly correlated ($r= 0.31$, $p= 0.001$; Figure 4.3). Partial RDA analysis also indicated that the diet and isotope relationship was significant ($F_{5,59}= 8.06$, $P< 0.001$, Adj. $R^2= 0.37$) and the strongest association among the datasets (Figure 4.3). Isotopic dendrograms and diet dendrograms had intermediate topological similarity scores (except for the analysis that included only species from Caño Agua Fría Viejo, which had low scores; Table 4.1, Figure 4.7). $\delta^{15}N$ was mainly associated with trophic level, being lower for herbivores/detritivores and higher for omnivores 2 and piscivores (Figure 4.6). $\delta^{13}C$ was lower for herbivores/detritivores when compared to all other trophic groups (Figure 4.6).

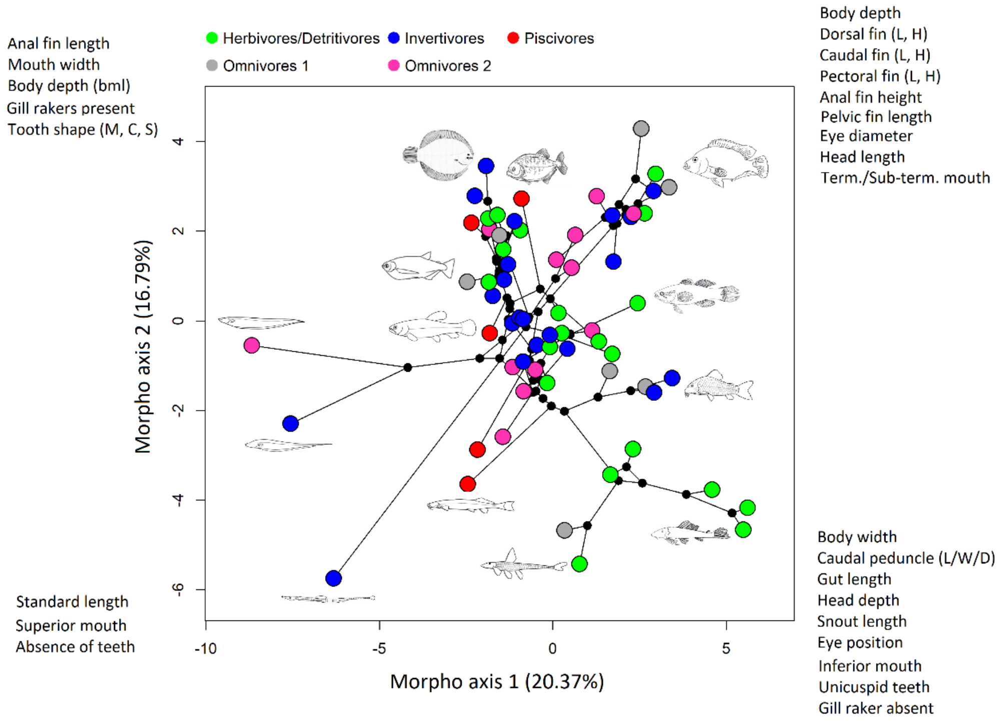

Figure 4.5 Projection of the phylogenetic tree into morphospace, which is represented by the first two axes of the Principal Coordinate Analysis (PCoA). Tree internal nodes are represented by small black dots. Tips of the tree are colored according to species trophic group based on diet analysis. Morphological traits associated with each side of the morphological space are also shown. L=Length, W=Width, D=Depth, H=Height, bml=Below middle line, M=Multicuspid, C=Conical, S=Serrated triangular.

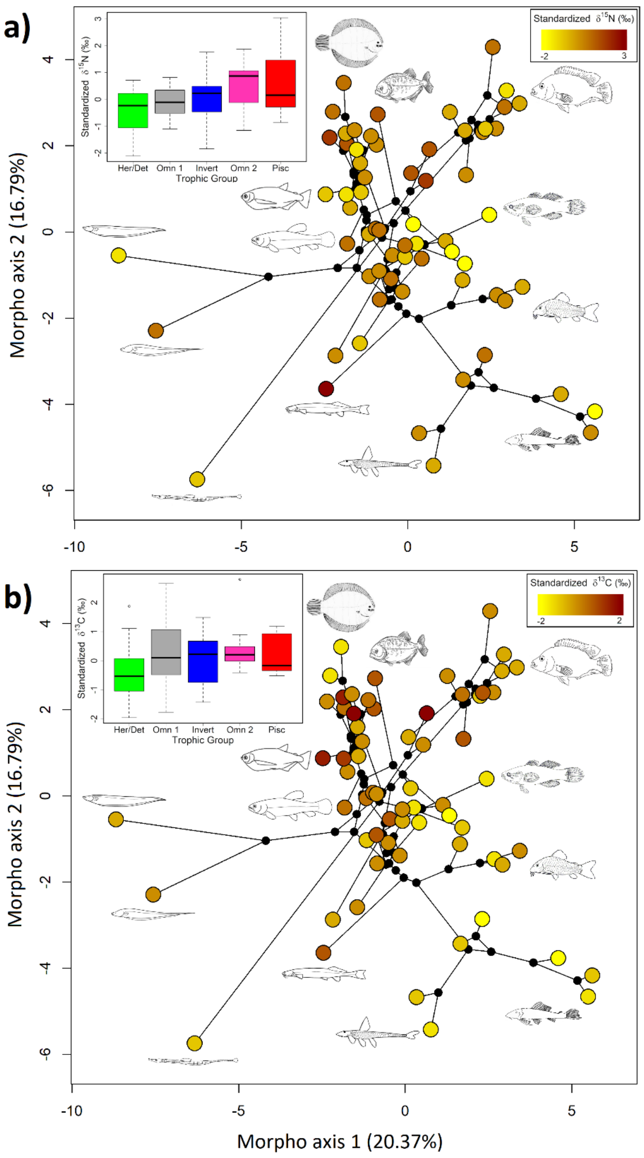

Figure 4.6 Projection of the phylogenetic tree into morphospace, which is represented by the first two axes of the Principal Coordinate Analysis (PCoA). Tree internal nodes are represented by small black dots. Tips of the tree (species) are colored according to its signature of either δ^{15}N (a) or δ^{13}C (b). Box plots showing variation of δ^{15}N (a) and δ^{13}C (b) across different trophic groups can be found in the superior left corner of each panel.

4.3.5. Sites differences

Site similarity was moderately associated with phylogenetic relatedness ($r = 0.39$, $p < 0.001$), weakly associated with diet ($r = 0.07$, $p = 0.03$) and isotopic ratios similarity ($r = 0.07$, $p = 0.04$), and not significantly associated with morphological traits similarity ($r = 0.02$, $p = 0.26$). Overall, topological similarity and phylogenetic signal conducted for each site individually generated similar patterns (e.g., phylogenetic signal was stronger in morphological traits than in diet and isotopic ratios) compared to the results of analysis conducted with both sites together (Table 4.1, 4.2; Figure C.3). However, the magnitude of correlations values and phylogenetic signals was typically higher in Caño Maraca than in Caño Água Fria Viejo (Table 4.1, 4.2).

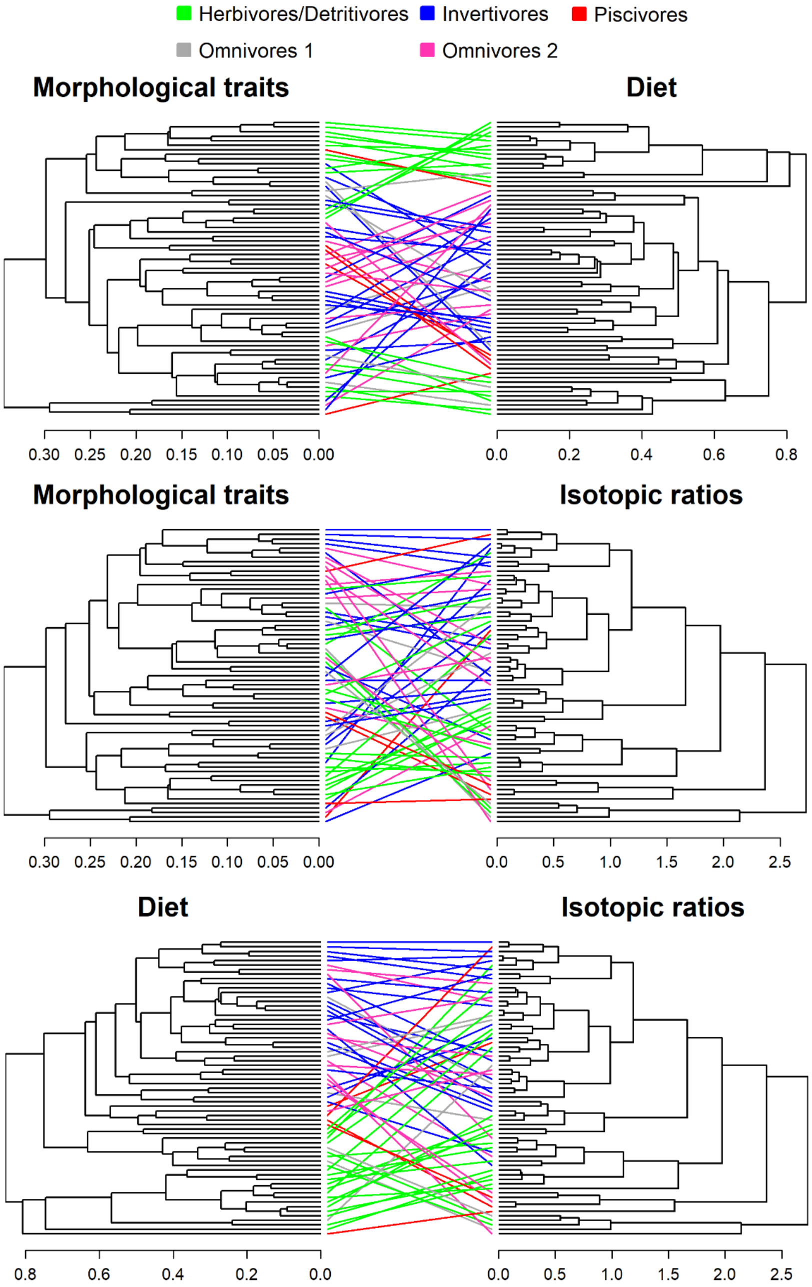

Figure 4.7 Tanglegrams constructed for pairwise comparisons between morphological traits and diet, morphological traits and isotopic ratios, and diet and isotopic ratios dendrograms. Dendograms were constructured using the UPGMA algorithm and using species of all sites combined. I used an untangle function (algorithm step2side) to improve the visualization of the tanglegrams. Colors represent different trophic groups. Tanglegrams constructed for each site separately can be found in Figure C.3.

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4.4. Discussion

Morphological traits of both tropical freshwater fish assemblages revealed a significant phylogenetic signal, corroborating my first hypothesis. Both phylogeny and morphological traits were associated with fish diets and isotopic ratios; however, morphological traits were stronger predictors of dietary and isotopic ratios than phylogenetic relationships, corroborating my second and third hypotheses. Diet and isotopic ratios were significantly correlated, indicating that species with similar isotopic ratios tend to have relatively high dietary overlap (hypothesis 4). Together, these findings lend some support for approaches in community ecology that rely on species traits to infer niche relationships (e.g., Kraft *et al.*, 2008; Côte *et al.*, 2019). However, high levels of unexplained variation in dietary and stable isotopic ratio data (>60%) suggest caution is warranted when interpreting patterns of community structure based on phylogenetic and morphological data. Although part of this variation may be caused by my methodology (e.g., body and sample size differences between datasets, preservation effects on isotopic ratios), morphology and phylogeny nonetheless may provide a blurred view of species niche relationships. This imprecision could limit their usefulness as proxies in certain kinds of studies that require high precision, such as those aiming to distinguish community assembly processes (Gerhold *et al*., 2015); however, morphological traits and phylogenetic relationships should be useful in macroecological studies, such as those exploring trophic diversification (Winemiller *et al.*, 1995; López-Fernández *et al*., 2012).

The significant phylogenetic signal for morphological traits indicates that closely related species are more morphologically similar than expected at random (Blomberg & Garland, 2002). Associations between phylogeny and morphological traits are expected under a random walk model of evolution (i.e., Brownian motion) that assumes changes are gradual and random due to either genetic drift or random fluctuations in natural selection (Losos, 2008). Other factors, including strong stabilizing selection and genetic constraints associated with pleiotropy, could promote conservatism in trait evolution (Wiens & Graham, 2005). However, I highlight that my method for assessing phylogenetic signal integrated multiple morphological traits, some of which could have evolved in response to different sources of selection (Cadotte *et al.*, 2017). Patterns of evolution for multiple-traits are often well described by Brownian motion models (Cooper & Purvis, 2010; Cadotte *et al.*, 2017), and, therefore, phylogenetic relationships could be particularly useful to predict general patterns of ecological similarity and function among species assemblages or taxa (Cavender-Bares *et al.*, 2009; Mouquet *et al.*, 2012).

Predicting community processes based on functional traits has been considered the "Holy Grail" in ecology (Lavorel & Garnier, 2002). My results indicated that morphological traits known to influence swimming and feeding performance can serve as proxies for the trophic ecology of freshwater fish. However, morphological traits only explained a moderate fraction of fish dietary variation (coefficient of determination and correlations between 0.12 and 0.33, depending on the method used). Multiple morphological traits may have redundant functions for feeding (Wainwright *et al*., 2005;

Zelditch *et al*., 2017), which would explain the limited predictive power of morphological traits in my study. Although not investigated in this study, individual feeding also could have influenced dietary patterns among species in my study and reduced the importance of species-averaged morphology as a valid proxy for trophic interactions. Specialized feeding by individuals has been shown in several fish species, but little is known about intraspecific variation in trophic niches (Bolnick *et al*., 2003, 2011). Moreover, many fish species have broad diets and display high levels of omnivory (Winemiller, 1990). Predator switching and broad trophic niches may be common in seasonal ecosystems that experience major fluctuations in abiotic conditions and resources availability (McMeans *et al*., 2015). Here, I restricted my analysis to periods when water levels were low (dry and transition periods), fish densities were high, aquatic resources were depleted, and diet breadth and interspecific diet overlap tended to be low (Winemiller, 1989; Peterson *et al*., 2017). Therefore, it is likely that the correlation between morphological traits and diets might have been even lower if we had considered a longer time interval that included all phases of the tropical hydrologic cycle. In this sense, inferences about species niches based only on morphological traits should be made with caution, with the acknowledgment that ecological performance depends on environmental conditions that vary in space and time (Kraft *et al*., 2015; Cadotte *et al*., 2019).

Diet was more strongly correlated with morphological traits than phylogeny, suggesting that morphological traits are the better predictor of trophic interactions. Indeed, partial Mantel analysis even indicated that the association of phylogeny with diets and isotopic ratios was not significant. Morphological traits are usually a stronger predictor of diet data than phylogeny because selective pressures can drive species from different clades to converge on similar phenotypes, allowing them to exploit similar resources (Grant *et al.*, 2004; Winemiller *et al*., 2015). Conversely, closely related species may undergo character displacement as a result of interspecific competition within areas of sympatry, or they may adapt to exploit different resources under different environmental conditions (Brown & Wilson, 1956; Schluter, 2000). Trophic diversification is observed in many freshwater fish families. For example, some Neotropical cichlids are specialized piscivores (*Cichla* spp.), others invertivores (*Aequidens* spp., *Geophagus* spp.), and others herbivores (*Uaru amphiacanthoides*). Interestingly, herbivory and detritivory, which require specialized gut morphology and physiology (e.g., long guts for longer passage time and enhanced nutritional absorption; Horn, 1989), occur in fishes from very different lineages, including poecilids, loricariids, callichthyids, prochilodontids, and curimatids. The weak association between phylogeny and diet might derive, in part, from the inclusion of neutral genetic sequences unrelated to natural selection during phylogenetic tree construction (Cadotte *et al.*, 2019). In any event, my results suggest that conclusions about species niches and community functional structure based on phylogenetic relationships alone can be misleading, a position argued by others (Mayfield & Levine, 2010; Gerhold *et al*., 2015).

Diet was significantly correlated with stable isotope ratios, likely reflecting differences in δ^{13}C of basal resources in food chains supporting consumers with various trophic niches, and trophic fractionation of δ^{15}N indicating vertical trophic positions

(Fry, 2006; Layman *et al*., 2012). The correlation between fish diet and stable isotope ratios was stronger than between morphological traits and isotopic ratios or between phylogeny and isotopic ratios. This indicates that error associated with inferred trophic isotopic enrichment, environmental influences on isotopic signatures of basal sources, effects of body size and metabolism on consumer isotopic ratios, and other factors is not large enough to completely degrade the signal revealing community trophic structure provided by isotopic ratios. On the other hand, morphology and phylogeny were usually more related to diet data than with isotopic ratios, probably reflecting the indirect relationship among trophic niche and stable isotopes (Caut *et al*., 2009). For example, many loricariid catfishes (Siluriformes) have diets dominated by detritus, algae, and micro-invertebrates, whereas soles (Pleuronectiformes: Achiridae) feed on both micro- and macro-invertebrates. These dietary patterns were completely lost in dendrograms based on stable isotope ratios. Without knowing the isotopic ratios of the basal resources, it is difficult to determine why some species associations were lost. The use of stable isotope ratios to infer trophic relationships can lead to misleading conclusions if variation in isotopic ratios of the basal resources in food chains supporting consumer biomass is not taken into account (Hoeinghaus & Zeug, 2008; Layman *et al*., 2012). In this sense, stable isotope ratios should be considered a complement rather than a substitute for diet data (Davis *et al*., 2012). Stable isotope ratios have the advantage of integrating assimilation of consumed items over time (i.e., several weeks to months depending on tissue type), provided that food resources have sufficiently distinct isotopic ratios (Layman *et al*., 2012). Dietary analysis provides much greater resolution of trophic niches, but the method merely provides a snapshot of items ingested prior to the organism's capture (e.g., Winemiller, 1990). Combined analysis of dietary and isotopic data can better reveal trophic patterns at the level of the individual organism, community, or taxon (Costa-Pereira *et al*., 2018).

Stable isotope ratios analyzed in my study were obtained from preserved specimens collected more than three decades ago. Prior research has shown that $\delta^{15}N$ tends to be slightly elevated and $\delta^{13}C$ is slightly lower in fish muscle tissue following fixation in formalin and storage in ethanol (Arrington & Winemiller, 2002; Edwards *et al.*, 2002; Sarakinos *et al.*, 2002; Kishe-Machumu *et al*., 2017). Given the relatively minor and consistent isotopic changes observed for preserved fish tissues, it has been proposed that archived specimens can provide a reliable data source for isotopic analysis aimed at revealing long-term trends (Edwards *et al.*, 2002; Sarakinos *et al.*, 2002). I found strong correlations between isotopic and dietary data, moderate correlations between isotopic and morphological data, and weak correlations between isotopic and phylogenetic data. These results further emphasize the importance of scientific collections for food web research. Millions of preserved specimens are housed in natural history collections worldwide, and these could be used to address many ecological questions using stable isotope analysis (Meineke *et al*., 2019). This archived material could advance research on topics ranging from food web ecology to community trophic structure and long-term changes associated with environmental impacts and climate change (Sarakinos *et al.*, 2002; Kishe-Machumu *et al*., 2017; Schmitt *et al*., 2018).

Species composition and their respective phylogenetic lineages differed between the studied sites. This mainly reflects the isolation and the geological history of the regions where Caño Maraca and Caño Agua Fría Viejo are located (South America and Central America, respectively). Not surprisingly, my analysis indicated that diets and isotopic signatures varied between sites. Phylogenetic signals and patterns of correlation between the different datasets (e.g., diet, morphology) were similar between sites, but values were usually lower for Caño Agua Fría Viejo when compared to analyses conducted for Caño Maraca or with both sites together. These differences could be caused by the low statistical power of my analysis due to a small sample size for Caño Agua Fria Viejo. Because it had more species, Caño Maraca might have contributed more to phylogenetic signal and topological similarity when both sites together. Alternatively, differences in the degree of longitudinal hydrological connectivity and dispersal or environmental fluctuation could have contributed to lower correlations and phylogenetic signal for Caño Agua Fria Viejo. Caño Agua Fría Viejo is located about 10 km from the Caribbean Sea (Winemiller, 1990), and its fish assemblage is open to invasion by estuarine and marine species. Caño Maraca is located further inland within the Orinoco Basin and has more extreme hydrological variation that creates harsh environmental conditions during the dry season (Winemiller, 1990). Seasonal reduction in habitat availability and quality generally reduces niche breadth and interspecific diet overlap (Winemiller, 1989; Winemiller & Pianka, 1990; Peterson *et al*., 2017), which might strengthen the association between morphology and diet. To investigate these possibilities, future studies exploring relationships between phylogeny, morphological traits, and trophic niche should include more locations and zoogeographic regions that span gradients fluvial connectivity and environmental conditions, including temporal variation.

Ecologists frequently use either phylogenetic or morphological similarity as a proxy for ecological similarity (Morales-Castilla *et al*., 2015). However, few studies have tested these assumed relationships, and this may be due to the great effort required to obtain sufficient empirical data for large numbers of species (Silva *et al*., 2019). My analysis of phylogenetic, morphological, dietary and isotopic data for diverse tropical fish assemblages showed that morphological traits had moderate correlations with diet and weak correlations with stable isotope ratios, whereas phylogeny had weak correlations with both dietary and isotopic data. With recent advances in genomics, phylogenetics and functional morphology as well as the compilation of associated data into public digital databases, phylogenetic and functional trait data are becoming more easily available. Despite these advantages, there are important factors that limit the use of phylogeny and morphological traits to infer niche relationships (Gerhold *et al*., 2015; Cadotte *et al.*, 2017, 2019; Funk *et al*., 2017). To enhance understanding of community assembly and ecological diversification, future research should further explore methods that integrate phylogeny, morphology and chemical tracers (e.g., bulk stable isotope ratios, amino-acid-specific stable isotope ratios, fatty acid signatures) for analysis of trophic ecology.

4.5. References

Abouheif E. 1999. A method for testing the assumption of phylogenetic independence in comparative data. *Evolutionary Ecology Research*, 1, 895–909.

Araújo M.S., Bolnick D.I., Machado G., Giaretta A.A. & dos Reis S.F. (2007) Using d 13 C stable isotopes to quantify individual-level diet variation. *Oecologia*, 152, 643–654. https://doi.org/10.1007/s00442-007-0687-1

Araújo M.S., Bolnick D.I., Martinelli L.A., Giaretta A.A. & Dos Reis S.F. (2009) Individual-level diet variation in four species of Brazilian frogs. *Journal of Animal Ecology*, 78, 848–856. https://doi.org/10.1111/j.1365-2656.2009.01546.x

Arrington D.A. & Winemiller K.O. (2002) Preservation effects on stable isotope analysis of fish muscle. *Transactions of the American Fisheries Society*, 131, 337–342. https://doi.org/10.1577/1548-8659(2002)131<0337:PEOSIA>2.0.CO;2

Arrington D.A., Winemiller K.O., Loftus W.F. & Akin, S. 2002. How often do fishes “run on empty”? *Ecology*, 83, 2145–2151. https://doi.org/10.1890/0012-9658(2002)083[2145:HODFRO]2.0.CO;2

Bastos R.F., Corrêa F., Winemiller K.O. & Garcia A.M. (2017) Are you what you eat? Effects of trophic discrimination factors on estimates of food assimilation and trophic position with a new estimation method. *Ecological Indicators*, 75, 234–241. https://doi.org/10.1016/j.ecolind.2016.12.007

Bell G. (2001) Neutral macroecology. *Science*, 293, 2413–2418. https://doi.org/10.1126/science.293.5539.2413

Bellwood D.R., Wainwright P.C., Fulton C.J. & Hoey A.S. (2006) Functional versatility supports coral reef biodiversity. *Proceedings of the Royal Society B*, 273, 101-107. https://doi.org/10.1098/rspb.2005.3276

Berlow E.L., Navarrete S.A., Briggs C.J., Power M.E. & Menge B.A. (1999) Quantifying variation in the strengths of species interactions. *Ecology*, 80, 2206-2224. https://doi.org/10.1890/0012-9658(1999)080[2206:QVITSO]2.0.CO;2

Blomberg S.P. & Garland T. (2002) Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. *Journal of Evolutionary Biology*, 15, 899–910. https://doi.org/10.1046/j.1420-9101.2002.00472.x

Blomberg S.P., Garland Jr.T. & Ives A.R. (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more mobile. *Evolution*, 57, 717–745. https://doi.org/10.1111/j.0014-3820.2003.tb00285.x

Bolnick D.I., Amarasekare P., Araújo M.S., Bürger R. Levine J.M., Novak M., Rudolf V.H.W., Schreiber S.J., Urban M.C. & Vasseur D.A. (2011) Why intraspecific trait variation matters in community ecology. *Trend in Ecology and Evolution*, 26, 183–192. https://doi.org/10.1016/j.tree.2011.01.009

Bolnick D.I., Svanbäck R., Fordyce J.A., Yang L.H., Davis J.M., Hulsey C.D. & Forister M.L. (2003) The ecology of individuals: incidence and implications of individual specialization. *American Naturalist*, 161, 1–28. https://doi.org/10.1086/343878

Bower L.M. & Winemiller K.O. (2019) Fish assemblage convergence along stream environmental gradients: an intercontinental analysis. *Ecography*, 42, 1691–1702. https://doi.org/10.1111/ecog.04690

Brown W.L. & Wilson E.O. (1956) Character displacement. *Systematic Zoology*, 5, 49–

64. https://doi.org/10.2307/2411924

Cachera M. & Le Loc'h F. (2017) Assessing the relationships between phylogenetic and functional singularities in sharks (Chondrichthyes). *Ecology and Evolution*, 7, 6292–6303. https://doi.org/10.1002/ece3.2871

Cadotte M.W., Carboni M., Si X. & Tatsumi S. (2019) Do traits and phylogeny support congruent community diversity patterns and assembly inferences? *Journal of Ecology*, 107, 2065–2077. https://doi.org/10.1111/1365-2745.13247

Cadotte M.W., Davies T.J. & Peres-Neto P.R. (2017) Why phylogenies do not always predict ecological differences. *Ecological Monographs*, 87, 535–551. https://doi.org/10.1002/ecm.1267

Caut S., Angulo E. & Courchamp F. (2009) Variation in discrimination factors (Δ15N and Δ13C): the effect of diet isotopic values and applications for diet reconstruction. *Journal of Applied Ecology*, 46, 443–453. https://doi.org/10.1111/j.1365-2664.2009.01620.x

Cavender-Bares J., Kozak K.H., Fine P.V.A. & Kembel S.W. (2009) The merging of community ecology and phylogenetic biology. *Ecology Letters*, 12, 693–715. https://doi.org/10.1111/j.1461-0248.2009.01314.x

Chang J., Rabosky D.L., Smith S.A. & Alfaro M.E. (2019) An R package and online resource for macroevolutionary studies using the ray-finned fish tree of life. *Methods in Ecology and Evolution*, 10, 1118–1124. https://doi.org/10.1111/2041-210x.13182

Chesson P.L. & Warner R.R. (1981) Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist*, 117, 923–943. https://doi.org/10.1086/283778

Cooper N. & Purvis A. (2010) Body size evolution in mammals: complexity in tempo and mode. *The American Naturalist*, 175, 727–738. https://doi.org/10.1086/652466

Cooper N., Rodríguez J. & Purvis A. (2008) A common tendency for phylogenetic overdispersion in mammalian assemblages. *Proceedings of the Royal Society B*, 275, 2031–2037. https://doi.org/10.1098/rspb.2008.0420

Costa-Pereira R., Rudolf V.H.W., Souza F.L. & Araújo M.S. (2018) Drivers of individual niche variation in coexisting species. *Journal of Animal Ecology*, 87, 1452–1464. https://doi.org/10.1111/1365-2656.12879

Côte J., Kuczynski L. & Grenouillet G. (2019) Spatial patterns and determinants of trait dispersion in freshwater fish assemblages across Europe. *Global Ecology and Biogeography*, 28, 826–838. https://doi.org/10.1111/geb.12896

Davis A.M., Blanchette M.L., Pusey B.J., Jardine T.D. & Pearson R.G. (2012) Gut content and stable isotope analyses provide complementary understanding of ontogenetic dietary shifts and trophic relationships among fishes in a tropical river. *Freshwater Biology*, 57, 2156–2172. https://doi.org/10.1111/j.1365-2427.2012.02858.x

Dietz E.J. (1983) Permutation tests for association between two distance matrices. *Systematic Zoology*, 32, 21–26. https://doi.org/10.1093/sysbio/32.1.21

Edwards M.S., Turner T.F. & Sharp Z.D. (2002) Short- and long-term effects of fixation and preservation on stable isotope values (δ13 C, δ15 N, δ34 S) of fluid-preserved museum specimens. *Copeia*, 2002, 1106–1112. https://doi.org/10.1643/0045-8511(2002)002[1106:SALTEO]2.0.CO;2

English P.A., Green D.J. & Nocera J.J. (2018) Stable isotopes from museum specimens may provide evidence of long-term change in the trophic ecology of a migratory aerial insectivore. *Frontiers in Ecology and Evolution*, 6, 14. https://doi.org/10.3389/fevo.2018.00014

Fraser D., Haupt R.J. & Barr W.A. (2018) Phylogenetic signal in tooth wear dietary niche proxies. *Ecology and Evolution*, 8, 5355–5368. https://doi.org/10.1002/ece3.4052

Freckleton R.P., Harvey P.H. & Pagel M. (2002) Phylogenetic analysis and comparative data: a test and review of evidence. *The American Naturalist*, 160, 712–726. https://doi.org/10.1086/343873

Fry B. (2006) *Stable isotope ecology*. Springer–Verlag, New York.

Funk J.L., Larson J.E., Ames G.M., Butterfield B.J., Cavender-Bares J., Firn J., Laughlin D.C., Sutton-Grier A.E., Williams L. & Wright J. (2017) Revisiting the Holy Grail: using plant functional traits to understand ecological processes. *Biological Reviews*, 92, 1156–1173. https://doi.org/10.1111/brv.12275

Galili T. (2015) dendextend: an R package for visualizing, adjusting and comparing trees of hierarchical clustering. *Bioinformatics*, 31, 3718–3720. https://doi.org/10.1093/bioinformatics/btv428

Gatz A.J.J. (1979) Community organization in fishes as indicated by morphological features. *Ecology*, 60, 711–718. https://doi.org/10.2307/1936608

Gerhold P., Cahill J.F., Winter M., Bartish I.V. & Prinzing A. (2015) Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Functional Ecology*, 29, 600–614. https://doi.org/10.1111/1365-2435.12425

Grant P.R., Grant B.R., Markert J.A., Keller L.F. & Petren K. (2004) Convergent evolution of Darwin ' s finches caused by introgressive hybridization and selection. *Evolution*, 58, 1588–1599. https://doi.org/10.1111/j.0014-3820.2004.tb01738.x

Greenwood P.H. (1989) *Ontogeny and evolution: saltatory or otherwise?* In: Brutton M. (ed.) Alternative life-history styles of animals. Kluwer Academic, Dordrecht. pp 245–259.

Harrison P.M., Gutowsky L.F.G., Martins E.G., Ward T.D., Patterson D.A., Cooke S.J & Power M. 2017. Individual isotopic specializations predict subsequent inter-individual variation in movement in a freshwater fish. *Ecology*, 98, 608–615. https://doi.org/10.1002/ecy.1681

HilleRisLambers J., Adler P.B., Harpole W.S., Levine J.M. & Mayfield M.M. (2012) Rethinking community assembly through the lens of coexistence theory. *Annual Review of Ecology, Evolution, and Systematics*, 43, 227–248. https://doi.org/10.1146/annurev-ecolsys-110411-160411

Hoeinghaus D.J. & Zeug S.C. (2008) Can stable isotope ratios provide for community-wide measures of trophic structure? Comment. *Ecology*, 89, 2353–2357. https://doi.org/10.1890/07-1143.1

Hopkins III J.B. & Kurle C.M. (2016) Measuring the realized niches of animals using stable isotopes: from rats to bears. *Methods in Ecology and Evolution*, 7, 210–221.

https://doi.org/10.1111/2041-210X.12446

Horn M.H. (1989) Biology of marine herbivorous fishes. *Oceanography and Marine Biology: An Annual Review*, 27, 167–272.

Hubbell S.P. (2001) *A unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton.

Hyslop E.J. (1980) Stomach contents analysis - A review of methods and their application. *Journal of Fish Biology*, 17, 411–429. https://doi.org/10.1111/j.1095-8649.1980.tb02775.x

Jombart T., Balloux F. & Dray S. (2010) adephylo: new tools for investigating the phylogenetic signal in biological traits. *Bioinformatics*, 26, 1907–1909. https://doi.org/10.1093/bioinformatics/btq292

Jordano P. (2016) Chasing ecological interactions. *PLOS Biology*, 14, e1002559. https://doi.org/10.1371/journal.pbio.1002559

Jung T.S., Stotyn S.A. & Czetwertynski S.M. (2015) Dietary overlap and potential competition in a dynamic ungulate community in Northwestern Canada. *The Journal of Wildlife Management*, 79, 1277–1285. https://doi.org/10.1002/jwmg.946

Kamilar J.M. & Cooper N. (2013) Phylogenetic singal in primate behaviour, ecology and life history. *Philosophical Transactions of the Royal Society B*, 368, 20120341. https://doi.org/10.1098/rstb.2012.0341

Keppeler F.W., Lanés L.E.K., Rolon A.S., Stenert C., Lehmann P., Reichard M. & Maltchik L. (2015) The morphology – diet relationship and its role in the coexistence of two species of annual fishes. Ecology of Freshwater Fish, 24, 77–

90. https://doi.org/10.1111/eff.12127

Kishe-Machumu M.A., van Rijssel J.C., Poste A., Hecky R.E. & Witte F. (2017) Stable isotope evidence from formalin–ethanol-preserved specimens indicates dietary shifts and increasing diet overlap in Lake Victoria cichlids. *Hydrobiologia*, 791, 155–173. https://doi.org/10.1007/s10750-016-2925-1

Kraft N.J.B., Godoy O. & Levine J.M. (2015) Plant functional traits and the multidimensional nature of species coexistence. *Proceedings of the National Academy of Sciences of the United States of America*, 112, 797–802. https://doi.org/10.1073/pnas.1413650112

Kraft N.J.B., Valencia R. & Ackerly D.D. (2008) Tree community assembly in an Amazonian forest. *Science*, 322, 580–582. https://doi.org/10.1126/science.1160662

Kuhner M.K. & Yamato J. (2015) Practical performance of tree comparison metrics. *Systematic Biology*, 64, 205–214. https://doi.org/10.1093/sysbio/syu085

Lavorel S. & Garnier E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology*, 16, 545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Layman C.A., Araujo M.S., Boucek R., Hammerschlag-Peyer C.M., Harrison E., Jud Z.R., Matich P., Rosenblatt A.E., Vaudo J.J. & Yeager L.A. (2012) Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biological Reviews*, 87, 545–562. https://doi.org/10.1111/j.1469-185X.2011.00208.x

Layman C.A., Arrington D.A., Montaña C.G. & Post D.M. (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology*, 88, 42–

48. https://doi.org/10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO;2

Legendre P. & Fortin M.J. (2010) Comparison of the Mantel test and alternative approaches for detecting complex multivariate relationships in the spatial analysis of genetic data. *Molecular Ecology Resources*, 10, 831–844. https://doi.org/10.1111/j.1755-0998.2010.02866.x

Legendre P., Fortin M.J. & Borcard D. (2015) Should the Mantel test be used in spatial analysis? *Methods in Ecology and Evolution*, 6, 1239–1247. https://doi.org/10.1111/2041-210X.12425

Legendre P. & Legendre L. (2012) *Numerical ecology*. Elsevier, Amsterdam.

Liem K.F. (1978) Modulatory multiplicity in the functional repertoire of the feeding mechanism in cichlid fishes. *Journal of Morphology*, 158, 323–360. https://doi.org/10.1002/jmor.1051580305

Lind E.M., Vincent J.B., Weiblen G.D., Cavender-Bares J. & Borer E.T. (2015) Trophic phylogenetics: Evolutionary influences on body size, feeding, and species associations in grassland arthropods. *Ecology*, 96, 998–1009. https://doi.org/10.1890/14-0784.1

Losos J.B. (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters*, 11, 995–1003. https://doi.org/10.1111/j.1461-0248.2008.01229.x

López-Fernández H., Winemiller K.O., Montaña C. & Honeycutt R.L. (2012) Diet-morphology correlations in the radiation of South American geophagine cichlids

(Perciformes: Cichlidae: Cichlinae). *PLoS One*, 7, e33997. https://doi.org/10.1371/journal.pone.0033997

Mantel N. (1967) The detection of disease clustering and a generalized regression approach. *Cancer Research*, 27, 209–220.

Mayfield M.M. & Levine J.M. (2010) Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, 13, 1085–1093. https://doi.org/10.1111/j.1461-0248.2010.01509.x

Mayr E. (1984) *Evolution of fish species flocks: A commentary*. In: Echelle A.A. & Kornfield I. (eds) Evolution of fish species flocks. University of Maine Press, Orono. pp 3–12

McGill B.J., Enquist B.J., Weiher E. & Westoby M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21, 178–185. https://doi.org/10.1016/j.tree.2006.02.002

McMeans B.C., Mccann K.S., Humphries M., Rooney N. & Fisk A.T. (2015) Food web structure in ecosystems. *Trends in Ecology & Evolution*, 30, 662–672. https://doi.org/10.1016/j.tree.2015.09.001

Meineke E.K., Davies T.J., Daru B.H. & Davis C.C. (2019) Biological collections for understanding biodiversity in the Anthropocene. *Philosophical Transactions of the Royal Society B*, 374, 20170386. https://doi.org/10.1098/rstb.2017.0386

Montaña C.G. & Winemiller K.O. (2013) Evolutionary convergence in Neotropical cichlids and Nearctic centrarchids: evidence from morphology, diet, and stable isotope analysis. *Biological Journal of the Linnean Society*, 109, 146–164.

https://doi.org/10.1111/bij.12021

Morales-Castilla I., Matias M.G., Gravel D. & Araújo M.B. (2015) Inferring biotic interactions from proxies. *Trends in Ecology & Evolution*, 30, 347–356. https://doi.org/10.1016/j.tree.2015.03.014

Mouquet N., Devictor V., Meynard C.N., Munoz F., Bersier L-F., Chave J., Couteron P., Dalecky A., Fontaine C., Gravel D., Hardy O.J., Jabot F., Lavergne S., Leibold M., Mouillot D., Münkemüller T., Pavoine S., Prinzing A., Rodrigues A.S.L., Rohr R.P.,Thébault E. & Thuiller W. (2012) Ecophylogenetics: advances and perspectives. *Biological Reviews,* 87, 769–785. https://doi.org/10.1111/j.1469-185X.2012.00224.x

Mouchet M. & Mason N.W.H. (2008) Towards a consensus for calculating dendrogram-based functional diversity indices. *Oikos*, 117, 794–800. https://doi.org/10.1111/j.0030-1299.2008.16594.x

Münkemüller T., Lavergne S., Bzeznik B., Dray S., Jombart T., Schiffers K. & Thuiller W. (2012) How to measure and test phylogenetic signal. *Methods in Ecology and Evolution*, 3, 743–756. https://doi.org/10.1111/j.2041-210X.2012.00196.x

Murdoch W.W. (1969) Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecological Monographs*, 39, 335–354. https://doi.org/10.2307/1942352

Nanthavong K., Harrison R.D., Millet J., Heinimann A. & Satdichanh M. (2015) Using plant functional traits and phylogenies to understand patterns of plant community assembly in a seasonal tropical forest in Lao PDR. *PLoS One*, 10, e0130151.

https://doi.org/10.1371/journal.pone.0130151

Nye T.M.W., Liò P. & Gilks W.R. (2006) A novel algorithm and web-based tool for comparing two alternative phylogenetic trees. *Bioinformatics*, 22, 117–119. https://doi.org/10.1093/bioinformatics/bti720

Oksanen J., Blanchet G., Friendly M., Kindt R., Legendre P., McGlinn D., Minchin P.R., O'Hara B., Simpson G.L., Solymos P., Stevens M.H.H., Szoecs E. & Wagner H. (2019) *vegan: Community ecology package*. R package version 2.5-6. Available at: https://cran.r-project.org/package=vegan (accessed 10 January 2020)

Peralta G. (2016) Merging evolutionary history into species interaction networks. *Functional Ecology*, 30, 1917–1925. https://doi.org/10.1111/1365-2435.12669

Peres-Neto A.P.R., Legendre P., Dray S. & Borcard D. (2006) Variation partitioning of species data matrices. *Ecology*, 87, 2614–2625. https://doi.org/10.1890/0012-9658(2006)87[2614:VPOSDM]2.0.CO;2

Peterson B.J. & Fry, B. (1987) Stable isotopes in ecosystem studies. *Annual Review of Ecology, Evolution, and Systematics*, 18, 293–320. https://doi.org/10.1146/annurev.es.18.110187.001453

Peterson C.C., Keppeler F.W., Saenz D.E., Bower L.M. & Winemiller K.O. (2017) Seasonal variation in fish trophic networks in two clear-water streams in the Central Llanos region, Venezuela. *Neotropical Ichthyology*, 15, e160125. https://doi.org/10.1590/1982-0224-20160125

Post D.M. (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, 83, 703–718. https://doi.org/10.1890/0012-

9658(2002)083[0703:USITET]2.0.CO;2

R Core Team (2019) *R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.* Available at: https://www.r-project.org/ (accessed 10 January 2020)

Rabosky D.L., Chang J., Title P.O., Cowman P.F., Sallan L., Friedman M., Kaschner K., Garilao C., Near T.J., Coll M. & Alfaro M.E. (2018) An inverse latitudinal gradient in speciation rate for marine fishes. *Nature*, 559, 392–395. https://doi.org/10.1038/s41586-018-0273-1

Revell L.J. (2012) phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, 3, 217–223. https://doi.org/10.1111/j.2041-210X.2011.00169.x

Robinson B.W. & Wilson D.S. (1998) Optimal foraging, specialization, and a solution to Liem's paradox. *The American Naturalist*, 151, 223–235. https://doi.org/10.1086/286113

Rocha M.R., Gaedke U. & Vasseur D.A. (2011) Functionally similar species have similar dynamics. *Journal of Ecology*, 99, 1453–1459. https://doi.org/10.1111/j.1365-2745.2011.01893.x

Rosi-Marshall E.J. & Wallace J.B. (2002) Invertebrate food webs along a stream resource gradient. *Freshwater Biology*, 47, 129–142. https://doi.org/10.1046/j.1365-2427.2002.00786.x

Sale P.F. (1977) Maintenance of high diversity in coral reef fish communities. *American Naturalist*, 111, 37–359. https://doi.org/10.1086/283164

Sarakinos H.C., Johnson M.L. & Zanden M.J.V. (2002) A synthesis of tissue-preservation effects on carbon and nitrogen stable isotope signatures. *Canadian Journal of Zoology*, 80, 381–387. https://doi.org/10.1139/z02-007

Schluter D. (2000) The ecology of adaptive radiation. Oxford University Press, Oxford.

Schmitt C.J., Cook J.A., Zamudio K.R. & Edwards S.V. (2018) Museum specimens of terrestrial vertebrates are sensitive indicators of environmental change in the Anthropocene. *Philosophical Transactions of the Royal Society B*, 374, 20170387. https://doi.org/10.1098/rstb.2017.0387

Silva M.J., Figueiredo B.R.S., Ramos R.T.C. & Medeiros E.S.F. (2010) Food resources used bu three species of fish in the semi-arid regions of Brazil. *Neotropical Icthyology*, 8, 825–833. https://doi.org/10.1590/S1679-62252010005000010

Silva V.E.L., Silva-Firmiano L.P.S., Teresa F.B., Batista V.S., Ladle R.J. & Fabré N.N. (2019) Functional traits of fish species: adjusting resolution to accurately express resource partitioning. *Frontiers in Marine Science*, 6, 303. https://doi.org/10.3389/fmars.2019.00303

Smith M.R. (2018) TreeSearch: phylogenetic tree search using custom optimality criteria. Available at: https://doi.org/10.5281/zenodo.815371 (accessed 10 January 2020)

Su G., Villéger S. & Brosse S. (2019) Morphological diversity of freshwater fishes differs between realms, but morphologically extreme species are widespread. *Global Ecology and Biogeography*, 28, 211–221. https://doi.org/10.1111/geb.12843

Takahashi T. & Koblmüller S. (2011) The adaptive radiation of cichlid fish in lake Tanganyika: a morphological perspective. *International Journal of Evolutionary Biology*, 2011, 620754. https://doi.org/10.4061/2011/620754

Toussaint A., Charpin N., Beauchard O., Grenouillet G., Oberdorff T., Tedesco P.A., Brosse S. & Villéger S. (2018) Non-native species led to marked shifts in functional diversity of the world freshwater fish faunas. *Ecology Letters*, 21, 1649–1659. https://doi.org/10.1111/ele.13141

Traill L.W., Lim M.L.M., Sodhi N.S. & Bradshaw C.J.A. (2010) Mechanisms driving change: altered species interactions and ecosystem function through global warming. *Journal of Animal Ecology*, 79, 937–947. https://doi.org/10.1111/j.1365-2656.2010.01695.x

Villamarín F., Jardine T.D., Bunn S.E., Marioni B. & Magnusson W.E. (2018) Body size is more important than diet in determining stable-isotope estimates of trophic position in crocodilians. *Scientific Reports*, 8, 2020. https://doi.org/10.1038/s41598-018-19918-6

Villéger S., Brosse S., Mouchet M., Mouillot D. & Vanni M.J. (2017) Functional ecology of fish: Current approaches and future challenges. *Aquatic Sciences*, 79, 783–801. https://doi.org/10.1007/s00027-017-0546-z

Votier S.C., Bearhop S., MacCormick A., Furness R.W. & Ratcliffe N. (2003) Assessing the diet of great skuas, Catharacta skua, using five different techniques. *Polar Biology*, 26, 20–26. https://doi.org/10.1007/s00300-002-0446-z

Xu J., Chai Y., Wang M., Dang H., Guo Y., Chen Y., Zhang C., Li T., Zhang L. & Yue

M. (2018) Shifts in plant community assembly processes across growth forms along a habitat severity gradient: A test of the plant-functional trait approach. *Frontiers in Plant Science*, 9, 180. https://doi.org/10.3389/fpls.2018.00180

Wainwright P.C., Alfaro M.E., Bolnick D.I. & Hulsey C.D. (2005) Many-to-one mapping of form to function: a general principle in organismal design? *Integrative and Comparative Biology*, 45, 256–262. https://doi.org/10.1093/icb/45.2.256

Wiens J.J. & Graham C.H. (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics*, 36, 519–539. https://doi.org/10.1146/annurev.ecolsys.36.102803.095431

Winemiller K.O. (1989) Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelan llanos. *Environmental Biology of Fishes*, 26, 177–199. https://doi.org/10.1007/BF00004815

Winemiller K.O. (1990) Spatial and temporal variation in tropical fish trophic networks. *Ecological Monographs*, 60, 331–367. https://doi.org/10.2307/1943061

Winemiller K.O. (1991) Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. *Ecological Monographs*, 61, 343–365. https://doi.org/10.2307/2937046

Winemiller K.O., Fitzgerald D.B., Bower L.M. & Pianka E.R. (2015) Functional traits, convergent evolution, and periodic tables of niches. *Ecology Letters*, 18, 737–751. https://doi.org/10.1111/ele.12462

Winemiller K.O., Kelso-Winemiller L.C. & Brenkert A.L. (1995) Ecomorphological diversification and convergence in fluvial cichlid fishes. Environmental Biology of

Fishes, 44, 235–261. https://doi.org/10.1007/978-94-017-1356-6_17

Winemiller K.O. & Pianka E.R. (1990) Organization in natural assemblages of desert lizards and tropical fishes. *Ecological Monographs*, 60, 27–55. https://doi.org/10.2307/1943025

Wootton J.T. & Emmerson M. (2005) Measurement of interaction strength in nature. *Annual Review of Ecology, Evolution, and Systematics*, 36, 419–444. https://doi.org/10.1146/annurev.ecolsys.36.091704.175535

Yodzis P. & Winemiller K. (1999) In search of operational trophospecies in a tropical food web. *Oikos*, 87, 327–340. https://doi.org/10.2307/3546748

Zanden M.J.V., Cabana G. & Rasmussen J.B. (1997) Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios (d15N) and literature dietary data. *Canadian Journal of Fisheries and Aquatic Sciences*, 54, 1142–1158. https://doi.org/10.1139/f97-016

Zelditch M.L., Ye J., Mitchell J.S. & Swiderski D.L. (2017) Rare ecomorphological convergence on a complex adaptive landscape: body size and diet mediate evolution of jaw shape in squirrels (Sciuridae). *Evolution*, 71, 633–649. https://doi.org/10.1111/evo.13168

5. CONCLUSIONS

Predation is one of the most important biological interactions affecting ecology and evolution (Abrams, 2000) and the structure of ecological communities and ecosystems (Paine, 1966; Terborgh *et al*., 2001; Estes *et al*., 2011). In recent decades, there have been extensive efforts to describe predator-prey interactions and food web structure (e.g., Beaver, 1985; Hildrew *et al.*, 1985; Winemiller, 1990; Thompson & Townsend, 2004). This has helped to advance food web theory (Pimm, 1982; Polis & Winemiller, 1996; McCann, 2011) and improve our capability to manage and restore ecosystems (Ripple & Beschta, 2012; Ritchie *et al*., 2012; McDonald-Madden *et al*., 2016). Of particular relevance is the finding that body size determines many aspects of predator-prey interactions, including predator foraging rate, prey availability, trophic niche width, and trophic level (Woodward *et al*., 2005). However, food web models and predictions are still quite crude (Jonsson *et al*., 2018), especially for diverse tropical systems where food webs seem to be less size based (Layman *et al.*, 2005; Ou *et al.*, 2017). My dissertation sought to expand previous studies by exploring the role of functional traits (body size and other traits) and phylogeny to determine predator-prey interactions, improving our understanding of how complex food webs composed of species with diverse feeding strategies are structured.

I showed that the association between body size and trophic level in freshwater and estuarine fishes is mainly indirect and may vary according to other functional traits. This helps to explain why previous studies have found weak trophic level–body size relationships (e.g., Riede *et al*., 2011; Potapov *et al*., 2019). The inclusion of other functional traits, such as gut length and mouth gape, and their involvement in direct and indirect causal pathways improved the explanatory capabilities of my statistical models. The correlation between trophic level and body size was only significant when carnivorous species were analyzed separately. Overall, predators with conical or triangular-serrated teeth, large mouths, and elongated/ and/or fusiform bodies tend to have strong positive trophic level–body size relationships, whereas primarily non-carnivorous species with unicuspid or multicuspid teeth, deep bodies and small to medium-sized mouth gapes tended to have negative relationships. In this sense, multi-trait models of assemblage trophic structure should be more useful for building predictive food web models than those based exclusively on body size. Simple food web models that assume a positive trophic level–body size relationship, such as the "fishing down food webs" model proposed by Pauly *et al.* (1998) for marine pelagic systems, should not be applied to rivers, wetlands, estuaries and other systems in which higher plants and detritus are important food resources for animals.

It is important to mention that species analyzed here are from tropical (Venezuela and Costa Rica) and sub-tropical regions (Texas [USA] and Zambia). These regions have higher proportions of non-carnivorous species than temperate and polar ecosystems (Wootton & Oemeke, 1992; Floeter *et al*., 2005; Behrens & Lafferty, 2007), which may partially explain the weak association between trophic level and body size found in this dissertation. Moreover, large predators living at higher temperatures, such as freshwater habitats in the tropics, may feed on highly abundant prey at the base of the food web in order to sustain their high energetic demands, further weakening trophic level-body size relationships (Dantas *et al.*, 2019). If this is the case, then the influence of body size on the structure of food webs might be greater at higher latitudes, a hypothesis that still needs to be tested.

Body size is a key element in the metabolic theory of ecology (Brown *et al.*, 2004) and allometric network theory (Martinez, 2020), two frameworks that attempt to integrate patterns and processes across different levels of organizations, from physiology to entire ecosystems. However, based on findings reported in this dissertation, it appears that the importance of body size as a determinant of food web structure has been overemphasized, while the importance of other functional traits has been overlooked. This was evident when I compared the relative capabilities for body size and other functional traits to explain variation in food web descriptors. For example, gut length was a more consistent predictor of food item size, trophic level and trophic niche width than was body size. Other traits, such as tooth shape and mouth gape, also were more strongly associated with trophic position than was body size. In prior studies of fish, body size was treated as a proxy for other relevant traits that affect ecological performance, such as brain size, mouth gape, and locomotion (McCann *et al.*, 2005; Rooney *et al.*, 2008; Arim *et al.*, 2010). Although convenient, this approach overlooks important causal relationships. In this sense, future studies should use examine relationships among multiple organism traits to predict predator-prey interactions and improve our understanding of food webs.

My dissertation builds on previous studies by analyzing species from multiple trophic guilds. However, it should be highlighted that my studies did not include some important components of freshwater and estuarine food webs. For example, ectoparasites and endoparasites are diverse in inland aquatic ecosystems (Poulin, 2016), with potential to regulate fish populations (Sindermann 1987). Parasites have special adaptations to attach (e.g., hooks) and feed (e.g., sucking and scrapping feeding apparatus) on aquatic animals that often are several orders of magnitude larger them themselves (Poulin, 2006). My analyses also did not incorporate functionally and taxonomically diverse free-living arthropods and other invertebrates that co-exist with fish in freshwater and estuarine ecosystems. Unlike most fish, many of these animals are not mouth-gape limited (Pimm, 1982; Arim *et al*., 2007) and use a variety of methods to capture (e.g., filter-feeding with an external silken net, social predation), ingest (e.g., phagocytosis, dismember prey into smaller pieces by chewing or using auxiliary appendices) and digest prey (e.g., extra-oral digestion by injecting digestive enzymes onto the prey) (Thorp & Covich, 2001; Merritt *et al.*, 2008). Inclusion of this diverse group in an analysis likely would further reduce the potential for body size to explain variation in food web structure, although their inclusion might improve predictions for certain systems (e.g., pelagic food chain: phytoplankton–> zooplankton–> zooplanktivorous fish–> piscivores fish; Potapov *et al*., 2019).

I found significant patterns of intercorrelation among phylogeny, morphology, diet and isotopic ratios. Morphology was a stronger predictor of diet than was phylogeny, and this provides support for approaches in community ecology that rely on species traits to infer niche relationships (e.g., Fitzgerald *et al*., 2017). However, high levels of unexplained variation in diet and isotopic data (>60%) indicate that certain morphological traits may have a redundant function (many-to-one), whereas others have multiple functions (one-to-many) (Wainwright *et al*., 2005; Zelditch *et al*., 2017). Whereas direct observation and measurement of predator-prey interactions provide the most robust information to guide the development of predictive food web models, species functional traits could serve as useful proxies for certain kinds of questions and analyses in community ecology, such as those exploring trophic diversification at macroecological scales (Winemiller et al. 1995; López-Fernández et al. 2012).

I also found that diet was significatively correlated with isotopic ratios (δ15N and δ13C) obtained from preserved specimens collected more than three decades ago. This result corroborates previous studies (e.g., Edwards *et al*., 2002; Sarakinos *et al.*, 2002) and indicates that isotopic signals reveal trophic structure despite potential error associated with estimates of trophic enrichment and variation associated with tissue preservation, metabolism, and other factors affecting isotopic ratios. Isotopic data from samples extracted from preserved species could be particularly useful to explore long-term changes in trophic niches associated with environmental impacts and climate change.

Recent advances in ecological modeling and computer science have made possible the development of individual-based (or agent-based) food web models that incorporate functional traits of individual organisms or life stages classes (Scotti et al. 2017). Such models allow organisms and populations to respond to both biotic environmental components (e.g., food, predators) as well as abiotic environmental components (e.g., temperature, water discharge) and therefore can simulate real-world scenarios as well as test ecological theories (DeAngelis & Grimm, 2014; Winemiller, 2017). I believe that relationships revealed in this dissertation contribute to a foundation for development of trait-based models capable of simulating aquatic and estuarine food webs and testing theories concerning community trophic structure and universal food web patterns.

5.1. References

Abrams P.A. (2000) The Evolution of predator-prey interactions. *Annual Review of Ecology and Systematics*, 31, 79–105. https://doi.org/10.1146/annurev.ecolsys.31.1.79

Arim M., Abades S.R., Laufer G., Loureiro M. & Marquet P.A. (2010) Food web structure and body size: trophic position and resource acquisition. *Oikos*, 119, 147–153. https://doi.org/10.1111/j.1600-0706.2009.17768.x

Beaver R.A. (1985) Geographical variation in food web structure in Nepenthes pitcher plants. *Ecological Entomology*, 10, 241–248. https://doi.org/10.1111/j.1365-2311.1985.tb00720.x

Behrens M.D. & Lafferty K.D. (2007) Temperature and diet effects on omnivorous fish performance: implications for the latitudinal diversity gradient in herbivorous fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, 64, 867–873. https://doi.org/10.1139/f07-063

Brose U., Jonsson T., Berlow E.L., Warren P., Banasek-Richter C., Bersier L., Blanchard J.L., Brey T., Carpenter S.R., Blandenier M-F.C., Cushing L., Dawah H.A., Dell T., Edwards F., Harper-Smith S., Jacob U., Ledger M.E., Marinez N.D., Memmott J., Mintenbeck K., Pinnegar J.K., Rall B.C., Rayner T.S., Reuman D.C., Ruess L., Ulrich W., Williams R.J., Woodward G. & Cohen J.E. (2006) Consumer–resource body-size relationships in natural food webs. *Ecology*, 87, 2411–2417. https://doi.org/10.1890/0012-9658(2006)87[2411:CBRINF]2.0.CO;2

Brown J.H., Gillooly J.F., Allen A.P., Savage V.M. & West G.B. (2004) Toward a metabolic theory of ecology. *Ecology*, 85, 1771–1789. https://doi.org/10.1890/03-9000

Dantas D.D.F., Caliman A., Guariento R.D., Angelini R., Carneiro L.S., Lima S.M.Q., Martinez P.A. & Attayde J.L. (2019) Climate effects on fish body size-trophic position relationship depend on ecosystem type. *Ecography*, 42, 1579–1586. https://doi.org/10.1111/ecog.04307

DeAngelis D.L. & Grimm V. (2014) Individual-based models in ecology after four decades. *F1000Prime Reports*, 6, 39. https://doi.org/10.12703/P6-39

Edwards M.S., Turner T.F. & Sharp Z.D. (2002) Short- and long-term effects of fixation and preservation on stable isotope values (δ13 C, δ15 N, δ34 S) of fluid-preserved museum specimens. *Copeia*, 2002, 1106–1112. https://doi.org/10.1643/0045-8511(2002)002[1106:SALTEO]2.0.CO;2

Estes J.A., Terborgh J., Brashares J.S., Power M.E., Berger J., Bond W.J., Carpenter S.R., Essington T.E., Holt R.D., Jackson J.B.C., Marquis R.J., Oksanen L., Oksanen T., Paine R.T., Pikitch E.K., Ripple W.J., Sandin S.A., Scheffer M., Schoener T.W., Shurin J.B., Sinclair A.R.E., Soulé M.E., Virtanen R. & Wardle D.A. (2011) Trophic downgrading of planet Earth. *Science*, 333, 301–306. https://doi.org/10.1126/science.1205106

Fitzgerald D.B., Winemiller K.O., Pérez M.H.S. & Sousa L.M. (2017) Seasonal changes in the assembly mechanisms structuring tropical fish communities. *Ecology*, 98, 21–31. https://doi.org/10.1002/ecy.1616

Floeter S.R., Behrens M.D., Ferreira C.E.L., Paddack M.J. & Horn M.H. (2005) Geographical gradients of marine herbivorous fishes: patterns and processes. *Marine Biology*, 147, 1435–1447. https://doi.org/10.1007/s00227-005-0027-0

Hildrew A.G., Townsend C. & Hasham A. (1985) The predatory Chironomidae of an iron-rich stream: feeding ecology and food web structure. *Ecological Entomology*, 10, 403–413. https://doi.org/10.1111/j.1365-2311.1985.tb00738.x

Jonsson T., Kaartinen R., Jonsson M. & Bommarco R. (2018) Predictive power of food web models based on body size decreases with trophic complexity. *Ecology Letters*, 21, 702–712. https://doi.org/10.1111/ele.12938

Layman C.A., Winemiller K.O., Arrington D.A. & Jepsen D.B. (2005) Body size and trophic position in a diverse tropical food web. *Ecology*, 86, 2530–2535. https://doi.org/10.1890/04-1098

López-Fernández H., Winemiller K.O., Montaña C. & Honeycutt R.L. (2012) Diet-morphology correlations in the radiation of South American geophagine cichlids (Perciformes: Cichlidae: Cichlinae). *PLoS One*, 7, e33997.

https://doi.org/10.1371/journal.pone.0033997

Martinez N.D. (2020) Allometric trophic networks from individuals to socio-ecosystems: consumer-resource theory of the ecological elephant in the room. *Frontiers in Ecology and Evolution*, 8, 92. https://doi.org/10.3389/fevo.2020.00092

McCann K.S. (2011) *Food webs,* Princeton University Press, New Jersey.

McCann K.S., Rasmussen J.B. & Umbanhowar J. (2005) The dynamics of spatially coupled food webs. *Ecology Letters*, 8, 513–523. https://doi.org/10.1111/j.1461-0248.2005.00742.x

McDonald-Madden E., Sabbadin R., Game E.T., Baxter P.W., Chadès I. & Possingham H.P. (2016) Using food-web theory to conserve ecosystems. *Nature communications*, 7, 10245. https://doi.org/10.1038/ncomms10245

Merritt R.W., Cummins K.W., & Berg M.B. (eds.) (2008) *An introduction to the aquatic insects of North America*. Kendall Hunt Publishing, Dubuque.

Ou C., Montaña C.G. & Winemiller K.O. (2017) Body size-trophic position relationships among fishes of the lower Mekong basin. *Royal Society Open Science*, 4, 160645. https://doi.org/10.1098/rsos.160645

Paine R.T. (1966) Food web complexity and species diversity. *American Naturalist*, 100, 65–75. https://doi.org/10.1086/282400

Pauly D., Christensen V., Dalsgaard J., Froese R. & Torres Jr.F. (1998) Fishing down marine food webs. *Science*, 279, 860–863. https://doi.org/10.1126/science.279.5352.860

Pimm S. (1982) *Food webs*, Chapman & Hall, London.

Polis G.A. & Winemiller K.O. (eds) (1996) *Food webs: integration of patterns and dynamics*, Chapman and Hall, New York.

Potapov A.M., Brose U., Scheu S. & Tiunov A.V. (2019) Trophic position of consumers and size structure of food webs across aquatic and terrestrial ecosystems. *The American Naturalist*, 194, 823–839. https://doi.org/10.1086/705811

Poulin R. (2016) Greater diversification of freshwater than marine parasites of fish. *International Journal for Parasitology*, 46, 275–279. https://doi.org/10.1016/j.ijpara.2015.12.002

Poulin R. (2006) *Evolutionary ecology of parasites*. Princeton University Press, Princeton.

Riede J.O., Brose U., Ebenman B., Jacob U., Thompson R., Townsend C.R. & Jonsson T. (2011) Stepping in Elton's footprints: a general scaling model for body masses and trophic levels across ecosystems. *Ecology Letters*, 14, 169–178. https://doi.org/10.1111/j.1461-0248.2010.01568.x

Ripple W.J. & Beschta R.L. (2012) Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. *Biological Conservation*, 145, 205–213. https://doi.org/10.1016/j.biocon.2011.11.005

Ritchie E.G., Elmhagen B., Glen A.S., Letnic M., Ludwig G. & McDonald R.A. (2012) Ecosystem restoration with teeth: what role for predators? *Trends in Ecology and Evolution*, 27, 265–271. https://doi.org/10.1016/j.tree.2012.01.001

Rooney N., McCann K.S. & Moore J.C. (2008) A landscape theory for food web architecture. *Ecology Letters*, 11, 867–881. doi: https://doi.org/10.1111/j.1461-

0248.2008.01193.x

Sarakinos H.C., Johnson M.L. & Zanden M.J.V. (2002) A synthesis of tissue-preservation effects on carbon and nitrogen stable isotope signatures. *Canadian Journal of Zoology*, 80, 381–387. https://doi.org/10.1139/z02-007

Scotti M., Hartvig M., Winemiller K.O., Li Y., Jauker F., Jordán F. & Dormann C. (2017) *Trait-based and process-oriented modeling in ecological network dynamics*. In: Moore J., Ruiter P., McCann K., & Wolters V. (eds) Adaptive food webs: stability and transitions of real and model ecosystems, Cambridge University Press, Cambridge. pp. 228-256

Sindermann C.J. (1987) Effects of parasites on fish populations: practical considerations. *International Journal for Parasitology*, 17, 371-382. https://doi.org/10.1016/0020-7519(87)90112-3

Terborgh J., Lopez L., Nuñez P., Rao M., Shahabuddin G., Orihuela G., Riveros M., Ascanio R., Adler G.H., Lambert T.D. & Balbas L. (2001) Ecological meltdown in predator-free forest fragments. *Science*, 294, 1923–1926. https://doi.org/10.1126/science.1064397

Thompson R.M. & Townsend C.R. (2004) Land-use influences on New Zealand stream communities: effects of species composition, functional organisation, and food-web structure. *New Zealand Journal of Marine and Freshwater Research*, 38, 595–608. https://doi.org/10.1080/00288330.2004.9517265

Thorp J.H., Covich A.P. (eds.) (2001) *Ecology and classification of North American freshwater invertebrates,* Academic Press, San Diego.

Wainwright P.C., Alfaro M.E., Bolnick D.I. & Hulsey C.D. (2005) Many-to-one mapping of form to function: a general principle in organismal design? *Integrative and Comparative Biology*, 45, 256–262. https://doi.org/10.1093/icb/45.2.256

Winemiller K.O. (1990) Spatial and temporal variation in tropical fish trophic networks. *Ecological Monographs*, 60, 331–367. https://doi.org/10.2307/1943061

Winemiller, K.O. (2017) *Food web dynamics when divergent life history strategies respond to environmental variation differently: a fisheries ecology perspective*. In: Moore J., de Ruiter P., McCann K., & Wolters V. (eds) Adaptive food webs: stability and transitions of real and model ecosystems, Cambridge University Press, Cambridge. pp. 306–323.

Winemiller K.O., Kelso-Winemiller L.C. & Brenkert A.L. (1995) Ecomorphological diversification and convergence in fluvial cichlid fishes. Environmental Biology of Fishes, 44, 235–261. https://doi.org/10.1007/978-94-017-1356-6_17

Woodward G., Ebenman B., Emmerson M., Montoya J., Olesen J., Valido A. & Warren P. (2005) Body size in ecological networks. *Trends in Ecology & Evolution*, 20, 402–409. https://doi.org/10.1016/j.tree.2005.04.005

Wootton J.T. & Oemke M.P. (1992) Latitudinal differences in fish community trophic structure, and the role of fish herbivory in a Costa Rican stream. *Environmental Biology of Fishes*, 35, 311-319. https://doi.org/10.1007/BF00001899

Zelditch M.L., Ye J., Mitchell J.S. & Swiderski D.L. (2017) Rare ecomorphological convergence on a complex adaptive landscape: body size and diet mediate evolution of jaw shape in squirrels (Sciuridae). *Evolution*, 71, 633–649.

https://doi.org/10.1111/evo.13168

APPENDIX A

SUPPORTING INFORMATION FOR THE MANUSCRIPT ENTITLED: THE RELATIONSHIP BETWEEN TROPHIC LEVEL AND BODY SIZE IN FISHES DEPENDS ON FUNCTIONAL TRAITS

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Table A.1 Number of individuals, species, families and orders of fish dissected for dietary analysis and included in this study. This information is separated according to the location where the fishes were collected. Details about the years and seasons when the fishes were collected are shown. Values in parentheses represent the number of individuals, species, families or orders of fish used for the analyses of mean trophic level (MTL) and the slope of the trophic level (TL)-body size relationship, respectively.

Location	**Main Sites**	**Sampling years**	**Seasons**	**N of individuals**	**N of species**	**N of families**	**N of orders**
Texas	Neches river, Brazos river	1993:6, 2009:11, 2013:14	Spring, Summer, Fall, Winter	1423 (1409,1286)	28 (21,11)	9 (6,3)	6 (5,3)
Texas	Mad Island Marsh Preserve	1998, 1999	Summer and Winter	4970 (4948,4828)	44 (33,23)	21 (16,13)	13 (9,8)
Costa Rica	Caño Agua Fría Viejo, Quebrada creek	1985	Low and high water	6098 (6041,5668)	91 (66,34)	28 (22,16)	16 (13,8)
Venezuela	Caño Maraca, Caño Volcan	1984	High, falling and low water	11698 (11682,11486)	90 (79,64)	30 (28,25)	6 (6,6)
Venezuela	Morichal Charcotico, Morichal Charcote	1995, 1996	High, falling and low water	3875 (3842,3564)	65 (50,32)	17 (12,11)	5 (4,4)
Zambezi	Upper Zambezi River floodplain	1989	Low, raising and high water	2277 (2220,1878)	71 (48,23)	13 (12,9)	7 (7,6)
			Total	30341 (30142,28710)	367 (283,179)	75 (67,54)	20 (17,14)

Table A.2 Trophic level estimates for the food items ingested by the fishes used in this study. All basal sources, including autotrophs and detritus, were placed in the trophic level 1. Primarily herbivorous taxa were considered as trophic level 2. Secondary and other high-level consumer taxa had trophic level that vary according to their main food types. For instance, a taxon that ingest primarily plants but also eats primary consumers, it was considered to feed at trophic level 2.25. A taxon that eats both plants and primary consumers at in similar proportions was considered to be at trophic level 2.5. If a taxon eats mostly primary consumers but also eat plants, it was considered to be at trophic level 2.75. In some cases, diet data were available for certain prey (e.g., *Palaemonetes pugio*), in which case I estimated the trophic level similarly to what was done with fishes using Adams *et al.* (1983) formula (for more details, see the main manuscript). References consulted for trophic level estimates are provided in the end of the table.

Food items	Trophic level
Detritus/Sediment	
Coarse detritus	1
Fine detritus	1
Vegetative detritus	1
Miscellaneous detritus	1
Sand	1
Algae	
Ruppia maritima	1
Oscillatoria	1
Chara sp.	1
Noctiluca spp.	2
Filamentous algae	1
Centric diatoms	1
Pennate diatoms	1
Diatoms	1
Golden brown algae	1
Brown algae	1
Nostocales (Blue green algae)	1
Other blue green algae	1
Green algae	1
Unicellular green algae	1
Polycystis	1
Desmids	1
Miscellaneous algae	1
Plants	
Wolffia sp.	1
Aquatic macrophytes	1

Table A.2 Continued.

Food items	**Trophic level**
Aquatic vegetation	1
Terrestrial vegetation	1
Leaf litter	1
Plant spores	1
Seeds	1
Fruits (soft tissues) and flowers	1
Woody vegetation	1
Miscellaneous vegetation	1
Protozoans	
Miscellaneous protozoans	2
Tubulinea	
Difflugiid	2.25
Bryozoa	
Miscellaneous Bryozoa	2.25
Rotifers	
Miscellaneous Rotifers	2.5
Sponge	
Miscellaneous sponge	2
Platyhelminthes	
Turbellaria	3
Nematoda	
Nematods (non-parasitic forms)	2.75
Nematophora	
Horsehair	3
Miscellaneous Nematophora	2.75
Annelids	
Oligochaeta	2.25
Polychaeta	2.5
Hirudinea (Leeches)	3.5
Molluscs	
Bivalvia	2
Clams	2
Gastropoda	2
Miscellaneous molluscs	2
Microcrustaceans	
Copepoda nauplii	2
Harpacticoida Copepoda	2.25

Table A.2 Continued.

Food items	Trophic level
Calanoida Copepoda	2.5
Cyclopoid Copepoda	2.5
Miscellaneous Copepoda	2.5
Ostracoda	2
Cladocera	2.25
Anostraca	2
Branchiopoda	2.25
Mysidacea	2
Penaeid shrimp post larvae	2
Decapoda larvae	2
Shrimp larvae	2
Miscellaneous microcrustacean	2.25
Crustacea	
Amphipoda (*Corophium* sp)	2.5
Amphipoda (*Gammarus* spp.)	2.5
Miscellaneous Amphipoda	2.5
Palaemonetes pugio	2.08
Penaeus setiferus	2.12
Thoracica	2
Brachyura (Crab zoea)	2
Dyspanopeus sayi	2
Callinectes sapidus	3.12
Dilocarcinus and *Callinectes* spp.	2.5
Cambaridae	2.5
Decapoda	2.5
Macrobranchium spp.	2.5
Palaemonidae	2.5
Penaeus aztecus	2.41
Dendrobranchiata (shrimps)	2.25
Dendrobranchiata (prawn)	2.5
Astacoidea (crayfish)	2.5
Miscellaneous Crustacea	2.5
Chilopoda	
Miscellaneous Chilopoda	3.5
Arachnids	
Hydracarina	3.25
Acarina terrestrial	3

Table A.2 Continued.

Food items	**Trophic level**
Miscellaneous Acarina	3
Araneae	3.5
Hexapods	
Collembola	2
Acrididae (Locust)	2
Coleoptera (Elmidae)	2
Coleoptera (Psephenidae)	2
Coleoptera (Hydrophilidae)	2.75
Coleoptera (Carabidae)	3.5
Coleoptera (Dysticidae)	3.5
Miscellaneous aquatic Coleoptera (adult)	2.5
Miscellaneous aquatic Coleoptera (larvae)	2.5
Miscellaneous terrestrial Coleoptera (adult)	2.5
Wood borer	2
Ephemeroptera (Ephemeridae)	2
Ephemeroptera (Heptageniidae)	2
Ephemeroptera (Leptophlebidae)	2
Ephemeroptera (Polymitarcidae)	2
Ephemeroptera (Baetidae)	2
Miscellaneous Ephemeroptera (nymph)	2
Miscellaneous Ephemeroptera (adult)	2
Diptera (Psychodidae)	2
Diptera (Ephydridae)	2.25
Diptera (Tipulidae)	2.25
Diptera (Ceratopogonidae)	2.75
Diptera (Tanypodinae)	2.75
Diptera (Chaboridae)	3
Diptera pupe (Chaboridae)	3
Diptera (Tabanidae)	3
Diptera (Chironomidae - larvae)	2.5
Diptera (Chironomidae - pupae)	2.5
Miscellaneous Diptera (larvae)	2.5
Miscellaneous Diptera (pupae)	2.5
Miscellaneous Diptera (adult)	2.5
Lepidoptera (adult)	2

Table A.2 Continued.

Food items	Trophic level
Lepidoptera (larvae)	2
Orthoptera (Gryllidae)	2.25
Miscellaneous Orthoptera	2
Isoptera	2
Trichoptera (Calamoceratidae)	2
Trichoptera (Limnephilidae)	2
Trichoptera (Hydropsychidae)	2.25
Trichoptera (Leptoceridae)	2.25
Trichoptera(Heptageniidae)	2.25
Miscellaneous Trichiptera (nymph)	2.25
Blattodea	2.25
Isopoda	2.25
Thysanoptera	2.25
Plecoptera	2.25
Hymenoptera (Formicidae)	2.5
Hymenoptera (Pteromalidae)	3
Miscellaneous Hymenoptera	2.5
Hemiptera (Corixidae)	2.5
Hemiptera (Naucoridae)	3.5
Hemiptera (Gerridae)	3.5
Hemiptera (Notonectidae)	3.5
Miscellaneous terrestrial Hemiptera	2.5
Miscellaneous aquatic Hemiptera	2.75
Miscellaneous Homoptera	2.75
Odonata (Coenagrionidae)	3.5
Odonata (Cordullidae)	3.5
Odonata (Gomphidae)	3.5
Odonata (Libellulidae)	3.5
Odonata (Adult)	3.5
Odonata (Nymphs)	3.5
Odonata (Zygoptera)	3.5
Miscellaneous Odonata	3.5
Neuroptera	3.25
Aquatic Neuroptera (Larvae)	3.25
Miscellaneous terrestrial insects	2.5
Miscellaneous aquatic insects	2.5
Miscellaneous insects (larvae)	2.5

Table A.2 Continued.

Food items	Trophic level
Miscellaneous insects	2.5
Unidentified invertebrates	
Miscellaneous terrestrial invertebrates	2.5
Miscellaneous aquatic invertebrates	2.5
Miscellaneous invertebrates	2.5
Chitin fragments	2.5
Miscellaneous Arthropoda	2.5
Miscellaneous worms	2.5
Non-fish Vertebrates	
Tadpoles	2.25
Frogs	3.5
Adult anurans	3.5
Amphibia Anura	3.5
Bird feather	2.5
Non-fish flesh	2.5
Pogona microlepidota	2.5
Lizard	2.75
Eggs	
Invertebrate eggs	2.5
Lucania parva eggs	3.01
Fish eggs	3.1
Miscellaneous eggs	2.5

References

Arcifa, M. S. 2000. Feeding habits of Chaoboridae larvae in a tropical Brazilian reservoir. Revista Brasileira de Biologia 60:591.

Arnett Jr, R. H. 2000. American insects: a handbook of the insects of America north of Mexico. CRC Press.

Baker, A., and A. McLachlan. 1979. Food preferences of Tanypodinae larvae (Diptera: Chironomidae). Hydrobiologia 62:283–288.

Barnes, R. 2003. Invertebrate zoology. Cengage Learning.

Brusca, R., and G. Brusca. 2003. Invertebrates. Sinauer Associates, Sunderland.

Castaño-Meneses, G., J. G. Palacios-Vargas, and L. Q. Cutz-Pool. 2004. Feeding habits of Collembola and their ecological niche. Anales del Instituto de Biologia, Universidad Nacional Autonoma de Mexico, Serie Zoologia 75:135–142.

Checon, H. H., E. V. Pardo, and A. C. Z. Amaral. 2017. Breadth and composition of polychaete diets and the importance of diatoms to species and trophic guilds. Helgoland Marine Research 70:1–11.

Joern, A. 1979. Feeding patterns in grasshoppers (Orthoptera: Acrididae): factors influencing diet specialization. Oecologia 38:325–347.

De Jong, H., P. Oosterbroek, J. Gelhaus, H. Reusch, and C. Young. 2008. Global diversity of craneflies (Insecta, Diptera: Tipulidea or Tipulidae sensu lato) in freshwater. Hydrobiologia 595:457–467.

Jumars, P. A., K. M. Dorgan, and S. M. Lindsay. 2015. Diet of worms emended: an update of Polychaete feeding guilds. Annual Review of Marine Science 7:497–520.

Keiper, J. B., W. E. Walton, and B. A. Foote. 2002. Biology and ecology of higher diptera from freshwater wetlands. Annual Review of Entomology 47:207–232.

Kiφrboe, T., and J. Titelman. 1998. Feeding, prey selection and prey encounter mechanisms in the heterotrophic dinoflagellate *Noctiluca scintillans*. Journal of Plankton Research 20:1615–1636.

Lima, J. de F., J. da S. Garcia, and T. C. da Silva. 2014. Natural diet and feeding habits of a freshwater prawn (Macrobrachium carcinus: Crustacea, Decapoda) in the estuary of the Amazon River. Acta Amazonica 44:235–244.

McDiarmid, R. W., and R. Altig. 1999. Tadpoles: the biology of anuran larvae. The University of Chicago Press, Chicago.

Merrit, R. W., K. W. Cummins, and M. B. Berg. 2008. An introduction to aquatic insects of North America. Kendall Hunt Publishers, Dubuque.

Morgan, M. D. 1980. Grazing and predation of the grass shrimp *Palaemonetes pugio*. Limnology and Oceanography 25:896–902.

Rossa-Feres, D. de C., J. Jim, and M. G. Fonseca. 2004. Diets of tadpoles from a temporary pond in southeastern Brazil (Amphibia, Anura). Revista Brasileira de Zoologia 21:745–754.

Thorp, J., and A. Covich. 2009. Ecology and classification of North American freshwater invertebrates. Academic Press.

Winemiller, K. O. 1990. Spatial and temporal variation in tropical fish trophic networks. Ecological Monographs 60: 331-367.

Table A.3 Functional traits measured for all species with more than 5 individuals dissected for the gut content analysis. Average values and their associated standard deviation, which is presented in parenthesis, are given for all continuous traits. N= Number of individuals measured. NA (Not available) are given when the number of individuals measured is equal to 1. In some cases, NA are given for some traits and not others in the same species. This happens because some traits could not be measured for all individuals.

Species	**N**	**Maximum body depth**	**Maximum body width**	**Gut length**	**Mouth orientation**	**Mouth width**	**Tooth shape**	**Gill raker shape**
Acestrorhynchus heterolepis	2	0.17 (0.02)	0.08 (0.01)	0.85 (0.00)	Terminal	0.69 (0.08)	Conical	Short/blunt/toothlike
Acestrorhynchus minimus	6	0.14 (0.01)	0.10 (0.01)	0.85 (NA)	Sub-terminal	0.72 (0.09)	Conical	Intermediate/long and sparse
Achirus lineatus	9	0.60 (0.02)	0.12 (0.01)	0.84 (0.44)	Terminal	0.56 (0.13)	Conical	Short/blunt/toothlike
Adinia xenica	3	0.41 (0.02)	0.23 (0.00)	2.86 (0.10)	Terminal	0.27 (0.02)	Conical	Short/blunt/toothlike
Adontosternarchus devenanzii	3	0.18 (0.00)	0.08 (0.00)	0.49 (NA)	Superior	0.60 (0.04)	Absent	Short/blunt/toothlike
Aequidens diadema	2	0.52 (0.03)	0.26 (0.01)	1.13 (0.16)	Terminal	0.45 (0.01)	Conical	Short/blunt/toothlike
Ageneiosus inermis	3	0.23 (0.01)	0.18 (0.02)	1.09 (0.29)	Terminal	1.03 (0.12)	Conical	Short/blunt/toothlike
Alfaro cultratus	3	0.30 (0.02)	0.15 (0.01)	0.63 (0.05)	Superior	0.59 (0.02)	Multicuspid	Short/blunt/toothlike
Amatitlania nigrofasciata	3	0.52 (0.02)	0.22 (0.00)	1.50 (0.09)	Terminal	0.40 (0.02)	Multicuspid	Short/blunt/toothlike
Ameiurus melas	3	0.23 (0.02)	0.20 (0.01)	1.87 (0.71)	Terminal	0.77 (0.06)	Unicuspid	Intermediate/long and sparse
Amphilophus alfari	3	0.47 (0.01)	0.21 (0.01)	1.04 (0.25)	Terminal	0.52 (0.03)	Multicuspid	Short/blunt/toothlike
Amphilophus citrinellus	3	0.48 (0.01)	0.20 (0.01)	1.10 (0.18)	Terminal	0.48 (0.05)	Multicuspid	Short/blunt/toothlike
Amphilophus diquis	3	0.48 (0.02)	0.19 (0.01)	1.44 (0.07)	Terminal	0.45 (0.05)	Conical	Short/blunt/toothlike
Amphilophus rostratus	4	0.48 (0.03)	0.20 (0.01)	1.16 (NA)	Terminal	0.55 (0.04)	Conical	Intermediate/long and sparse
Anchoa mitchilli	3	0.23 (0.01)	0.08 (0.01)	0.52 (0.00)	Terminal	1.08 (0.05)	Conical	Long and comb-like
Andinoacara pulcher	5	0.49 (0.02)	0.25 (0.00)	1.23 (0.14)	Terminal	0.43 (0.04)	Multicuspid	Short/blunt/toothlike
Anguilla rostrate	3	0.07 (0.00)	0.05 (0.00)	0.28 (0.00)	Superior	0.59 (0.06)	Multicuspid	Absent

Table A.3 Continued.

Species	N	Maximum body depth	Maximum body width	Gut length	Mouth orientation	Mouth width	Tooth shape	Gill raker shape
Aphyocharax erythrurus	3	0.28 (0.01)	0.14 (0.00)	0.65 (0.06)	Terminal	0.51 (0.05)	Multicuspid	Long and comb-like
Apistogramma hoignei	3	0.39 (0.02)	0.19 (0.01)	1.11 (0.14)	Terminal	0.36 (0.07)	Multicuspid	Absent
Aplocheilichthys johnstoni	3	0.19 (0.01)	0.14 (0.00)	0.53 (0.01)	Superior	0.50 (0.02)	Conical	Intermediate/long and sparse
Aplocheilichthys katangae	3	0.25 (0.01)	0.16 (0.01)	0.63 (0.05)	Superior	0.54 (0.04)	Conical	Intermediate/long and sparse
Archocentrus centrarchus	3	0.55 (0.02)	0.19 (0.00)	1.22 (0.17)	Terminal	0.44 (0.03)	Multicuspid	Intermediate/long and sparse
Archocentrus multispinosus	3	0.57 (0.02)	0.24 (0.01)	3.96 (0.75)	Terminal	0.36 (0.02)	Multicuspid	Intermediate/long and sparse
Ariopsis felis	4	0.20 (0.01)	0.19 (0.02)	1.62 (0.26)	Terminal	0.62 (0.05)	Unicuspid	Intermediate/long and sparse
Astronotus ocellatus	3	0.52 (0.02)	0.23 (0.01)	1.16 (0.13)	Terminal	0.57 (0.05)	Multicuspid	Short/blunt/toothlike
Astyanax bimaculatus	6	0.39 (0.08)	0.14 (0.02)	1.19 (0.10)	Terminal	0.63 (0.06)	Multicuspid	Intermediate/long and sparse
Astyanax fasciatus	3	0.39 (0.01)	0.15 (0.01)	1.14 (0.16)	Terminal	0.56 (0.05)	Multicuspid	Intermediate/long and sparse
Astyanax maximus	3	0.42 (0.02)	0.22 (0.12)	1.09 (0.05)	Terminal	0.47 (0.20)	Multicuspid	Long and comb-like
Astyanax superbus	3	0.35 (0.02)	0.12 (0.01)	1.15 (0.00)	Terminal	0.76 (0.08)	Multicuspid	Intermediate/long and sparse
Atherinella hubbsi	3	0.16 (0.01)	0.12 (0.00)	0.50 (0.05)	Terminal	0.45 (0.02)	Multicuspid	Long and comb-like
Atractosteus spatula	4	0.12 (0.01)	0.11 (0.01)	0.88 (NA)	Terminal	0.69 (0.08)	Conical	Absent
Awaous banana	3	0.17 (0.01)	0.14 (0.01)	1.18 (0.11)	Sub-terminal	0.57 (0.11)	Conical	Short/blunt/toothlike
Awaous tajasica	1	0.19 (NA)	0.15 (NA)	0.59 (NA)	Sub-terminal	0.57 (NA)	Conical	Short/blunt/toothlike
Bairdiella chrysoura	3	0.32 (0.01)	0.13 (0.01)	0.63 (0.07)	Terminal	1.27 (0.13)	Conical	Intermediate/long and sparse
Barbus annectens	3	0.24 (0.01)	0.13 (0.01)	0.67 (0.08)	Sub-terminal	0.43 (0.02)	Absent	Short/blunt/toothlike
Barbus barotseensis	3	0.29 (0.00)	0.14 (0.00)	0.80 (0.04)	Terminal	0.40 (0.02)	Absent	Short/blunt/toothlike
Barbus bifrenatus	3	0.27 (0.00)	0.14 (0.00)	0.97 (0.06)	Sub-terminal	0.44 (0.04)	Absent	Intermediate/long and sparse
Barbus multilineatus	3	0.31 (0.01)	0.15 (0.00)	0.95 (0.05)	Sub-terminal	0.42 (0.03)	Absent	Short/blunt/toothlike

Table A.3 Continued.

Species	N	Maximum body depth	Maximum body width	Gut length	Mouth orientation	Mouth width	Tooth shape	Gill raker shape
Barbus paludinosus	3	0.28 (0.01)	0.13 (0.01)	0.97 (0.11)	Terminal	0.43 (0.05)	Absent	Short/blunt/toothlike
Barbus poechii	3	0.32 (0.00)	0.15 (0.00)	1.02 (0.07)	Terminal	0.46 (0.01)	Absent	Short/blunt/toothlike
Barbus radiatus	7	0.28 (0.01)	0.15 (0.01)	0.88 (0.04)	Sub-terminal	0.40 (0.01)	Absent	Short/blunt/toothlike
Belonesox belizanus	3	0.16 (0.02)	0.14 (0.02)	0.33 (0.02)	Superior	0.57 (0.08)	Multicuspid	Absent
Brachychalcinus orbicularis	3	0.63 (0.02)	0.13 (0.01)	0.74 (0.03)	Superior	0.59 (0.04)	Multicuspid	Intermediate/long and sparse
Brachyhypopomus brevirostris	3	0.07 (0.01)	0.04 (0.01)	0.21 (0.04)	Sub-terminal	0.33 (0.05)	Absent	Short/blunt/toothlike
Brachyhypopomus occidentalis	3	0.08 (0.00)	0.04 (0.00)	0.17 (0.03)	Sub-terminal	0.34 (0.04)	Absent	Short/blunt/toothlike
Brachyrhaphis parismina	3	0.28 (0.02)	0.19 (0.01)	0.64 (0.06)	Superior	0.50 (0.06)	Multicuspid	Short/blunt/toothlike
Brachyrhaphis rhabdophora	3	0.29 (0.02)	0.18 (0.01)	0.75 (0.09)	Superior	0.43 (0.03)	Conical	Intermediate/long and sparse
Brevoortia patronus	3	0.38 (0.01)	0.11 (0.00)	5.05 (0.47)	Terminal	0.44 (0.06)	Absent	Long and comb-like
Brycinus lateralis	3	0.29 (0.02)	0.13 (0.01)	1.23 (0.05)	Terminal	0.49 (0.08)	Multicuspid	Long and comb-like
Brycon guatemalensis	3	0.31 (0.02)	0.13 (0.01)	1.41 (0.15)	Sub-terminal	0.58 (0.02)	Multicuspid	Intermediate/long and sparse
Brycon whitei	4	0.31 (0.01)	0.14 (0.01)	1.51 (0.41)	Terminal	0.66 (0.07)	Multicuspid	Intermediate/long and sparse
Bryconamericus deuterodonoides	3	0.29 (0.01)	0.14 (0.01)	1.14 (0.19)	Terminal	0.50 (0.04)	Multicuspid	Short/blunt/toothlike
Bryconamericus motatanensis	3	0.36 (0.01)	0.14 (0.00)	1.35 (0.09)	Terminal	0.51 (0.01)	Multicuspid	Intermediate/long and sparse
Bryconops alburnoides	3	0.24 (0.01)	0.11 (0.01)	0.72 (0.18)	Terminal	0.50 (0.04)	Multicuspid	Intermediate/long and sparse
Bryconops giacopinii	50	0.25 (0.01)	0.12 (0.01)	0.80 (0.10)	Sub-terminal	0.56 (0.07)	Multicuspid	Short/blunt/toothlike
Bunocephalus amaurus	5	0.13 (0.01)	0.29 (0.02)	0.50 (0.09)	Terminal	0.31 (0.02)	Unicuspid	Short/blunt/toothlike
Caquetaia kraussii	6	0.46 (0.03)	0.19 (0.01)	1.13 (0.15)	Terminal	0.54 (0.05)	Conical	Intermediate/long and sparse

Table A.3 Continued.

Species	**N**	**Maximum body depth**	**Maximum body width**	**Gut length**	**Mouth orientation**	**Mouth width**	**Tooth shape**	**Gill raker shape**
Carlana eigenmanni	3	0.40 (0.01)	0.12 (0.00)	1.13 (NA)	Terminal	0.49 (0.01)	Multicuspid	Intermediate/long and sparse
Catoprion mento	3	0.55 (0.07)	0.13 (0.02)	0.91 (0.14)	Superior	0.68 (0.08)	Triangular serrated	Intermediate/long and sparse
Centropomus parallelus	3	0.28 (0.01)	0.15 (0.01)	0.63 (0.05)	Terminal	0.80 (0.06)	Conical	Intermediate/long and sparse
Centropomus pectinatus	3	0.31 (0.01)	0.13 (0.00)	0.66 (0.05)	Superior	0.73 (0.05)	Unicuspid	Short/blunt/toothlike
Centropomus undecimalis	6	0.24 (0.01)	0.10 (0.01)	0.60 (0.12)	Terminal	0.92 (0.07)	Conical	Intermediate/long and sparse
Characidium pellucidum	3	0.19 (0.02)	0.12 (0.01)	0.62 (0.02)	Terminal	0.26 (0.02)	Unicuspid	Intermediate/long and sparse
Characidium pteroides	2	0.18 (0.01)	0.11 (0.00)	0.64 (0.00)	Terminal	0.42 (0.03)	Unicuspid	Intermediate/long and sparse
Characidium steindachneri	2	0.24 (0.03)	0.10 (0.00)	0.60 (0.03)	Terminal	0.43 (0.03)	Unicuspid	Intermediate/long and sparse
Charax condei	3	0.30 (0.01)	0.10 (0.01)	0.63 (0.01)	Sub-terminal	0.84 (0.09)	Conical	Intermediate/long and sparse
Charax gibbosus	3	0.38 (0.02)	0.12 (0.00)	0.63 (0.07)	Superior	0.79 (0.03)	Conical	Intermediate/long and sparse
Cheirodontops geayi	6	0.31 (0.01)	0.12 (0.01)	0.59 (0.04)	Superior	0.54 (0.01)	Multicuspid	Long and comb-like
Cichla orinocensis	1	0.30 (NA)	0.14 (NA)	1.07 (NA)	Terminal	1.05 (NA)	Conical	Intermediate/long and sparse
Cichlasoma orinocense	3	0.55 (0.01)	0.28 (0.02)	1.17 (0.09)	Terminal	0.41 (0.03)	Multicuspid	Short/blunt/toothlike
Citharichthys spilopterus	6	0.44 (0.01)	0.06 (0.02)	0.56 (0.07)	Terminal	0.75 (0.28)	Conical	Intermediate/long and sparse
Clarias gariepinus	3	0.16 (0.00)	0.16 (0.01)	0.78 (0.12)	Terminal	0.81 (0.05)	Conical	Intermediate/long and sparse
Clarias ngamensis	3	0.17 (0.02)	0.15 (0.02)	0.86 (0.09)	Terminal	0.74 (0.04)	Conical	Intermediate/long and sparse
Clarias stappersii	3	0.17 (0.00)	0.15 (0.01)	0.90 (0.11)	Terminal	0.88 (0.09)	Conical	Intermediate/long and sparse
Clarias theodorae	3	0.13 (0.01)	0.10 (0.01)	0.76 (0.11)	Sub-terminal	0.70 (0.06)	Conical	Long and comb-like
Copella eigenmanni	3	0.16 (0.01)	0.09 (0.00)	0.75 (0.16)	Superior	0.70 (0.01)	Conical	Short/blunt/toothlike

Table A.3 Continued.

Species	N	Maximum body depth	Maximum body width	Gut length	Mouth orientation	Mouth width	Tooth shape	Gill raker shape
Coptodon rendalli	3	0.50 (0.01)	0.19 (0.02)	7.38 (0.23)	Terminal	0.60 (0.06)	Conical	Intermediate/long and sparse
Corydoras aeneus	3	0.41 (0.03)	0.30 (0.02)	1.14 (0.11)	Inferior	0.23 (0.03)	Absent	Absent
Corydoras habrosus	3	0.34 (0.01)	0.27 (0.01)	1.03 (0.03)	Inferior	0.33 (0.02)	Absent	Absent
Corydoras septentrionalis	3	0.39 (0.01)	0.28 (0.01)	0.94 (0.06)	Sub-terminal	0.27 (0.02)	Absent	Absent
Corynopoma riisei	3	0.30 (0.01)	0.13 (0.00)	0.84 (0.05)	Superior	0.61 (0.05)	Multicuspid	Intermediate/long and sparse
Creagrutus melasma	3	0.32 (0.01)	0.16 (0.01)	0.97 (0.06)	Sub-terminal	0.49 (0.03)	Multicuspid	Short/blunt/toothlike
Crenicichla geayi	3	0.21 (0.01)	0.18 (0.01)	0.87 (0.11)	Superior	0.64 (0.08)	Multicuspid	Short/blunt/toothlike
Crenicichla saxatilis	3	0.24 (0.01)	0.16 (0.02)	0.77 (0.03)	Superior	0.87 (0.08)	Conical	Short/blunt/toothlike
Cryptoheros sajica	5	0.51 (0.00)	0.21 (0.01)	1.90 (0.04)	Terminal	0.33 (0.02)	Conical	Short/blunt/toothlike
Cryptoheros septemfasciatus	3	0.50 (0.04)	0.21 (0.01)	1.12 (0.24)	Terminal	0.62 (0.07)	Conical	Short/blunt/toothlike
Ctenobrycon spilurus	3	0.46 (0.00)	0.13 (0.01)	0.69 (0.02)	Terminal	0.53 (0.01)	Multicuspid	Long and comb-like
Ctenogobius boleosoma	3	0.18 (0.01)	0.12 (0.03)	0.47 (0.04)	Sub-terminal	0.86 (0.17)	Conical	Short/blunt/toothlike
Ctenogobius claytonia	3	0.19 (0.01)	0.19 (0.01)	0.72 (0.00)	Sub-terminal	0.56 (0.02)	Multicuspid	Short/blunt/toothlike
Curimata cyprinoides	3	0.37 (0.01)	0.15 (0.02)	8.18 (0.28)	Sub-terminal	0.53 (0.06)	Absent	Intermediate/long and sparse
Curimatopsis evelynae	19	0.27 (0.01)	0.14 (0.02)	5.89 (2.07)	Terminal	0.61 (0.11)	Absent	Short/blunt/toothlike
Cynodonichthys isthmensis	3	0.21 (0.00)	0.19 (0.00)	0.38 (0.04)	Superior	0.48 (0.08)	Multicuspid	Short/blunt/toothlike
Cynoscion arenarius	3	0.26 (0.01)	0.12 (0.01)	0.82 (0.02)	Terminal	0.72 (0.04)	Conical	Intermediate/long and sparse
Cynoscion nebulosus	3	0.24 (0.01)	0.11 (0.01)	0.67 (0.09)	Terminal	0.86 (0.09)	Conical	Intermediate/long and sparse
Cyphocharax spilurus	37	0.29 (0.03)	0.15 (0.01)	13.77 (1.50)	Terminal	0.50 (0.10)	Absent	Short/blunt/toothlike
Cyphomyrus discorhynchus	3	0.32 (0.01)	0.11 (0.01)	0.69 (0.02)	Sub-terminal	0.39 (0.03)	Multicuspid	Short/blunt/toothlike

Table A.3 Continued.

Species	N	Maximum body depth	Maximum body width	Gut length	Mouth orientation	Mouth width	Tooth shape	Gill raker shape
Cyprinodon variegatus variegatus	3	0.41 (0.01)	0.21 (0.03)	2.54 (0.38)	Terminal	0.37 (0.03)	Conical	Intermediate/long and sparse
Cyprinus carpio	3	0.36 (0.05)	0.19 (0.02)	3.07 (0.87)	Sub-terminal	0.35 (0.01)	Absent	Long and comb-like
Dormitator latifrons	3	0.30 (0.02)	0.16 (0.01)	2.12 (0.26)	Terminal	0.60 (0.08)	Conical	Long and comb-like
Dormitator maculatus	3	0.33 (0.01)	0.22 (0.02)	1.56 (0.44)	Terminal	0.50 (0.01)	Unicuspid	Absent
Dorosoma cepedianum	6	0.37 (0.02)	0.12 (0.01)	2.83 (0.27)	Terminal	0.46 (0.08)	Absent	Long and comb-like
Dorosoma petenense	3	0.34 (0.01)	0.11 (0.01)	1.81 (0.21)	Terminal	0.70 (0.09)	Absent	Long and comb-like
Eigenmannia virescens	3	0.16 (0.01)	0.07 (0.00)	0.28 (0.01)	Terminal	0.38 (0.04)	Absent	Short/blunt/toothlike
Eleotris amblyopsis	3	0.22 (0.02)	0.27 (0.01)	0.49 (0.10)	Superior	0.58 (0.06)	Multicuspid	Short/blunt/toothlike
Eleotris picta	3	0.20 (0.00)	0.19 (0.01)	0.74 (0.05)	Superior	0.67 (0.07)	Conical	Short/blunt/toothlike
Eleotris Pisonis	3	0.24 (0.02)	0.27 (0.02)	0.62 (0.07)	Superior	0.60 (0.06)	Multicuspid	Short/blunt/toothlike
Entomocorus gameroi	4	0.28 (0.00)	0.22 (0.00)	0.75 (NA)	Terminal	0.53 (0.02)	Absent	Intermediate/long and sparse
Eucinostomus jonesii	1	0.36 (NA)	0.13 (NA)	0.78 (NA)	Terminal	0.46 (NA)	Conical	Short/blunt/toothlike
Evorthodus lyricus	3	0.23 (0.00)	0.21 (0.00)	1.63 (0.14)	Sub-terminal	0.55 (0.07)	Unicuspid	Absent
Fundulus confluentus	6	0.24 (0.02)	0.17 (0.02)	0.70 (0.06)	Terminal	0.39 (0.04)	Conical	Short/blunt/toothlike
Fundulus grandis	3	0.26 (0.01)	0.16 (0.01)	0.63 (0.02)	Terminal	0.58 (0.06)	Conical	Short/blunt/toothlike
Fundulus pulvereus	3	0.22 (0.01)	0.16 (0.00)	0.68 (0.07)	Superior	0.38 (0.03)	Conical	Short/blunt/toothlike
Gephyrocharax Valencia	3	0.28 (0.00)	0.11 (0.01)	0.76 (0.20)	Superior	0.56 (0.03)	Multicuspid	Intermediate/long and sparse
Gobiomorus dormitory	3	0.17 (0.01)	0.19 (0.01)	0.39 (0.07)	Superior	0.64 (0.04)	Multicuspid	Short/blunt/toothlike
Gobiomorus maculatus	3	0.20 (0.00)	0.15 (0.00)	0.51 (0.02)	Terminal	0.84 (0.04)	Conical	Short/blunt/toothlike
Gobiosoma bosc	3	0.21 (0.01)	0.13 (0.01)	0.53 (0.13)	Terminal	0.83 (0.08)	Conical	Short/blunt/toothlike
Gobiosoma robustum	4	0.19 (0.02)	0.12 (0.02)	0.53 (0.10)	Terminal	0.81 (0.15)	Conical	Short/blunt/toothlike

Table A.3 Continued.

Species	N	Maximum body depth	Maximum body width	Gut length	Mouth orientation	Mouth width	Tooth shape	Gill raker shape
Gobiosoma spes	5	0.19 (0.01)	0.14 (0.01)	0.82 (0.12)	Terminal	0.92 (0.08)	Conical	Short/blunt/toothlike
Gymnotus carapo	3	0.14 (0.01)	0.08 (0.00)	0.47 (0.04)	Superior	0.62 (0.07)	Multicuspid	Short/blunt/toothlike
Gymnotus cylindricus	3	0.08 (0.00)	0.05 (0.00)	0.98 (NA)	Superior	0.54 (0.03)	Absent	Short/blunt/toothlike
Hemicaranx amblyrhynchus	3	0.45 (0.01)	0.11 (0.01)	0.93 (0.21)	Terminal	0.81 (0.11)	Conical	Intermediate/long and sparse
Hemichromis elongatus	3	0.36 (0.03)	0.17 (0.01)	1.20 (0.24)	Superior	0.72 (0.06)	Multicuspid	Long and comb-like
Hemichromis fasciatus	3	0.37 (0.00)	0.17 (0.01)	0.92 (0.19)	Terminal	0.66 (0.08)	Conical	Intermediate/long and sparse
Hemigrammocharax machadoi	3	0.22 (0.00)	0.12 (0.00)	0.52 (0.03)	Sub-terminal	0.29 (0.02)	Conical	Intermediate/long and sparse
Hemigrammocharax multifasciatus	3	0.20 (0.03)	0.12 (0.00)	0.69 (0.05)	Sub-terminal	0.34 (0.02)	Conical	Intermediate/long and sparse
Hemigrammus analis	94	0.25 (0.02)	0.13 (0.01)	1.11 (NA)	Terminal	0.60 (0.08)	Multicuspid	Intermediate/long and sparse
Hemigrammus barrigonae	21	0.27 (0.04)	0.14 (0.01)	0.85 (0.17)	Terminal	0.57 (0.06)	Multicuspid	Intermediate/long and sparse
Hemigrammus bellottii	3	0.31 (0.01)	0.12 (0.01)	0.86 (0.12)	Terminal	0.45 (0.05)	Multicuspid	Short/blunt/toothlike
Hemigrammus elegans	6	0.32 (0.01)	0.12 (0.01)	1.10 (0.00)	Terminal	0.52 (0.03)	Multicuspid	Intermediate/long and sparse
Hemigrammus marginatus	3	0.32 (0.02)	0.11 (0.00)	0.72 (0.05)	Terminal	0.59 (0.03)	Multicuspid	Intermediate/long and sparse
Hemigrammus micropterus	10	0.25 (0.01)	0.11 (0.01)	0.73 (0.06)	Terminal	0.64 (0.05)	Multicuspid	Intermediate/long and sparse
Hemigrammus microstomus	23	0.25 (0.01)	0.12 (0.01)	0.77 (0.03)	Terminal	0.70 (0.24)	Multicuspid	Intermediate/long and sparse
Hemigrammus rhodostomus	17	0.25 (0.02)	0.13 (0.01)	1.49 (0.91)	Terminal	0.46 (0.10)	Multicuspid	Intermediate/long and sparse
Hemigrammus rodwayi	3	0.33 (0.01)	0.12 (0.01)	0.77 (0.06)	Terminal	0.56 (0.03)	Multicuspid	Intermediate/long and sparse
Hemigrammus stictus	4	0.29 (0.01)	0.11 (0.00)	1.21 (0.16)	Terminal	0.58 (0.08)	Multicuspid	Intermediate/long and sparse

Table A.3 Continued.

Species	N	Maximum body depth	Maximum body width	Gut length	Mouth orientation	Mouth width	Tooth shape	Gill raker shape
Hemigrammus vorderwinkleri	3	0.33 (0.01)	0.14 (0.00)	0.85 (0.16)	Terminal	0.48 (0.04)	Multicuspid	Intermediate/long and sparse
Hepsetus odoe	3	0.23 (0.03)	0.12 (0.01)	0.68 (0.12)	Terminal	0.65 (0.05)	Conical	Intermediate/long and sparse
Heterocharax macrolepis	3	0.33 (0.01)	0.12 (0.01)	0.70 (0.08)	Superior	0.63 (0.08)	Conical	Intermediate/long and sparse
Hippopotamyrus ansorgii	1	0.24 (NA)	0.10 (NA)	0.72 (NA)	Sub-terminal	0.40 (NA)	Multicuspid	Short/blunt/toothlike
Hoplerythrinus unitaeniatus	3	0.25 (0.01)	0.20 (0.01)	0.95 (0.02)	Terminal	0.74 (0.02)	Conical	Intermediate/long and sparse
Hoplias malabaricus	3	0.21 (0.01)	0.18 (0.01)	0.57 (0.03)	Superior	0.73 (0.06)	Conical	Short/blunt/toothlike
Hoplosternum littorale	3	0.31 (0.01)	0.27 (0.00)	1.34 (0.19)	Inferior	0.40 (0.01)	Absent	Short/blunt/toothlike
Hydrocynus vittatus	3	0.28 (0.01)	0.12 (0.01)	1.20 (0.38)	Terminal	0.54 (0.03)	Triangular serrated	Intermediate/long and sparse
Hyphessobrycon metae	3	0.28 (0.01)	0.13 (0.01)	0.48 (0.10)	Terminal	0.67 (0.02)	Multicuspid	Intermediate/long and sparse
Hyphessobrycon savagei	3	0.44 (0.02)	0.12 (0.00)	1.12 (0.13)	Terminal	0.65 (0.03)	Multicuspid	Intermediate/long and sparse
Hyphessobrycon sweglesi	19	0.30 (0.02)	0.14 (0.01)	1.13 (0.14)	Superior	0.68 (0.10)	Multicuspid	Intermediate/long and sparse
Hyphessobrycon tortuguerae	2	0.35 (0.02)	0.11 (0.01)	0.95 (0.00)	Terminal	0.65 (0.02)	Multicuspid	Intermediate/long and sparse
Hypoptopoma machadoi	4	0.21 (0.01)	0.27 (0.01)	5.14 (0.75)	Inferior	0.34 (0.01)	Unicuspid	Long and comb-like
Hypostomus argus	3	0.22 (0.03)	0.33 (0.03)	13.30 (2.65)	Inferior	0.28 (0.04)	Unicuspid	Absent
Hypostomus plecostomoides	4	0.23 (0.00)	0.27 (0.01)	13.30 (0.00)	Inferior	0.25 (0.03)	Unicuspid	Long and comb-like
Ictalurus punctatus	3	0.22 (0.01)	0.17 (0.01)	0.88 (0.12)	Sub-terminal	0.62 (0.04)	Unicuspid	Short/blunt/toothlike
Ictiobus bubalus	3	0.38 (0.04)	0.18 (0.01)	2.70 (0.51)	Sub-terminal	0.27 (0.03)	Absent	Long and comb-like
Iguanodectes spilurus	3	0.18 (0.01)	0.09 (0.00)	1.02 (0.03)	Terminal	0.60 (0.03)	Multicuspid	Intermediate/long and sparse

Table A.3 Continued.

Species	**N**	**Maximum body depth**	**Maximum body width**	**Gut length**	**Mouth orientation**	**Mouth width**	**Tooth shape**	**Gill raker shape**
Jupiaba abramoides	3	0.28 (0.02)	0.13 (0.01)	0.94 (0.11)	Terminal	0.59 (0.08)	Multicuspid	Intermediate/long and sparse
Labeo lunatus	3	0.28 (0.02)	0.16 (0.02)	9.32 (0.42)	Inferior	0.51 (0.07)	Absent	Short/blunt/toothlike
Lagodon rhomboides	3	0.40 (0.01)	0.16 (0.02)	1.03 (0.04)	Terminal	0.46 (0.08)	Multicuspid	Intermediate/long and sparse
Leiostomus xanthurus	3	0.34 (0.01)	0.13 (0.02)	1.05 (0.03)	Sub-terminal	0.50 (0.05)	Conical	Intermediate/long and sparse
Lepisosteus oculatus	6	0.10 (0.01)	0.09 (0.01)	0.70 (0.05)	Terminal	0.49 (0.06)	Conical	Absent
Lepisosteus osseus	3	0.08 (0.00)	0.08 (0.00)	0.68 (0.01)	Terminal	0.43 (0.01)	Conical	Absent
Lepomis cyanellus	3	0.39 (0.00)	0.19 (0.02)	0.78 (0.03)	Terminal	0.64 (0.05)	Conical	Intermediate/long and sparse
Lepomis gulosus	3	0.45 (0.01)	0.20 (0.02)	0.85 (0.06)	Terminal	0.62 (0.02)	Conical	Intermediate/long and sparse
Lepomis humilis	3	0.36 (0.01)	0.16 (0.01)	0.96 (0.25)	Terminal	0.64 (0.02)	Conical	Intermediate/long and sparse
Lepomis macrochirus	3	0.46 (0.02)	0.17 (0.01)	0.97 (0.03)	Terminal	0.52 (0.07)	Conical	Long and comb-like
Lepomis megalotis	3	0.48 (0.01)	0.19 (0.01)	0.99 (0.07)	Terminal	0.53 (0.04)	Conical	Short/blunt/toothlike
Lepomis microlophus	3	0.41 (0.00)	0.17 (0.01)	1.11 (0.10)	Terminal	0.55 (0.06)	Conical	Short/blunt/toothlike
Lepomis miniatus	3	0.48 (0.02)	0.20 (0.03)	0.79 (0.13)	Terminal	0.48 (0.03)	Conical	Intermediate/long and sparse
Leporinus friderici	3	0.36 (0.02)	0.19 (0.01)	1.45 (0.35)	Sub-terminal	0.39 (0.00)	Triangular serrated	Intermediate/long and sparse
Loricariichthys brunneus	3	0.13 (0.00)	0.20 (0.00)	1.12 (0.08)	Inferior	0.28 (0.02)	Absent	Short/blunt/toothlike
Lucania parva	3	0.25 (0.01)	0.14 (0.01)	0.64 (0.23)	Terminal	0.45 (0.02)	Conical	Short/blunt/toothlike
Lutjanus argentiventris	3	0.39 (0.02)	0.19 (0.01)	0.49 (0.02)	Terminal	0.59 (0.02)	Conical	Intermediate/long and sparse
Lutjanus Colorado	3	0.37 (0.01)	0.17 (0.01)	0.70 (0.00)	Terminal	0.63 (0.14)	Conical	Intermediate/long and sparse
Lutjanus jocu	3	0.39 (0.01)	0.19 (0.01)	0.82 (NA)	Terminal	0.81 (0.02)	Conical	Short/blunt/toothlike
Lutjanus novemfasciatus	3	0.34 (0.01)	0.17 (0.01)	0.59 (0.10)	Terminal	0.86 (0.12)	Conical	Intermediate/long and sparse
Marcusenius macrolepidotus	6	0.26 (0.04)	0.10 (0.02)	0.51 (0.12)	Superior	0.47 (0.07)	Conical	Intermediate/long and sparse

Table A.3 Continued.

Species	**N**	**Maximum body depth**	**Maximum body width**	**Gut length**	**Mouth orientation**	**Mouth width**	**Tooth shape**	**Gill raker shape**
Markiana geayi	5	0.47 (0.01)	0.16 (0.01)	1.33 (0.23)	Terminal	0.58 (0.01)	Multicuspid	Intermediate/long and sparse
Mastacembelus frenatus	6	0.08 (0.01)	0.05 (0.00)	0.48 (0.11)	Terminal	0.40 (0.06)	Conical	Absent
Menidia beryllina	3	0.18 (0.01)	0.10 (0.01)	0.70 (0.05)	Terminal	0.61 (0.05)	Conical	Intermediate/long and sparse
Menidia peninsulae	3	0.20 (0.00)	0.11 (0.01)	0.55 (0.03)	Terminal	0.68 (0.04)	Conical	Long and comb-like
Metynnis hypsauchen	3	0.86 (0.02)	0.14 (0.01)	2.99 (0.68)	Terminal	0.51 (0.03)	Multicuspid	Long and comb-like
Microglanis iheringi	3	0.22 (0.02)	0.29 (0.01)	0.55 (0.04)	Terminal	0.66 (0.02)	Unicuspid	Short/blunt/toothlike
Microgobius gulosus	3	0.19 (0.01)	0.10 (0.02)	0.48 (0.08)	Terminal	1.03 (0.13)	Conical	Short/blunt/toothlike
Microphis lineatus	3	0.05 (0.00)	0.04 (0.00)	0.36 (0.02)	Superior	0.43 (0.05)	Absent	Absent
Micropogonias undulatus	3	0.33 (0.01)	0.11 (0.01)	0.91 (0.04)	Sub-terminal	0.72 (0.12)	Conical	Intermediate/long and sparse
Micropterus punctulatus	3	0.26 (0.01)	0.15 (0.00)	1.05 (0.05)	Terminal	0.79 (0.06)	Conical	Intermediate/long and sparse
Micropterus salmoides	3	0.29 (0.02)	0.15 (0.02)	1.04 (0.03)	Terminal	0.78 (0.13)	Conical	Short/blunt/toothlike
Mikrogeophagus ramirezi	3	0.42 (0.01)	0.16 (0.01)	1.20 (0.07)	Terminal	0.53 (0.02)	Conical	Short/blunt/toothlike
Moenkhausia copei	86	0.29 (0.02)	0.13 (0.01)	1.20 (0.21)	Terminal	0.59 (0.09)	Multicuspid	Intermediate/long and sparse
Moenkhausia lepidura	42	0.29 (0.03)	0.13 (0.01)	1.05 (0.18)	Terminal	0.53 (0.07)	Multicuspid	Intermediate/long and sparse
Mormyrus lacerda	3	0.23 (0.01)	0.14 (0.02)	0.99 (0.00)	Sub-terminal	0.31 (0.08)	Conical	Short/blunt/toothlike
Mugil cephalus	3	0.24 (0.01)	0.18 (0.05)	4.17 (0.31)	Terminal	0.41 (0.11)	Absent	Intermediate/long and sparse
Mugil curema	3	0.28 (0.01)	0.11 (0.02)	2.31 (0.48)	Terminal	0.52 (0.09)	Unicuspid	Long and comb-like
Myloplus rubripinnis	1	0.75 (NA)	0.17 (NA)	2.50 (NA)	Terminal	0.69 (NA)	Multicuspid	Intermediate/long and sparse
Mylossoma duriventre	3	0.77 (0.03)	0.15 (0.01)	1.88 (0.03)	Terminal	0.68 (0.03)	Multicuspid	Intermediate/long and sparse
Ochmacanthus alternus	3	0.15 (0.01)	0.18 (0.01)	0.42 (0.06)	Inferior	0.71 (0.06)	Unicuspid	Absent
Odontostilbe pulchra	3	0.34 (0.01)	0.12 (0.01)	1.02 (0.02)	Terminal	0.60 (0.01)	Multicuspid	Long and comb-like

Table A.3 Continued.

Species	**N**	**Maximum body depth**	**Maximum body width**	**Gut length**	**Mouth orientation**	**Mouth width**	**Tooth shape**	**Gill raker shape**
Oreochromis andersonii	3	0.43 (0.02)	0.18 (0.02)	5.03 (1.46)	Terminal	0.56 (0.09)	Conical	Long and comb-like
Oreochromis macrochir	3	0.49 (0.02)	0.17 (0.01)	7.15 (1.57)	Terminal	0.51 (0.04)	Conical	Long and comb-like
Parachromis dovii	3	0.38 (0.01)	0.20 (0.01)	0.90 (0.22)	Superior	0.65 (0.15)	Conical	Short/blunt/toothlike
Parachromis friedrichsthalii	3	0.43 (0.01)	0.22 (0.01)	0.84 (0.12)	Superior	0.50 (0.06)	Multicuspid	Short/blunt/toothlike
Paralichthys lethostigma	3	0.46 (0.02)	0.08 (0.01)	0.59 (0.12)	Terminal	0.67 (0.08)	Conical	Intermediate/long and sparse
Paraneetroplus maculicauda	3	0.55 (0.01)	0.19 (0.01)	2.06 (0.41)	Terminal	0.46 (0.03)	Unicuspid	Short/blunt/toothlike
Parapristella georgiae	59	0.25 (0.02)	0.13 (0.01)	1.07 (0.03)	Terminal	0.67 (0.10)	Multicuspid	Intermediate/long and sparse
Parauchenoglanis ngamensis	3	0.21 (0.01)	0.19 (0.02)	0.93 (0.06)	Terminal	0.72 (0.07)	Unicuspid	Intermediate/long and sparse
Petrocephalus catostoma	3	0.36 (0.02)	0.09 (0.00)	0.62 (0.06)	Sub-terminal	0.82 (0.12)	Unicuspid	Intermediate/long and sparse
Phallichthys amates	3	0.38 (0.01)	0.21 (0.01)	4.76 (0.72)	Superior	0.54 (0.02)	Unicuspid	Intermediate/long and sparse
Pharyngochromis acuticeps	6	0.37 (0.01)	0.18 (0.00)	1.17 (0.13)	Terminal	0.61 (0.04)	Conical	Short/blunt/toothlike
Piabucina erythrinoides	3	0.21 (0.01)	0.15 (0.01)	1.12 (0.03)	Superior	0.59 (0.05)	Multicuspid	Short/blunt/toothlike
Pimelodella linami	3	0.20 (0.00)	0.18 (0.01)	0.63 (0.10)	Sub-terminal	0.50 (0.02)	Absent	Short/blunt/toothlike
Pimelodella metae	3	0.19 (0.02)	0.18 (0.01)	0.47 (0.03)	Sub-terminal	0.48 (0.02)	Absent	Absent
Pimelodus blochii	3	0.26 (0.02)	0.19 (0.01)	0.93 (0.05)	Terminal	0.59 (0.03)	Unicuspid	Intermediate/long and sparse
Poecilia gillii	3	0.34 (0.01)	0.21 (0.01)	3.18 (0.43)	Terminal	0.51 (0.02)	Unicuspid	Intermediate/long and sparse
Poecilia latipinna	3	0.35 (0.04)	0.19 (0.03)	2.58 (0.28)	Superior	0.41 (0.07)	Conical	Short/blunt/toothlike
Poecilia Mexicana	3	0.30 (0.01)	0.17 (0.02)	2.58 (0.29)	Superior	0.47 (0.04)	Conical	Intermediate/long and sparse
Poecilia reticulata	3	0.27 (0.01)	0.22 (0.00)	1.84 (0.21)	Superior	0.42 (0.02)	Unicuspid	Intermediate/long and sparse

Table A.3 Continued.

Species	**N**	**Maximum body depth**	**Maximum body width**	**Gut length**	**Mouth orientation**	**Mouth width**	**Tooth shape**	**Gill raker shape**
Poecilia sphenops	3	0.34 (0.03)	0.22 (0.01)	4.07 (0.63)	Superior	0.35 (0.05)	Conical	Intermediate/long and sparse
Poeciliopsis turrubarensis	3	0.27 (0.00)	0.17 (0.01)	1.39 (0.10)	Superior	0.30 (0.03)	Conical	Intermediate/long and sparse
Pogonias cromis	3	0.37 (0.02)	0.16 (0.03)	1.10 (0.09)	Sub-terminal	0.57 (0.10)	Conical	Short/blunt/toothlike
Pollimyrus castelnaui	3	0.29 (0.01)	0.09 (0.01)	0.62 (0.03)	Sub-terminal	0.67 (0.10)	Unicuspid	Short/blunt/toothlike
Pomadasys crocro	3	0.33 (0.01)	0.19 (0.01)	0.63 (0.06)	Sub-terminal	0.65 (0.07)	Multicuspid	Short/blunt/toothlike
Pomoxis annularis	3	0.37 (0.02)	0.13 (0.00)	0.81 (0.02)	Terminal	0.80 (0.07)	Conical	Long and comb-like
Pomoxis nigromaculatus	3	0.42 (0.03)	0.14 (0.03)	0.98 (0.21)	Superior	0.69 (0.11)	Conical	Long and comb-like
Pristobrycon striolatus	2	0.56 (0.00)	0.18 (0.02)	4.78 (0.32)	Superior	0.63 (0.08)	Triangular serrated	Intermediate/long and sparse
Prochilodus mariae	3	0.41 (0.01)	0.19 (0.01)	3.38 (0.17)	Sub-terminal	0.65 (0.05)	Absent	Absent
Pseudocrenilabrus nicholsi	3	0.38 (0.01)	0.19 (0.01)	0.88 (0.06)	Terminal	0.56 (0.06)	Conical	Short/blunt/toothlike
Pseudophallus mindii	3	0.03 (0.00)	0.03 (0.00)	0.22 (0.01)	Superior	0.34 (0.02)	Absent	Short/blunt/toothlike
Pseudophallus starksii	3	0.04 (0.01)	0.03 (0.01)	0.25 (0.01)	Superior	0.33 (0.10)	Absent	Absent
Pterygoplichthys multiradiatus	3	0.21 (0.03)	0.30 (0.02)	15.82 (0.00)	Inferior	0.29 (0.02)	Unicuspid	Absent
Pygocentrus cariba	3	0.56 (0.01)	0.23 (0.00)	1.27 (0.13)	Superior	0.68 (0.01)	Triangular serrated	Intermediate/long and sparse
Pygopristis denticulate	3	0.61 (0.01)	0.14 (0.01)	1.03 (NA)	Terminal	0.73 (0.03)	Multicuspid	Intermediate/long and sparse
Pyrrhulina lugubris	5	0.25 (0.01)	0.14 (0.00)	0.71 (0.10)	Superior	0.61 (0.06)	Multicuspid	Short/blunt/toothlike
Rachovia maculipinnis	4	0.29 (0.00)	0.21 (0.01)	0.56 (NA)	Superior	0.52 (0.04)	Conical	Short/blunt/toothlike
Rhamdia nicaraguensis	3	0.18 (0.00)	0.19 (0.01)	0.82 (0.11)	Sub-terminal	0.59 (0.08)	Unicuspid	Intermediate/long and sparse
Rhamdia quelen	3	0.21 (0.01)	0.19 (0.01)	1.17 (NA)	Terminal	0.63 (0.02)	Unicuspid	Intermediate/long and sparse

Table A.3 Continued.

Species	**N**	**Maximum body depth**	**Maximum body width**	**Gut length**	**Mouth orientation**	**Mouth width**	**Tooth shape**	**Gill raker shape**
Rhamphichthys marmoratus	6	0.10 (0.00)	0.04 (0.00)	0.41 (0.20)	Sub-terminal	0.33 (0.07)	Absent	Short/blunt/toothlike
Rineloricaria caracasensis	3	0.12 (0.00)	0.17 (0.01)	2.87 (0.25)	Inferior	0.27 (0.02)	Unicuspid	Absent
Roeboides dayi	6	0.38 (0.02)	0.11 (0.01)	0.84 (0.11)	Terminal	0.75 (0.09)	Multicuspid	Intermediate/long and sparse
Roeboides guatemalensis	3	0.36 (0.02)	0.11 (0.00)	0.93 (0.04)	Terminal	0.65 (0.04)	Multicuspid	Short/blunt/toothlike
Sargochromis carlottae	3	0.43 (0.02)	0.17 (0.00)	0.93 (0.02)	Terminal	0.72 (0.14)	Conical	Short/blunt/toothlike
Sargochromis codringtonii	6	0.40 (0.02)	0.16 (0.02)	1.10 (0.15)	Terminal	0.69 (0.09)	Conical	Short/blunt/toothlike
Sargochromis giardia	3	0.48 (0.01)	0.20 (0.02)	1.73 (0.55)	Terminal	0.59 (0.18)	Conical	Short/blunt/toothlike
Satanoperca daemon	3	0.38 (0.01)	0.16 (0.00)	1.07 (0.18)	Sub-terminal	0.61 (0.06)	Conical	Short/blunt/toothlike
Satanoperca jurupari	6	0.42 (0.01)	0.18 (0.01)	1.19 (0.35)	Sub-terminal	0.64 (0.12)	Conical	Short/blunt/toothlike
Schilbe intermedius	3	0.28 (0.01)	0.12 (0.01)	0.67 (0.24)	Superior	1.21 (0.13)	Conical	Intermediate/long and sparse
Schizodon isognathus	3	0.28 (0.01)	0.17 (0.01)	1.83 (0.00)	Terminal	0.44 (0.03)	Triangular serrated	Intermediate/long and sparse
Sciaenops ocellatus	3	0.26 (0.01)	0.15 (0.03)	0.73 (0.13)	Terminal	0.65 (0.14)	Conical	Intermediate/long and sparse
Serrabrycon magoi	3	0.26 (0.00)	0.12 (0.01)	0.61 (0.07)	Terminal	0.62 (0.04)	Multicuspid	Intermediate/long and sparse
Serranochromis altus	3	0.40 (0.03)	0.18 (0.01)	1.32 (0.23)	Superior	0.54 (0.02)	Conical	Short/blunt/toothlike
Serranochromis angusticeps	3	0.39 (0.02)	0.16 (0.04)	1.07 (0.02)	Superior	0.59 (0.16)	Conical	Short/blunt/toothlike
Serranochromis macrocephalus	3	0.39 (0.03)	0.18 (0.01)	1.24 (0.39)	Superior	0.74 (0.01)	Conical	Short/blunt/toothlike
Serranochromis robustus	3	0.36 (0.02)	0.17 (0.02)	0.79 (0.12)	Terminal	0.90 (0.27)	Conical	Short/blunt/toothlike
Serrasalmus eigenmanni	2	0.51 (0.05)	0.14 (0.02)	0.85 (NA)	Terminal	0.68 (0.06)	Triangular serrated	Short/blunt/toothlike

Table A.3 Continued.

Species	**N**	**Maximum body depth**	**Maximum body width**	**Gut length**	**Mouth orientation**	**Mouth width**	**Tooth shape**	**Gill raker shape**
Serrasalmus medinai	8	0.60 (0.01)	0.17 (0.02)	1.65 (0.05)	Superior	0.69 (0.03)	Triangular serrated	Short/blunt/toothlike
Serrasalmus rhombeus	3	0.57 (0.03)	0.16 (0.02)	1.10 (0.30)	Terminal	0.86 (0.05)	Triangular serrated	Short/blunt/toothlike
Sicydium plumieri	3	0.17 (0.00)	0.15 (0.01)	2.59 (0.19)	Sub-terminal	0.67 (0.08)	Unicuspid	Absent
Sphoeroides annulatus	3	0.29 (0.01)	0.28 (0.02)	0.95 (NA)	Terminal	0.30 (0.04)	Unicuspid	Short/blunt/toothlike
Sphoeroides testudineus	3	0.31 (0.04)	0.31 (0.05)	1.06 (0.06)	Terminal	0.28 (0.02)	Unicuspid	Short/blunt/toothlike
Steindachnerina argentea	3	0.39 (0.02)	0.19 (0.00)	12.48 (0.83)	Sub-terminal	0.52 (0.06)	Absent	Absent
Sternopygus macrurus	3	0.11 (0.00)	0.04 (0.00)	0.35 (0.01)	Terminal	0.45 (0.08)	Conical	Short/blunt/toothlike
Strongylura timucu	6	0.05 (0.00)	0.05 (0.01)	0.42 (0.01)	Terminal	0.53 (0.01)	Conical	Absent
Synbranchus marmoratus	6	0.05 (0.00)	0.04 (0.00)	0.63 (0.02)	Sub-terminal	0.72 (0.03)	Conical	Absent
Syngnathus scovelli	3	0.04 (0.01)	0.03 (0.00)	0.28 (0.01)	Superior	0.36 (0.03)	Absent	Short/blunt/toothlike
Synodontis leopardinus	3	0.27 (0.02)	0.25 (0.01)	1.61 (0.25)	Inferior	0.49 (0.12)	Unicuspid	Long and comb-like
Synodontis macrostigma	3	0.26 (0.02)	0.21 (0.00)	2.78 (0.82)	Sub-terminal	0.47 (0.05)	Unicuspid	Intermediate/long and sparse
Synodontis nigromaculatus	3	0.24 (0.01)	0.25 (0.01)	2.36 (0.43)	Inferior	0.52 (0.03)	Unicuspid	Long and comb-like
Synodontis woosnami	3	0.26 (0.01)	0.22 (0.03)	2.20 (0.13)	Inferior	0.57 (0.06)	Unicuspid	Long and comb-like
Tetragonopterus argenteus	3	0.58 (0.03)	0.18 (0.01)	1.47 (0.13)	Terminal	0.66 (0.01)	Multicuspid	Long and comb-like
Thoracocharax stellatus	3	0.58 (0.01)	0.15 (0.01)	0.80 (0.01)	Superior	0.67 (0.03)	Multicuspid	Short/blunt/toothlike
Tilapia ruweti	6	0.39 (0.02)	0.18 (0.01)	3.13 (0.73)	Terminal	0.57 (0.12)	Multicuspid	Short/blunt/toothlike
Tilapia sparrmanii	3	0.50 (0.02)	0.21 (0.01)	4.66 (0.45)	Terminal	0.52 (0.06)	Conical	Intermediate/long and sparse

Table A.3 Continued.

Species	**N**	**Maximum body depth**	**Maximum body width**	**Gut length**	**Mouth orientation**	**Mouth width**	**Tooth shape**	**Gill raker shape**
Trachelyopterus galeatus	3	0.28 (0.02)	0.28 (0.00)	0.85 (0.17)	Superior	0.54 (0.02)	Unicuspid	Absent
Trinectes paulistanus	3	0.55 (0.02)	0.12 (0.00)	0.66 (0.00)	Sub-terminal	0.50 (0.05)	Conical	Short/blunt/toothlike
Triportheus orinocensis	3	0.37 (0.01)	0.14 (0.00)	1.12 (0.05)	Superior	0.57 (0.07)	Multicuspid	Long and comb-like
Triportheus venezuelensis	3	0.36 (0.01)	0.14 (0.00)	0.97 (0.02)	Superior	0.60 (0.02)	Multicuspid	Long and comb-like
Xenagoniates bondi	3	0.24 (0.01)	0.08 (0.00)	0.60 (0.00)	Superior	0.61 (0.04)	Conical	Intermediate/long and sparse

Table A.4 List with all species with more than 5 individuals used in the analyses of MTL. N=number of individuals analyzed, SL= standard length.

Species	**N**	**MTL**	**Mean SL (mm)**	**Mean body mass (g)**
Acestrorhynchus heterolepis	5	3.94	111.40	28.79
Acestrorhynchus minimus	19	4.09	48.37	1.37
Achirus lineatus	44	3.28	35.03	2.50
Adinia xenica	57	2.11	22.03	0.29
Adontosternarchus devenanzii	59	3.32	92.75	2.65
Aequidens diadema	20	3.50	54.20	3.62
Ageneiosus inermis	15	3.78	105.15	23.87
Alfaro cultratus	409	3.32	32.88	0.59
Amatitlania nigrofasciata	221	2.71	37.09	1.27
Ameiurus melas	8	2.96	165.38	178.97
Amphilophus alfari	63	3.12	37.14	6.44
Amphilophus citrinellus	112	3.20	78.12	39.93
Amphilophus diquis	7	3.03	41.36	2.40
Amphilophus rostratus	12	2.81	123.65	63.22
Anchoa mitchilli	773	2.92	30.74	0.35
Ancistrus triradiatus	93	2.08	45.38	1.31
Andinoacara pulcher	639	3.00	41.07	2.89
Anguilla rostrate	8	3.51	93.96	2.36
Aphyocharax erythrurus	266	3.40	29.41	0.52
Apistogramma hoignei	194	3.13	22.05	0.25
Aplocheilichthys johnstoni	66	3.19	26.27	0.23
Aplocheilichthys katangae	6	3.03	24.77	0.18
Archocentrus centrarchus	187	3.25	29.57	1.39
Archocentrus multispinosus	21	2.01	54.18	5.72
Ariopsis felis	61	3.66	240.28	218.27
Astronotus ocellatus	87	3.30	94.18	44.57
Astyanax bimaculatus	374	2.59	40.65	2.08
Astyanax fasciatus	587	2.66	47.72	3.81
Astyanax maximus	179	2.59	47.87	4.32
Astyanax superbus	10	3.23	52.40	3.24
Atherinella hubbsi	198	3.27	48.25	1.52
Atractosteus spatula	19	3.36	756.95	5319.42
Awaous banana	7	3.09	80.36	10.35
Awaous tajasica	5	2.82	96.30	18.14
Bairdiella chrysoura	163	3.38	36.48	1.91
Barbus annectens	8	2.41	28.84	0.35

Table A.4 Continued.

Species	**N**	**MTL**	**Mean SL (mm)**	**Mean body mass (g)**
Barbus barotseensis	9	3.11	25.62	0.25
Barbus bifrenatus	5	2.00	35.86	0.69
Barbus multilineatus	5	2.22	25.52	0.25
Barbus paludinosus	54	2.50	66.09	5.07
Barbus poechii	50	2.09	64.43	5.03
Barbus radiatus	8	2.78	38.65	0.89
Belonesox belizanus	72	3.75	63.70	5.93
Brachychalcinus orbicularis	19	3.04	33.14	0.87
Brachyhypopomus brevirostris	61	3.32	110.10	2.37
Brachyhypopomus occidentalis	64	3.27	110.11	2.27
Brachyrhaphis parismina	53	3.42	22.91	0.19
Brachyrhaphis rhabdophora	37	3.04	27.60	0.28
Brevoortia patronus	523	2.04	27.29	0.36
Brycinus lateralis	19	2.66	85.19	9.86
Brycon guatemalensis	126	2.34	179.62	171.22
Brycon whitei	17	2.19	214.76	197.75
Bryconamericus deuterodonoides	157	2.56	24.19	0.28
Bryconamericus motatanensis	458	3.00	30.39	0.61
Bryconops alburnoides	18	3.39	33.56	0.33
Bryconops giacopinii	112	3.52	41.99	1.31
Bunocephalus amaurus	151	3.10	38.21	0.54
Caquetaia kraussii	341	3.41	47.01	8.87
Carlana eigenmanni	9	2.00	46.96	2.16
Catoprion mento	23	3.59	41.26	2.53
Centropomus parallelus	5	3.31	87.14	15.62
Centropomus pectinatus	58	3.33	132.74	85.88
Centropomus undecimalis	10	3.16	212.50	359.60
Characidium pellucidum	25	3.31	17.04	0.08
Characidium pteroides	55	3.27	17.85	0.09
Characidium steindachneri	190	3.28	24.24	0.23
Charax condei	71	3.53	26.00	0.35
Charax gibbosus	216	3.47	49.13	3.60
Cheirodontops geayi	88	3.25	23.03	0.23
Cichla orinocensis	16	4.15	187.94	241.94
Cichlasoma orinocense	225	2.79	43.52	4.21
Citharichthys spilopterus	79	3.22	39.02	2.25

Table A.4 Continued.

Species	**N**	**MTL**	**Mean SL (mm)**	**Mean body mass (g)**
Clarias gariepinus	23	3.68	388.53	795.45
Clarias ngamensis	26	3.51	381.42	449.07
Clarias stappersii	9	3.95	169.90	56.15
Clarias theodorae	77	3.77	140.59	39.48
Copella eigenmanni	38	2.81	20.11	0.07
Corydoras aeneus	154	2.90	34.15	1.43
Corydoras habrosus	203	2.75	17.15	0.19
Corydoras septentrionalis	129	3.17	33.17	1.37
Corynopoma riisei	241	3.43	29.23	0.53
Creagrutus melasma	311	2.85	23.52	0.26
Crenicichla geayi	116	3.41	60.95	3.14
Crenicichla saxatilis	18	3.75	63.72	7.00
Cryptoheros sajica	18	3.43	35.78	1.83
Cryptoheros septemfasciatus	14	3.14	30.58	3.10
Ctenobrycon spilurus	355	2.49	34.36	1.05
Ctenogobius boleosoma	70	2.40	23.65	0.14
Ctenogobius claytonia	101	3.00	36.81	0.57
Curimata cyprinoides	16	2.26	130.43	62.66
Curimatopsis evelynae	146	2.13	21.15	0.27
Cynodonichthys isthmensis	249	3.36	26.74	0.20
Cynoscion arenarius	9	3.41	41.56	16.92
Cynoscion nebulosus	74	3.26	69.19	80.41
Cyphocharax spilurus	248	2.04	28.53	0.86
Cyphomyrus discorhynchus	8	3.50	106.45	16.13
Cyprinodon variegatus variegatus	130	2.03	23.66	0.51
Cyprinus carpio	6	2.07	341.83	1279.29
Dormitator latifrons	6	3.69	49.00	1.60
Dormitator maculatus	220	2.20	45.66	1.40
Dorosoma cepedianum	264	2.11	199.01	203.35
Dorosoma petenense	5	2.11	35.60	0.80
Eigenmannia virescens	138	3.37	98.75	1.70
Eleotris amblyopsis	525	3.41	44.01	1.33
Eleotris picta	16	3.26	76.32	8.59
Eleotris pisonis	105	3.37	74.94	7.35
Entomocorus gameroi	55	3.31	32.43	0.88
Eucinostomus jonesii	5	3.22	67.58	7.94

Table A.4 Continued.

Species	**N**	**MTL**	**Mean SL (mm)**	**Mean body mass (g)**
Evorthodus lyricus	79	2.15	28.01	0.49
Fundulus confluentus	7	3.16	34.76	1.91
Fundulus grandis	94	2.66	33.63	1.88
Fundulus pulvereus	10	3.13	28.07	0.96
Gephyrocharax valencia	333	3.27	28.54	0.45
Gnathocharax steindachneri	38	3.73	17.24	0.09
Gobiomorus dormitor	147	3.44	66.43	11.30
Gobiomorus maculatus	12	3.25	94.88	14.99
Gobiosoma bosc	121	2.85	22.38	0.21
Gobiosoma robustum	10	2.69	18.00	0.10
Gobiosoma spes	9	3.42	25.92	0.29
Gymnotus carapo	281	3.52	145.42	16.19
Gymnotus cylindricus	20	3.31	123.09	8.43
Hemicaranx amblyrhynchus	13	3.23	28.95	0.77
Hemichromis elongatus	27	3.67	62.10	7.15
Hemichromis fasciatus	6	3.99	105.05	31.53
Hemigrammus analis	170	2.68	16.98	0.09
Hemigrammus barrigonae	197	2.61	23.41	0.25
Hemigrammus bellottii	153	3.21	14.03	0.05
Hemigrammus elegans	132	3.19	22.07	0.22
Hemigrammus marginatus	32	3.18	16.06	0.08
Hemigrammus micropterus	212	2.86	23.64	0.25
Hemigrammus microstomus	204	2.29	20.62	0.16
Hemigrammus newboldi	50	2.96	16.10	0.09
Hemigrammus rhodostomus	99	3.06	22.52	0.22
Hemigrammus rodwayi	5	3.02	20.80	0.17
Hemigrammus stictus	168	2.67	21.08	0.18
Hemigrammus vorderwinkleri	107	3.07	14.42	0.05
Hepsetus odoe	71	3.99	206.63	78.45
Heterocharax macrolepis	102	3.66	22.81	0.20
Hippopotamyrus ansorgii	29	3.29	131.93	19.71
Hoplerythrinus unitaeniatus	92	3.85	96.00	21.07
Hoplias malabaricus	413	3.58	65.63	26.04
Hoplosternum littorale	61	2.91	92.36	40.66
Hydrocynus vittatus	133	3.95	221.85	380.71
Hyphessobrycon metae	40	3.56	22.12	0.21
Hyphessobrycon savagei	34	3.23	32.89	0.71

Table A.4 Continued.

Species	**N**	**MTL**	**Mean SL (mm)**	**Mean body mass (g)**
Hyphessobrycon sweglesi	30	3.24	14.93	0.06
Hyphessobrycon tortuguerae	6	3.40	33.57	0.78
Hypoptopoma machadoi	40	2.11	43.12	0.97
Hypoptopoma spectabile	79	2.08	21.31	0.08
Hypostomus argus	87	2.08	79.97	24.55
Hypostomus plecostomoides	5	2.02	90.76	27.36
Ictalurus punctatus	24	3.41	361.42	1373.78
Ictiobus bubalus	16	2.41	122.02	188.22
Iguanodectes spilurus	27	2.59	49.33	1.04
Jupiaba abramoides	35	2.72	74.99	10.27
Labeo lunatus	14	2.01	172.81	97.00
Lagodon rhomboides	346	2.73	38.94	2.77
Leiostomus xanthurus	493	3.25	38.42	1.74
Lepisosteus oculatus	235	3.72	470.64	1113.21
Lepisosteus osseus	84	3.86	764.37	4783.62
Lepomis cyanellus	90	3.45	56.17	8.69
Lepomis gulosus	62	3.58	67.29	16.13
Lepomis humilis	48	3.34	52.82	5.18
Lepomis macrochirus	91	3.38	56.92	7.52
Lepomis megalotis	95	3.24	70.77	16.37
Lepomis microlophus	20	3.16	81.69	23.76
Lepomis miniatus	22	3.29	65.37	10.35
Leporinus friderici	70	2.37	86.45	18.53
Loricariichthys brunneus	41	2.36	165.72	86.58
Lucania parva	119	3.01	24.49	1.02
Lutjanus argentiventris	16	3.36	120.50	40.99
Lutjanus colorado	8	3.20	326.25	827.41
Lutjanus jocu	56	3.52	140.64	103.52
Lutjanus novemfasciatus	8	3.31	154.88	92.24
Marcusenius macrolepidotus	76	3.29	122.22	23.79
Markiana geayi	257	2.50	53.19	4.29
Mastacembelus frenatus	7	3.11	89.01	3.47
Menidia beryllina	476	3.01	37.86	0.71
Menidia peninsulae	44	2.87	29.02	0.29
Metynnis hypsauchen	239	2.16	55.63	5.70
Microglanis iheringi	166	3.29	26.51	0.33
Microgobius gulosus	7	3.28	27.26	0.21

Table A.4 Continued.

Species	N	MTL	Mean SL (mm)	Mean body mass (g)
Microphis lineatus	180	3.29	101.57	0.64
Micropogonias undulatus	442	3.16	30.43	1.86
Micropterus punctulatus	109	3.61	126.07	119.87
Micropterus salmoides	99	3.84	178.51	259.14
Microsternarchus bilineatus	10	3.30	80.50	0.75
Mikrogeophagus ramirezi	212	2.52	21.42	0.30
Moenkhausia copei	132	3.51	31.95	0.65
Moenkhausia lepidura	29	3.52	49.86	2.49
Mormyrus lacerda	108	3.13	151.79	41.45
Mugil cephalus	423	2.02	142.19	183.94
Mugil curema	8	3.49	36.41	3.97
Myloplus rubripinnis	24	2.04	46.46	3.16
Mylossoma duriventre	8	2.15	116.94	63.52
Nannocharax machadoi	5	3.38	21.46	0.08
Nannocharax multifasciatus	6	3.28	28.12	0.19
Ochmacanthus alternus	245	3.64	29.04	0.22
Odontostilbe pulchra	338	2.45	24.18	0.28
Oreochromis andersonii	20	2.06	199.30	290.09
Oreochromis macrochir	44	2.02	128.58	109.39
Parachromis dovii	150	3.40	66.96	36.91
Parachromis friedrichsthalii	484	3.40	48.03	8.83
Paralichthys lethostigma	27	3.49	177.68	384.02
Paraneetroplus maculicauda	180	2.38	121.56	85.73
Parapristella georgiae	134	3.42	25.91	0.34
Parauchenoglanis ngamensis	5	3.42	144.96	42.71
Petrocephalus catostoma	43	3.51	57.26	4.06
Phallichthys amates	336	2.07	32.81	0.51
Pharyngochromis acuticeps	28	3.30	79.88	15.73
Piabucina erythrinoides	281	3.11	59.35	3.46
Pimelodella cruxenti	11	3.43	76.91	9.06
Pimelodella linami	176	3.12	64.14	3.66
Pimelodella metae	188	3.30	45.25	1.43
Pimelodella odynea	6	3.42	62.85	3.38
Pimelodus blochii	8	2.85	127.99	35.54
Poecilia gillii	310	2.05	44.06	1.72
Poecilia latipinna	84	2.02	24.46	0.21
Poecilia mexicana	11	3.02	64.45	4.13

Table A.4 Continued.

Species	**N**	**MTL**	**Mean SL (mm)**	**Mean body mass (g)**
Poecilia reticulata	210	2.43	18.68	0.08
Poecilia sphenops	14	2.78	61.11	4.02
Poeciliopsis turrubarensis	15	2.90	41.34	0.77
Pogonias cromis	36	3.32	231.53	653.34
Pollimyrus castelnaui	72	3.19	50.54	1.33
Pomadasys crocro	78	3.32	140.90	156.51
Pomoxis annularis	302	3.57	96.69	64.34
Pomoxis nigromaculatus	14	3.80	133.66	89.15
Pristobrycon striolatus	11	3.47	51.82	5.23
Prochilodus mariae	64	2.13	146.98	87.90
Pseudocrenilabrus nicholsi	43	3.28	26.38	0.61
Pseudophallus mindii	6	3.09	98.77	0.55
Pseudophallus starksii	21	3.34	107.50	0.71
Pterygoplichthys multiradiatus	54	2.11	139.06	89.89
Pygocentrus cariba	202	3.31	91.01	57.78
Pygopristis denticulata	79	2.81	55.10	6.56
Pyrrhulina lugubris	293	3.34	29.71	0.24
Rachovia maculipinnis	101	3.32	21.16	0.18
Rhamdia guatemalensis	105	3.07	80.06	9.58
Rhamdia quelen	168	3.47	91.09	20.61
Rhamphichthys marmoratus	16	3.19	215.85	20.42
Rineloricaria caracasensis	67	2.34	72.96	6.66
Roeboides dayi	657	3.48	39.95	1.81
Roeboides guatemalensis	20	3.76	65.14	5.72
Sargochromis carlottae	51	3.36	91.82	39.50
Sargochromis codringtonii	147	2.78	94.38	33.56
Sargochromis giardi	54	3.23	127.24	94.74
Satanoperca daemon	42	2.76	81.19	14.00
Satanoperca jurupari	7	2.57	79.14	16.92
Schilbe intermedius	284	3.59	108.53	15.42
Schizodon isognathus	91	2.09	105.55	37.37
Sciaenops ocellatus	60	3.79	422.22	1869.74
Serrabrycon magoi	117	3.73	23.10	0.24
Serranochromis altus	27	3.99	227.62	445.14
Serranochromis angusticeps	44	3.61	170.55	195.19
Serranochromis macrocephalus	78	3.91	176.79	188.67

Table A.4 Continued.

Species	N	MTL	Mean SL (mm)	Mean body mass (g)
Serranochromis robustus	89	3.74	233.24	483.52
Serrasalmus eigenmanni	72	3.72	38.92	6.08
Serrasalmus medinai	62	3.33	27.09	1.76
Serrasalmus rhombeus	50	3.75	41.22	8.79
Sicydium plumieri	14	3.01	42.12	0.80
Sphoeroides annulatus	8	3.11	152.75	110.81
Sphoeroides testudineus	28	3.32	66.56	18.41
Steindachnerina argentea	101	2.42	49.76	4.06
Sternopygus macrurus	5	3.34	149.60	5.89
Strongylura timucu	6	3.49	258.47	79.88
Synbranchus marmoratus	84	2.98	196.91	23.39
Syngnathus scovelli	14	3.31	65.01	0.19
Synodontis leopardinus	43	3.08	62.62	9.66
Synodontis macrostigma	7	3.20	43.60	1.83
Synodontis nigromaculatus	24	3.04	143.34	75.48
Synodontis woosnami	88	2.52	70.08	12.47
Tetragonopterus argenteus	144	2.79	45.61	2.47
Thoracocharax stellatus	179	3.45	29.04	0.67
Tilapia rendalli	78	2.05	93.26	73.00
Tilapia ruweti	11	2.02	42.08	2.21
Tilapia sparrmanii	85	2.14	80.88	20.63
Trachelyopterus galeatus	179	3.25	66.00	10.03
Trinectes paulistanus	60	3.44	28.19	1.42
Triportheus orinocensis	250	2.63	53.24	3.79
Triportheus venezuelensis	54	2.48	94.27	14.44
Xenagoniates bondi	15	3.68	38.28	0.51

Table A.5 Estimated marginal means of MTL based on Bayesian phylogenetic linear mixed models performed on 100 different trees are presented for different types of tooth shape, mouth orientation and gill raker. The models were run with standard length as proxy for body size.

Levels	Marginal means of MTL	Credible intervals (Lower / Upper)
Tooth shape		
Absence	2.83	2.80 / 2.85
Unicuspid	2.98	2.95 / 3.00
Multicuspid	2.99	2.97 / 3.01
Conical	3.12	3.10 / 3.14
Triangular serrated	3.45	3.39 / 3.50
Mouth orientation		
Superior	3.25	3.24 / 3.27
Terminal	3.04	3.03 / 3.06
Subterminal	3.03	3.00 / 3.05
Inferior	2.96	2.93 / 2.99
Gill raker shape		
Absent	3.12	3.11 / 3.14
Short	3.11	3.09 / 3.12
Intermidiate	3.05	3.03 / 3.07
Comb-like	3	2.99 / 3.02

Table A.6 Estimated marginal means of MTL based on Bayesian phylogenetic linear mixed models performed on 100 different trees are presented for different types of tooth shape, mouth orientation and gill raker. The models were run with body mass as proxy for body size.

Levels	Marginal means of MTL	Credible intervals (Lower / Upper)
Tooth shape		
Absence	2.81	2.79 / 2.83
Unicuspid	2.96	2.92 / 2.98
Multicuspid	2.96	2.95 / 2.99
Conical	3.11	3.09 / 3.12
Triangular serrated	3.4	3.34 / 3.46
Mouth orientation		
Superior	3.23	3.21 / 3.24
Terminal	3.03	3.01 / 3.04
Subterminal	3	2.98 / 3.02
Inferior	2.94	2.90 / 2.96
Gill raker shape		
Absent	3.12	3.10 / 3.14
Short	3.08	3.06 / 3.09
Intermidiate	3.02	3.01 / 3.04
Comb-like	2.97	2.96 / 2.99

Table A.7 Estimated marginal means of the mean trophic level (MTL) of carnivorous fishes based on Bayesian phylogenetic linear mixed models are presented for different types of tooth shape, mouth orientation and gill raker. Estimated marginal means take into account the uncertainty associated with the phylogenetic similarity of species (100 trees). The models were run with standard length as proxy for body size.

Levels	**Marginal means of MTL**	**Credible intervals**
Tooth shape		
Absent	3.09	3.08 / 3.10
Unicuspid	3.24	3.22 / 3.25
Multicuspid	3.18	3.16 / 3.19
Conical	3.24	3.22 / 3.26
Triangular serrated	3.63	3.59 / 3.68
Mouth orientation		
Superior	3.4	3.39 / 3.40
Terminal	3.27	3.27 / 3.28
Sub-terminal	3.28	3.27 / 3.29
Inferior	3.15	3.13 / 3.16
Gill raker shape		
Absent	3.31	3.30 / 3.32
Short	3.26	3.25 / 3.26
Intermidiate	3.3	3.28 / 3.30
Comb-like	3.24	3.23 / 3.25

Table A.8 Estimated marginal means of the mean trophic level (MTL) of carnivorous fish based on Bayesian phylogenetic linear mixed models are presented for different types of tooth shape, mouth orientation and gill raker. Estimated marginal means take into account the uncertainty associated with the phylogenetic similarity of species (100 trees). The models were run with body mass as proxy for body size.

Levels	**Marginal means of MTL**	**Credible intervals**
Tooth shape		
Absent	3.11	3.09 / 3.13
Unicuspid	3.23	3.20 / 3.24
Multicuspid	3.17	3.16 / 3.18
Conical	3.25	3.22 / 3.26
Triangular serrated	3.59	3.56 / 3.65
Mouth position		
Superior	3.4	3.38 / 3.40
Terminal	3.28	3.27 / 3.28
Sub-terminal	3.27	3.26 / 3.28
Inferior	3.13	3.10 / 3.14
Gill raker shape		
Absent	3.32	3.31 / 3.33
Short	3.24	3.23 / 3.25
Intermidiate	3.29	3.27 / 3.29
Comb-like	3.23	3.21 / 3.24

Table A.9 Estimated marginal means of the mean trophic level (MTL) of non-carnivorous fish based on Bayesian phylogenetic linear mixed models are presented for different types of tooth shape, mouth orientation and gill raker. Estimated marginal means take into account the uncertainty associated with the phylogenetic similarity of species (100 trees). The models were run with standard length as proxy for body size.

Levels	Marginal means of MTL	Credible intervals
Tooth shape		
Absent	2.17	2.16 / 2.18
Unicuspid	2.25	2.24 / 2.26
Multicuspid	2.17	2.14 / 2.21
Conical	2.18	2.17 / 2.18
Triangular serrated	2.2	2.18 / 2.21
Mouth orientation		
Superior	2.22	2.21 / 2.23
Terminal	2.12	2.11 / 2.13
Sub-terminal	2.25	2.23 / 2.26
Inferior	2.19	2.16 / 2.21
Gill raker shape		
Absent	2.21	2.19 / 2.23
Short	2.21	2.20 / 2.22
Intermidiate	2.15	2.14 / 2.16
Comb-like	2.21	2.20 / 2.22

Table A.10 Estimated marginal means of the mean trophic level (MTL) of non-carnivorous fish based on Bayesian phylogenetic linear mixed models are presented for different types of tooth shape, mouth orientation and gill raker. Estimated marginal means take into account the uncertainty associated with the phylogenetic similarity of species (100 trees). The models were run with body mass as proxy for body size.

Levels	Marginal means of MTL	Credible intervals
Tooth shape		
Absent	2.17	2.15 / 2.18
Unicuspid	2.25	2.24 / 2.26
Multicuspid	2.18	2.14 / 2.21
Conical	2.18	2.17 / 2.18
Triangular serrated	2.19	2.17 / 2.21
Mouth orientation		
Superior	2.22	2.21 / 2.23
Terminal	2.12	2.11 / 2.13
Subterminal	2.25	2.24 / 2.26
Inferior	2.18	2.16 / 2.21
Gill raker shape		
Absent	2.21	2.19 / 2.22
Short	2.21	2.20 / 2.22
Intermidiate	2.15	2.14 / 2.15
Comb-like	2.21	2.20 / 2.21

Table A.11 Intercepts and slopes for the trophic level (TL) – body size (standard length and body mass) relationship generated by semi-parametric mixed models for all species with more than 30 individuals dissected. Body size range and sample size is also presented.

Species	N	Range SL (mm)	SL - TL Intercept (CI)	SL - TL Slope (CI)	Range Body mass (grams)	Body mass - TL Intercept (CI)	Body mass - TL Slope (CI)
Achirus lineatus	38	17.4/74.5	3.72(2.32/5.06)	-0.06(-0.47/0.31)	0.2/18.3	3.44(3.27/3.6)	-0.03(-0.18/0.11)
Adinia xenica	57	14/29.4	3.1(1.22/4.8)	-0.29(-0.87/0.29)	0.07/0.65	2.09(1.71/2.43)	-0.03(-0.3/0.22)
Adontosternarchus devenanzii	59	16.2/144	2.19(1.07/3.45)	0.24(-0.03/0.5)	0.01/8.66	3.26(3.12/3.39)	0.1(0/0.19)
Alfaro cultratus	409	11.4/65.5	3.94(3.52/4.4)	-0.18(-0.31/-0.06)	0.02/3.6	3.26(3.19/3.32)	-0.06(-0.1/-0.02)
Amatitlania nigrofasciata	221	11.8/73.9	6.21(5.58/6.8)	-0.98(-1.15/-0.81)	0.03/7.24	2.62(2.56/2.69)	-0.34(-0.4/-0.29)
Cribroheros alfari	63	12.9/129.5	4.04(3.51/4.55)	-0.27(-0.43/-0.12)	0.06/59.81	3.06(2.94/3.18)	-0.1(-0.15/-0.04)
Amphilophus citrinellus	112	15.5/208	3.44(3.02/3.82)	-0.05(-0.15/0.04)	0.1/247.85	3.23(3.13/3.33)	-0.02(-0.05/0.01)
Anchoa mitchilli	773	15.7/67.5	1.76(1.27/2.22)	0.33(0.21/0.48)	0.03/3.54	3.07(3/3.14)	0.11(0.07/0.16)
Ancistrus triradiatus	93	12.7/81.2	2.26(1.39/3.14)	-0.05(-0.28/0.18)	0.01/6.47	2.09(1.98/2.18)	0(-0.08/0.07)
Andinoacara pulcher	639	8.5/89	4.38(4.09/4.67)	-0.38(-0.46/-0.3)	0.02/19.42	3.04(3.01/3.08)	-0.13(-0.16/-0.1)
Aphyocharax erythrurus	266	13.7/42.6	3.3(2.26/4.29)	0.04(-0.26/0.34)	0.05/1.51	3.4(3.3/3.5)	0.01(-0.1/0.11)
Apistogramma hoignei	180	13.4/32.5	4.62(3.61/5.8)	-0.5(-0.85/-0.14)	0.05/0.73	2.87(2.68/3.07)	-0.2(-0.32/-0.07)
Micropanchax johnstoni	66	15.2/33.4	3.87(2.16/5.6)	-0.23(-0.74/0.31)	0.04/0.47	3(2.65/3.35)	-0.12(-0.34/0.09)
Archocentrus centrarchus	187	13.9/85.7	4.55(3.98/5.05)	-0.39(-0.55/-0.22)	0.07/17.34	3.16(3.09/3.24)	-0.14(-0.19/-0.08)
Ariopsis felis	61	150/340	3.53(1.55/5.36)	0.04(-0.31/0.39)	43.65/588.98	3.46(2.77/4.2)	0.04(-0.1/0.17)
Astronotus ocellatus	87	16.2/230	3.46(2.75/4.09)	-0.03(-0.18/0.12)	0.11/327.48	3.32(3.15/3.49)	-0.01(-0.06/0.04)
Astyanax bimaculatus	368	14.9/91.5	3.56(2.97/4.19)	-0.28(-0.44/-0.11)	0.08/19.23	2.62(2.57/2.67)	-0.09(-0.15/-0.04)
Astyanax fasciatus	587	12.7/126	4.09(3.77/4.41)	-0.38(-0.46/-0.29)	0.04/46.25	2.73(2.69/2.77)	-0.12(-0.15/-0.1)
Astyanax metae	179	20.9/101	2.67(2.13/3.26)	-0.02(-0.18/0.12)	0.21/24.16	2.6(2.52/2.67)	-0.01(-0.06/0.04)
Atherinella hubbsi	198	9.7/101	2.78(2.25/3.29)	0.13(-0.01/0.27)	0.01/9.17	3.27(3.21/3.34)	0.05(0/0.1)
Bairdiella chrysoura	163	9.2/142.8	3.47(2.84/4.1)	-0.03(-0.21/0.15)	0.02/59.88	3.37(3.3/3.45)	-0.01(-0.07/0.05)
Enteromius paludinosus	54	50.4/77.7	2.97(0.64/5.17)	-0.1(-0.63/0.45)	2.19/8.11	2.55(2.03/3.05)	-0.02(-0.34/0.29)

Table A.11 Continued.

Species	**N**	**Range SL (mm)**	**SL - TL Intercept (CI)**	**SL - TL Slope (CI)**	**Range Body mass (grams)**	**Body mass - TL Intercept (CI)**	**Body mass - TL Slope (CI)**
Enteromius poechii	50	43.6/92.5	3.49(1.41/5.61)	-0.33(-0.84/0.17)	1.46/14.36	2.41(1.99/2.82)	-0.21(-0.46/0.06)
Belonesox belizanus	72	17/173.4	3.66(2.71/4.51)	0.04(-0.19/0.25)	0.05/77.31	3.73(3.61/3.86)	0.01(-0.07/0.08)
Brachyhypopomus brevirostris	61	34.2/184	3.62(2.24/4.98)	-0.06(-0.36/0.23)	0.05/9.17	3.32(3.2/3.46)	-0.03(-0.15/0.08)
Brachyhypopomus occidentalis	64	64/215	3.46(1.68/5.21)	-0.03(-0.42/0.34)	0.37/14.72	3.28(3.13/3.44)	-0.04(-0.21/0.14)
Brachyrhaphis parismina	53	8.8/38.3	2.13(1.1/3.02)	0.43(0.14/0.76)	0.01/0.68	3.75(3.48/4)	0.15(0.05/0.25)
Brachyrhaphis rhabdophora	37	15/42	3.21(1.41/4.91)	-0.04(-0.57/0.49)	0.04/0.91	3.02(2.67/3.37)	-0.01(-0.23/0.21)
Brevoortia patronus	523	18.2/51.6	2.74(2.07/3.36)	-0.19(-0.4/-0.01)	0.09/2.13	1.97(1.88/2.06)	-0.06(-0.13/0.01)
Brycon guatemalensis	126	12.5/405	4.38(3.7/5.03)	-0.4(-0.53/-0.27)	0.03/1244.19	2.92(2.71/3.11)	-0.14(-0.18/-0.09)
Knodus deuterodonoides	157	16.3/38.6	2.42(1.12/3.72)	0.04(-0.37/0.46)	0.08/1.11	2.64(2.41/2.85)	0.06(-0.1/0.2)
Bryconamericus motatanensis	458	12.7/49.6	4.21(3.67/4.81)	-0.36(-0.53/-0.2)	0.04/2.41	2.91(2.85/2.97)	-0.12(-0.18/-0.07)
Bryconops giacopinii	112	25/56	2.05(0.47/3.78)	0.39(-0.07/0.82)	0.26/2.94	3.49(3.39/3.58)	0.19(0/0.38)
Bunocephalus amaurus	151	17/59.4	4.55(3.43/5.62)	-0.39(-0.7/-0.09)	0.04/1.81	2.96(2.85/3.09)	-0.16(-0.27/-0.05)
Caquetaia kraussii	341	14/230	3.22(2.89/3.56)	0.05(-0.04/0.14)	0.08/335.11	3.4(3.35/3.45)	0.02(-0.01/0.05)
Centropomus pectinatus	58	20.4/410	2.08(1.21/2.88)	0.28(0.1/0.45)	0.14/1195.33	3.02(2.79/3.24)	0.1(0.04/0.16)
Characidium pteroides	55	15/22	4.45(2.51/6.72)	-0.42(-1.19/0.27)	0.05/0.17	2.53(1.79/3.29)	-0.3(-0.62/0.01)
Characidium steindachneri	190	16.7/29.4	3.52(1.81/5.15)	-0.05(-0.58/0.46)	0.08/0.4	3.22(2.87/3.54)	-0.04(-0.27/0.17)
Charax condei	71	17/38	2.29(0.37/4)	0.41(-0.14/0.97)	0.09/1.06	3.75(3.45/4.04)	0.22(-0.04/0.44)
Charax gibbosus	216	16.2/104.9	2.89(2.32/3.38)	0.15(0.02/0.3)	0.08/23.65	3.44(3.37/3.51)	0.05(0.01/0.1)
Cheirodontops geayi	88	12.2/27.9	3.29(1.58/5.16)	-0.02(-0.62/0.53)	0.03/0.41	3.17(2.8/3.57)	-0.05(-0.29/0.21)
Cichlasoma orinocense	225	12.6/106	5.37(4.92/5.78)	-0.7(-0.82/-0.58)	0.06/32.8	2.89(2.83/2.96)	-0.24(-0.28/-0.2)
Citharichthys spilopterus	79	13.4/92.4	2.57(1.91/3.22)	0.18(0/0.37)	0.04/15.97	3.24(3.13/3.35)	0.07(0/0.13)
Clarias theodorae	77	40.6/229	0.46(-0.76/1.69)	0.67(0.43/0.93)	0.79/128.21	2.89(2.59/3.19)	0.27(0.18/0.36)
Copella eigenmanni	38	13/25	4.15(2.44/5.93)	-0.47(-1.05/0.12)	0.02/0.13	2.34(1.75/2.98)	-0.16(-0.39/0.05)
Corydoras aeneus	154	16.8/45	4.31(2.85/5.91)	-0.43(-0.85/0.02)	0.18/3.05	2.96(2.87/3.05)	-0.2(-0.38/-0.02)

Table A.11 Continued.

Species	N	Range SL (mm)	SL - TL Intercept (CI)	SL - TL Slope (CI)	Range Body mass (grams)	Body mass - TL Intercept (CI)	Body mass - TL Slope (CI)
Corydoras habrosus	203	14.2/24.7	2.67(1.19/4)	0.04(-0.44/0.55)	0.11/0.54	2.83(2.5/3.18)	0.06(-0.15/0.25)
Corydoras septentrionalis	129	18.4/45.8	4.41(3.07/5.81)	-0.34(-0.76/0.03)	0.23/3.26	3.21(3.12/3.29)	-0.17(-0.33/-0.01)
Corynopoma riisei	241	12.5/42.7	3.22(2.41/4.07)	0.07(-0.19/0.3)	0.03/1.52	3.45(3.35/3.54)	0.01(-0.07/0.1)
Creagrutus melasma	311	9.5/32.7	4.29(3.32/5.26)	-0.47(-0.77/-0.15)	0.01/0.67	2.62(2.45/2.78)	-0.16(-0.27/-0.06)
Crenicichla geayi	106	19.8/124.6	2.8(2.04/3.51)	0.15(-0.03/0.33)	0.06/17.08	3.34(3.25/3.43)	0.05(-0.01/0.11)
Ctenobrycon spilurus	355	10.8/52.1	5.57(4.96/6.11)	-0.87(-1.04/-0.71)	0.03/3.2	2.43(2.38/2.48)	-0.3(-0.36/-0.24)
Ctenogobius boleosoma	70	12.7/35.5	2.32(0.81/3.81)	0.03(-0.44/0.51)	0.02/0.41	2.59(2.17/3)	0.08(-0.11/0.27)
Ctenogobius claytonii	101	13.7/61.1	3.61(2.69/4.52)	-0.16(-0.43/0.09)	0.03/1.97	2.94(2.81/3.07)	-0.07(-0.16/0.03)
Curimatopsis evelynae	146	14/39	1.27(0.37/2.31)	0.27(-0.06/0.58)	0.06/1.45	2.33(2.14/2.52)	0.13(0.01/0.24)
Cynodonichthys isthmensis	249	6.7/46.7	3.43(2.84/4)	-0.01(-0.19/0.16)	0.00/0.87	3.34(3.21/3.47)	-0.01(-0.07/0.05)
Cynoscion nebulosus	74	14.3/425	2.63(2.08/3.23)	0.16(0.01/0.3)	0.06/1665.14	3.21(3.09/3.32)	0.06(0.01/0.11)
Cyphocharax spilurus	248	15/64	2.24(1.63/2.83)	-0.05(-0.24/0.12)	0.08/6.5	2.04(1.96/2.11)	-0.01(-0.07/0.05)
Cyprinodon variegatus	130	8.8/43.4	2.29(1.67/2.89)	-0.09(-0.28/0.11)	0.01/2.45	2.01(1.9/2.13)	-0.02(-0.08/0.04)
Dormitator maculatus	220	15/89.6	4.36(3.64/5.07)	-0.58(-0.76/-0.38)	0.04/8.45	2.19(2.13/2.26)	-0.2(-0.26/-0.13)
Dorosoma cepedianum	264	26/345	2.3(1.87/2.74)	-0.04(-0.12/0.05)	0.31/765.97	2.17(2.03/2.31)	-0.01(-0.04/0.02)
Eigenmannia virescens	138	30.2/174.1	2.93(1.72/4.1)	0.11(-0.16/0.36)	0.04/7.75	3.36(3.27/3.44)	0.04(-0.06/0.14)
Eleotris amblyopsis	525	16/93.7	3.06(2.62/3.47)	0.1(-0.02/0.21)	0.05/9.45	3.41(3.37/3.45)	0.03(-0.01/0.07)
Eleotris pisonis	105	19.4/123.8	3.4(2.7/4.11)	-0.01(-0.17/0.16)	0.09/22.29	3.38(3.26/3.49)	0(-0.06/0.05)
Entomocorus gameroi	55	17.9/40.8	3.32(1.54/5.26)	0.01(-0.56/0.51)	0.14/1.68	3.3(3.16/3.43)	-0.03(-0.28/0.22)
Evorthodus lyricus	79	12.2/53.4	2.34(1.36/3.35)	-0.06(-0.36/0.24)	0.03/2.54	2.16(2/2.32)	0(-0.11/0.11)
Fundulus grandis	94	15.5/75.8	1.24(0.24/2.35)	0.39(0.09/0.7)	0.11/19.34	2.63(2.54/2.73)	0.15(0.05/0.25)
Gephyrocharax valencia	333	13/39.1	3.7(2.63/4.77)	-0.15(-0.45/0.19)	0.04/1.13	3.23(3.11/3.33)	-0.05(-0.17/0.06)
Gnathocharax steindachneri	38	2/25	3.47(2.4/4.43)	0.14(-0.25/0.47)	0/0.26	3.76(3.4/4.11)	0.02(-0.11/0.14)
Gobiomorus dormitor	147	16.4/238	3.09(2.64/3.62)	0.08(-0.04/0.2)	0.05/158.39	3.42(3.34/3.5)	0.03(-0.01/0.07)

Table A.11 Continued.

Species	N	Range SL (mm)	SL - TL Intercept (CI)	SL - TL Slope (CI)	Range Body mass (grams)	Body mass - TL Intercept (CI)	Body mass - TL Slope (CI)
Gobiosoma bosc	121	9.2/39.8	2.27(1.2/3.31)	0.19(-0.14/0.54)	0.01/1.04	2.99(2.77/3.23)	0.09(-0.04/0.2)
Gymnotus carapo	281	18.7/306	3.05(2.67/3.48)	0.09(0.01/0.18)	0.02/88.55	3.46(3.39/3.54)	0.03(0/0.06)
Hemigrammus analis	170	14/23	-1.05(-4.24/0.38)	1.32(0.82/2.45)	0.05/0.23	4.05(3.59/4.5)	0.56(0.38/0.74)
Hemigrammus barrigonae	197	19/35	1.53(-0.18/3.12)	0.36(-0.17/0.88)	0.13/0.82	2.93(2.63/3.24)	0.22(0.02/0.43)
Hemigrammus bellottii	153	10/19	2.65(1.17/4.2)	0.2(-0.38/0.77)	0.02/0.13	3.4(2.78/4.02)	0.06(-0.14/0.26)
Hemigrammus elegans	132	15/32.8	4.34(3.12/5.74)	-0.38(-0.83/0.02)	0.06/0.67	2.9(2.63/3.17)	-0.19(-0.33/-0.02)
Hemigrammus marginatus	32	14/25	2.49(0.57/4.37)	0.24(-0.43/0.94)	0.05/0.29	3.47(2.73/4.16)	0.11(-0.17/0.38)
Hemigrammus micropterus	212	16/35	3.17(1.68/4.54)	-0.09(-0.54/0.37)	0.07/0.8	2.82(2.58/3.09)	-0.02(-0.19/0.15)
Hemigrammus microstomus	204	14/24	2.69(0.73/4.53)	-0.1(-0.75/0.51)	0.05/0.26	2.43(1.93/2.94)	0.05(-0.2/0.35)
Hemigrammus newboldi	50	13/29	1.89(0.48/3.38)	0.36(-0.15/0.9)	0.04/0.46	3.4(2.87/3.9)	0.17(-0.03/0.35)
Hemigrammus rhodostomus	99	19/27	4.52(2.56/6.64)	-0.45(-1.15/0.17)	0.13/0.37	2.58(2.1/3.04)	-0.32(-0.62/-0.02)
Hemigrammus stictus	168	14/31	4.78(3.18/6.46)	-0.68(-1.24/-0.17)	0.05/0.57	2.12(1.78/2.53)	-0.29(-0.5/-0.09)
Hemigrammus vorderwinkleri	107	11/18	3.01(1.27/4.8)	0.05(-0.65/0.68)	0.02/0.11	3.07(2.36/3.81)	-0.01(-0.24/0.25)
Hepsetus odoe	71	110/324	0.99(-0.8/2.72)	0.57(0.24/0.9)	9.68/258.26	2.87(2.37/3.38)	0.28(0.15/0.39)
Heterocharax macrolepis	102	16/29	3.93(2.22/5.6)	-0.06(-0.62/0.46)	0.07/0.4	3.49(3.11/3.87)	-0.1(-0.33/0.12)
Hoplerythrinus unitaeniatus	79	58/155	3.04(1.25/4.97)	0.22(-0.2/0.61)	3.19/65.21	3.74(3.26/4.21)	0.13(-0.06/0.29)
Hoplias malabaricus	413	4.3/355	2.99(2.76/3.23)	0.15(0.09/0.21)	0/910.33	3.55(3.5/3.6)	0.05(0.03/0.07)
Hoplosternum littorale	61	11.1/172	3.89(3.23/4.58)	-0.23(-0.39/-0.08)	0.06/160.47	3.13(2.94/3.32)	-0.08(-0.14/-0.03)
Hydrocynus vittatus	133	76.5/654	2.28(1.41/3.09)	0.32(0.17/0.48)	6.7/4564.11	3.38(3.13/3.66)	0.12(0.06/0.17)
Hyphessobrycon metae	40	17/29	3.07(0.93/5.11)	0.19(-0.5/0.85)	0.09/0.46	3.59(3.03/4.14)	-0.01(-0.32/0.35)
Hyphessobrycon savagei	34	20/40.5	3.88(1.73/5.98)	-0.16(-0.79/0.43)	0.15/1.29	3.16(2.94/3.35)	-0.18(-0.5/0.16)
Hyphessobrycon sweglesi	30	12/23	3.18(1.16/5.05)	0.02(-0.68/0.76)	0.03/0.22	3.19(2.39/4)	-0.02(-0.3/0.27)
Hypoptopoma machadoi	40	23.8/60.5	3.19(1.56/4.81)	-0.29(-0.73/0.14)	0.11/2.5	2.11(1.95/2.26)	-0.08(-0.25/0.09)
Hypoptopoma spectabile	79	16.7/26.5	2.39(0.64/4.25)	-0.09(-0.71/0.47)	0.03/0.16	2.37(1.76/2.92)	0.11(-0.12/0.32)

Table A.11 Continued.

Species	N	Range SL (mm)	SL - TL Intercept (CI)	SL - TL Slope (CI)	Range Body mass (grams)	Body mass - TL Intercept (CI)	Body mass - TL Slope (CI)
Hypostomus argus	87	15.1/190	2.2(1.7/2.79)	-0.04(-0.17/0.09)	0.1/136.28	2.12(1.98/2.24)	-0.01(-0.06/0.03)
Jupiaba abramoides	35	58/92.4	4.66(2.39/6.99)	-0.44(-0.99/0.08)	4.52/18.46	3.48(2.85/4.07)	-0.33(-0.6/-0.06)
Lagodon rhomboides	346	12/124.3	5.84(5.47/6.21)	-0.87(-0.98/-0.77)	0.04/56.24	2.77(2.72/2.82)	-0.29(-0.32/-0.26)
Leiostomus xanthurus	493	10.7/100	4.01(3.63/4.4)	-0.22(-0.32/-0.11)	0.03/21.38	3.25(3.21/3.29)	-0.07(-0.11/-0.04)
Lepisosteus oculatus	235	248/910	2.57(1.26/4.02)	0.18(-0.05/0.4)	137.36/7045.4	3.21(2.66/3.75)	0.08(0/0.16)
Lepisosteus osseus	84	290/1254	3.18(1.43/4.91)	0.11(-0.16/0.37)	220.62/18607.64	3.36(2.58/4.14)	0.06(-0.04/0.15)
Lepomis cyanellus	90	19/113	3.01(2.1/3.87)	0.1(-0.1/0.34)	0.19/48.43	3.39(3.24/3.53)	0.04(-0.03/0.12)
Lepomis gulosus	62	21.2/126.9	3.37(2.2/4.52)	0.06(-0.23/0.33)	0.29/78.13	3.53(3.29/3.77)	0.02(-0.08/0.12)
Lepomis humilis	48	30/80.6	3.74(2.07/5.47)	-0.09(-0.55/0.32)	0.77/16.55	3.41(3.13/3.7)	-0.06(-0.24/0.12)
Lepomis macrochirus	91	12/114	3.63(2.99/4.29)	-0.07(-0.23/0.1)	0.04/41.51	3.41(3.29/3.52)	-0.03(-0.08/0.03)
Lepomis megalotis	95	34.8/129.9	2.92(1.76/4.21)	0.06(-0.23/0.35)	1.4/88.69	3.17(2.91/3.44)	0.02(-0.07/0.13)
Leporinus friderici	70	28.9/252	2.72(1.14/4.19)	-0.07(-0.41/0.28)	0.46/356.7	2.41(2.07/2.77)	-0.02(-0.15/0.11)
Loricariichthys brunneus	41	80/224	3.57(1.95/5.28)	-0.23(-0.58/0.08)	6.15/185.92	2.8(2.29/3.3)	-0.1(-0.23/0.02)
Lucania parva	119	13.1/36.8	2.19(1.04/3.31)	0.25(-0.09/0.62)	0.11/3.43	3.03(2.94/3.12)	0.1(-0.02/0.22)
Lutjanus jocu	56	49.2/260	2.21(0.66/3.78)	0.24(-0.05/0.59)	4.16/486.21	2.99(2.44/3.51)	0.13(0/0.25)
Marcusenius macrolepidotus	76	71/176	2.45(1.04/3.89)	0.16(-0.13/0.47)	4.2/56.84	3.07(2.69/3.41)	0.08(-0.04/0.2)
Markiana geayi	257	16.8/94	4.1(3.55/4.76)	-0.42(-0.58/-0.27)	0.1/19	2.65(2.57/2.73)	-0.15(-0.2/-0.09)
Menidia beryllina	476	11.6/80.5	1.46(1.03/1.94)	0.42(0.3/0.55)	0.02/4.79	3.12(3.07/3.17)	0.15(0.11/0.2)
Menidia peninsulae	44	15.4/41.3	3.12(1.5/4.69)	-0.09(-0.55/0.4)	0.04/0.7	2.85(2.54/3.17)	-0.01(-0.22/0.19)
Metynnis hypsauchen	239	32/76	6.54(5.11/8.12)	-1.09(-1.48/-0.73)	0.92/14.7	2.9(2.69/3.11)	-0.45(-0.57/-0.32)
Microglanis iheringi	166	16/37.6	2.67(1.36/3.85)	0.18(-0.17/0.59)	0.07/0.88	3.4(3.21/3.58)	0.09(-0.06/0.22)
Microphis lineatus	180	66/197.8	2.22(0.91/3.65)	0.22(-0.08/0.52)	0.15/4.39	3.34(3.24/3.45)	0.09(-0.02/0.21)
Micropogonias undulatus	442	11.5/215	3.07(2.75/3.43)	0.02(-0.08/0.12)	0.03/202.89	3.16(3.11/3.22)	0(-0.03/0.04)
Micropterus punctulatus	109	28.04/460	3.06(2.36/3.65)	0.13(-0.01/0.27)	0.39/2262.3	3.48(3.3/3.64)	0.05(0/0.09)

Table A.11 Continued.

Species	N	Range SL (mm)	SL - TL Intercept (CI)	SL - TL Slope (CI)	Range Body mass (grams)	Body mass - TL Intercept (CI)	Body mass - TL Slope (CI)
Micropterus salmoides	99	34.9/383	3.2(2.44/3.96)	0.12(-0.02/0.28)	0.94/1427.54	3.64(3.39/3.87)	0.04(0/0.1)
Mikrogeophagus ramirezi	212	13/38	2.21(1.29/3.09)	0.12(-0.19/0.41)	0.06/1.51	2.61(2.44/2.76)	0.06(-0.05/0.16)
Moenkhausia copei	132	21/46	2.92(1.26/4.66)	0.18(-0.33/0.66)	0.17/1.91	3.54(3.41/3.67)	0.06(-0.15/0.27)
Mormyrus lacerda	108	102/368	2.29(0.86/3.53)	0.18(-0.08/0.45)	9.21/343.31	2.83(2.5/3.2)	0.08(-0.02/0.19)
Mugil cephalus	423	11.7/390	1.95(1.74/2.16)	0.02(-0.03/0.06)	0.03/1206.07	2.01(1.95/2.07)	0.01(-0.01/0.02)
Ochmacanthus alternus	245	13.1/37.9	4.93(3.87/6)	-0.4(-0.7/-0.07)	0.02/0.46	3.36(3.18/3.56)	-0.16(-0.28/-0.05)
Odontostilbe pulchra	338	11.9/35.7	4.63(3.66/5.52)	-0.66(-0.96/-0.38)	0.03/0.86	2.14(1.99/2.28)	-0.23(-0.33/-0.13)
Oreochromis macrochir	44	41/249	2.36(1.28/3.42)	-0.07(-0.3/0.16)	1.9/425.2	2.12(1.81/2.44)	-0.02(-0.11/0.05)
Parachromis dovii	150	8.5/266	3.2(2.91/3.48)	0.06(-0.02/0.13)	0.01/461.73	3.4(3.32/3.47)	0.02(-0.01/0.04)
Parachromis friedrichsthalii	484	12.4/170	3.6(3.35/3.86)	-0.05(-0.12/0.01)	0.05/135.32	3.41(3.37/3.46)	-0.02(-0.04/0)
Vieja maculicauda	180	19.8/240	3.66(3.19/4.12)	-0.28(-0.37/-0.18)	0.21/380.74	2.69(2.57/2.83)	-0.09(-0.13/-0.06)
Parapristella georgiae	134	19/32	5(3.58/6.68)	-0.5(-1/-0.05)	0.13/0.62	3.11(2.88/3.33)	-0.28(-0.46/-0.09)
Petrocephalus catostoma	43	44/74	2.97(0.76/5.06)	0.16(-0.38/0.68)	1.82/8.17	3.33(2.94/3.76)	0.13(-0.17/0.41)
Phallichthys amates	336	13/55	2.71(2.02/3.38)	-0.19(-0.38/0.02)	0.02/2.12	2.02(1.94/2.1)	-0.05(-0.12/0.01)
Lebiasina erythrinoides	281	14.6/154	4.06(3.63/4.47)	-0.24(-0.34/-0.13)	0.03/32.44	3.12(3.07/3.18)	-0.08(-0.12/-0.05)
Pimelodella linami	176	45.5/91.9	3.82(2/5.53)	-0.16(-0.59/0.27)	1.3/10.08	3.24(2.98/3.47)	-0.09(-0.28/0.1)
Pimelodella metae	188	20.7/68.4	3.15(2.05/4.25)	0.04(-0.25/0.33)	0.13/4.35	3.3(3.22/3.36)	0.02(-0.1/0.12)
Poecilia gillii	310	12.7/93.2	2.42(1.96/2.85)	-0.09(-0.22/0.02)	0.02/11.07	2.05(1.99/2.1)	-0.03(-0.07/0.01)
Poecilia latipinna	84	8.8/41.3	2.23(1.19/3.13)	-0.07(-0.35/0.26)	0.01/0.87	2.05(1.83/2.27)	0.01(-0.09/0.12)
Poecilia reticulata	210	9/28.3	4.75(3.9/5.59)	-0.8(-1.09/-0.51)	0.01/0.26	1.75(1.47/2.01)	-0.25(-0.35/-0.16)
Pogonias cromis	36	13.9/752	3.02(2.15/3.96)	0.05(-0.12/0.22)	0.06/9277.17	3.23(2.89/3.54)	0.02(-0.04/0.08)
Pollimyrus castelnaui	72	30/62.5	3.43(1.66/5.24)	-0.06(-0.53/0.39)	0.29/2.3	3.2(3.08/3.31)	-0.03(-0.27/0.17)
Pomadasys crocro	78	20/375	3.08(2.55/3.58)	0.06(-0.05/0.17)	0.15/1080.37	3.26(3.11/3.41)	0.02(-0.02/0.06)
Pomoxis annularis	302	14/293	3.14(2.82/3.46)	0.1(0.03/0.17)	0.06/643.6	3.49(3.42/3.57)	0.03(0.01/0.06)

Table A.11 Continued.

Species	N	Range SL (mm)	SL - TL Intercept (CI)	SL - TL Slope (CI)	Range Body mass (grams)	Body mass - TL Intercept (CI)	Body mass - TL Slope (CI)
Prochilodus mariae	64	101/250	3.2(1.43/4.99)	-0.22(-0.57/0.15)	24.71/361.33	2.56(1.95/3.18)	-0.1(-0.25/0.04)
Pseudocrenilabrus nicholsi	43	16.9/41.6	3.68(2.18/5.04)	-0.11(-0.55/0.33)	0.13/1.98	3.23(3.04/3.43)	-0.06(-0.23/0.12)
Pterygoplichthys multiradiatus	54	13.8/235	2.43(1.74/3.1)	-0.06(-0.21/0.08)	0.08/233.88	2.19(1.99/2.41)	-0.02(-0.08/0.03)
Pygocentrus cariba	202	13/248	3.31(2.9/3.75)	-0.01(-0.1/0.09)	0.05/634.23	3.31(3.21/3.42)	0(-0.03/0.03)
Pygopristis denticulata	79	26/94	4.11(2.84/5.53)	-0.35(-0.69/-0.01)	0.48/29.77	3.03(2.81/3.24)	-0.13(-0.26/-0.02)
Pyrrhulina lugubris	293	16/38.1	5.53(4.47/6.58)	-0.65(-0.96/-0.34)	0.03/0.47	2.93(2.77/3.12)	-0.25(-0.37/-0.15)
Rachovia maculipinnis	101	12.3/32.6	3.05(1.81/4.19)	0.08(-0.29/0.49)	0.03/0.57	3.37(3.09/3.66)	0.03(-0.11/0.17)
Rhamdia guatemalensis	105	26.4/180	2.5(1.6/3.48)	0.11(-0.1/0.34)	0.27/73.35	2.99(2.82/3.15)	0.05(-0.03/0.13)
Rhamdia quelen	168	16.6/201	3.24(2.68/3.78)	0.06(-0.07/0.18)	0.09/140.43	3.43(3.31/3.55)	0.02(-0.02/0.06)
Rineloricaria caracasensis	67	25/121	4.82(3.7/5.85)	-0.58(-0.83/-0.32)	0.13/24.21	2.61(2.44/2.75)	-0.21(-0.28/-0.12)
Roeboides dayi	657	13.8/104	2.34(1.96/2.67)	0.31(0.22/0.42)	0.05/23.58	3.48(3.44/3.51)	0.11(0.07/0.14)
Sargochromis carlottae	51	44.2/220	3.47(2.16/4.68)	-0.02(-0.29/0.27)	2.55/314.24	3.36(3.03/3.68)	0(-0.11/0.1)
Sargochromis codringtonii	147	48.2/220	2.9(1.95/3.87)	-0.03(-0.24/0.19)	3.21/309.52	2.82(2.57/3.05)	-0.01(-0.08/0.07)
Sargochromis giardi	54	64.6/277	2.49(1.11/3.66)	0.16(-0.09/0.45)	7.74/619.25	2.92(2.56/3.33)	0.08(-0.02/0.17)
Satanoperca daemon	42	34/119	2.11(0.32/3.83)	0.16(-0.24/0.56)	0.83/39.08	2.56(2.13/2.95)	0.1(-0.07/0.26)
Schilbe intermedius	284	56.6/208	0.5(-0.3/1.34)	0.64(0.48/0.84)	1.48/84.95	3.05(2.92/3.2)	0.24(0.17/0.29)
Schizodon isognathus	91	62.9/260	0.98(-0.39/2.26)	0.26(-0.04/0.54)	4.85/367.85	1.78(1.46/2.1)	0.1(0.01/0.21)
Sciaenops ocellatus	60	232/600	1.83(-0.01/3.67)	0.33(0.02/0.63)	269.23/4701.49	2.69(1.92/3.49)	0.15(0.04/0.26)
Serrabrycon magoi	117	20/30	4.21(2.4/5.89)	-0.16(-0.69/0.42)	0.15/0.51	3.52(3.14/3.86)	-0.14(-0.38/0.09)
Serranochromis angusticeps	44	44.6/340	3.96(2.84/5.17)	-0.07(-0.31/0.16)	1.92/980.94	3.72(3.33/4.08)	-0.03(-0.1/0.06)
Serranochromis macrocephalus	78	52.6/306	2.8(1.63/3.81)	0.23(0.02/0.45)	2.99/701.03	3.5(3.15/3.84)	0.09(0.02/0.16)
Serranochromis robustus	89	49.3/422	3.51(2.52/4.47)	0.04(-0.14/0.23)	2.67/1948.54	3.61(3.28/3.97)	0.02(-0.04/0.08)
Serrasalmus eigenmanni	72	14.6/147.5	2.28(1.6/2.95)	0.41(0.22/0.6)	0.08/126.42	3.7(3.6/3.82)	0.14(0.07/0.2)
Serrasalmus medinai	62	11/80.6	1.49(0.72/2.22)	0.59(0.36/0.83)	0.03/18.17	3.53(3.39/3.67)	0.19(0.12/0.27)

Table A.11 Continued.

Species	N	Range SL (mm)	SL - TL Intercept (CI)	SL - TL Slope (CI)	Range Body mass (grams)	Body mass - TL Intercept (CI)	Body mass - TL Slope (CI)
Serrasalmus rhombeus	50	15/195	2.34(1.47/3.25)	0.38(0.14/0.63)	0.08/300.68	3.7(3.57/3.84)	0.13(0.05/0.21)
Steindachnerina argentea	101	12.1/92.4	3.14(2.33/4.01)	-0.2(-0.42/0.02)	0.04/20.23	2.48(2.37/2.6)	-0.07(-0.14/0.01)
Synbranchus marmoratus	84	40/550	3.16(2.42/3.84)	-0.03(-0.17/0.11)	0.1/240.7	3.01(2.86/3.13)	-0.01(-0.06/0.04)
Synodontis leopardinus	43	39.8/167	3.3(1.99/4.71)	-0.04(-0.4/0.27)	1.25/89.89	3.11(2.89/3.33)	-0.03(-0.15/0.1)
Synodontis woosnami	88	42.8/169	1.69(0.67/2.72)	0.21(-0.05/0.44)	1.59/95.3	2.39(2.21/2.57)	0.09(-0.01/0.17)
Tetragonopterus argenteus	144	37.5/82.6	3.87(2.39/5.39)	-0.27(-0.68/0.11)	1.21/13.16	2.89(2.74/3.02)	-0.13(-0.28/0.03)
Thoracocharax stellatus	179	13.1/42.4	3.39(2.18/4.56)	0.01(-0.33/0.38)	0.06/1.93	3.45(3.36/3.55)	0.01(-0.13/0.14)
Coptodon rendalli	78	32.6/276	2.46(1.68/3.24)	-0.08(-0.27/0.08)	1.07/678.49	2.15(1.95/2.34)	-0.03(-0.09/0.03)
Tilapia sparrmanii	85	27.6/124.8	3.42(2.52/4.21)	-0.29(-0.48/-0.09)	0.58/53.54	2.4(2.19/2.57)	-0.1(-0.17/-0.03)
Trachelyopterus galeatus	179	11.2/115	3.88(3.27/4.46)	-0.14(-0.29/-0.01)	0.04/42.01	3.34(3.23/3.45)	-0.05(-0.1/0)
Trinectes paulistanus	60	13.6/62.9	3.53(2.57/4.4)	-0.02(-0.29/0.27)	0.09/9.68	3.44(3.3/3.55)	-0.01(-0.11/0.09)
Triportheus orinocensis	250	18.2/132	4.79(4.27/5.32)	-0.56(-0.69/-0.42)	0.1/39.1	2.76(2.7/2.83)	-0.19(-0.24/-0.15)
Triportheus venezuelensis	54	72/115	4.01(1.8/6.39)	-0.36(-0.88/0.14)	6.28/25.79	3.14(2.5/3.9)	-0.26(-0.53/0)

Table A.12 Estimated marginal means of the slope of the trophic level (TL)–standard length relationship based on Bayesian phylogenetic linear mixed models performed on 100 different trees are presented for different types of tooth shape, mouth orientation and gill raker. The models were run with standard length as proxy for body size.

Levels	**Marginal means of the TL-SL slope**	**Credible intervals (Lower / Upper)**
Tooth shape		
Absence	-0.06	-0.06 / -0.06
Unicuspid	-0.17	-0.18 / -0.17
Multicuspid	-0.16	-0.16 / -0.16
Conical	0.01	0.01 / 0.02
Triangular serrated	0.32	0.31 / 0.33
Mouth orientation		
Upper	-0.02	-0.02 / -0.01
Terminal	0.00	-0.01 / 0.00
Subterminal	-0.02	-0.03 / -0.02
Inferior	-0.01	-0.01 / 0.00
Gill raker shape		
Absent	-0.07	-0.07 / -0.07
Short	0.05	0.05 / 0.05
Intermidiate	0.00	0.00 / 0.01
Comb-like	-0.03	-0.04 / -0.03

Table A.13 Estimated marginal means of the slope of the trophic level (TL)–body mass relationship based on Bayesian phylogenetic linear mixed models performed on 100 different trees are presented for different types of tooth shape, mouth orientation and gill raker. The models were run with body mass as proxy for body size.

Levels	Marginal means of the TL-body mass slope	Credible intervals (Lower / Upper)
Tooth shape		
Absence	-0.03	-0.03 / -0.03
Unicuspid	-0.06	-0.07 / -0.06
Multicuspid	-0.06	-0.06 / -0.06
Conical	0.01	0.01 / 0.02
Triangular serrated	0.12	0.11 / 0.13
Mouth orientation		
Upper	-0.01	-0.01 / -0.01
Terminal	0	0.00 / 0.00
Subterminal	0	0.00 / 0.00
Inferior	-0.01	-0.01 / 0.00
Gill raker shape		
Absent	-0.03	-0.03 / -0.03
Short	0.03	0.02 / 0.03
Intermidiate	0	0.00 / 0.00
Comb-like	-0.01	-0.02 / -0.01

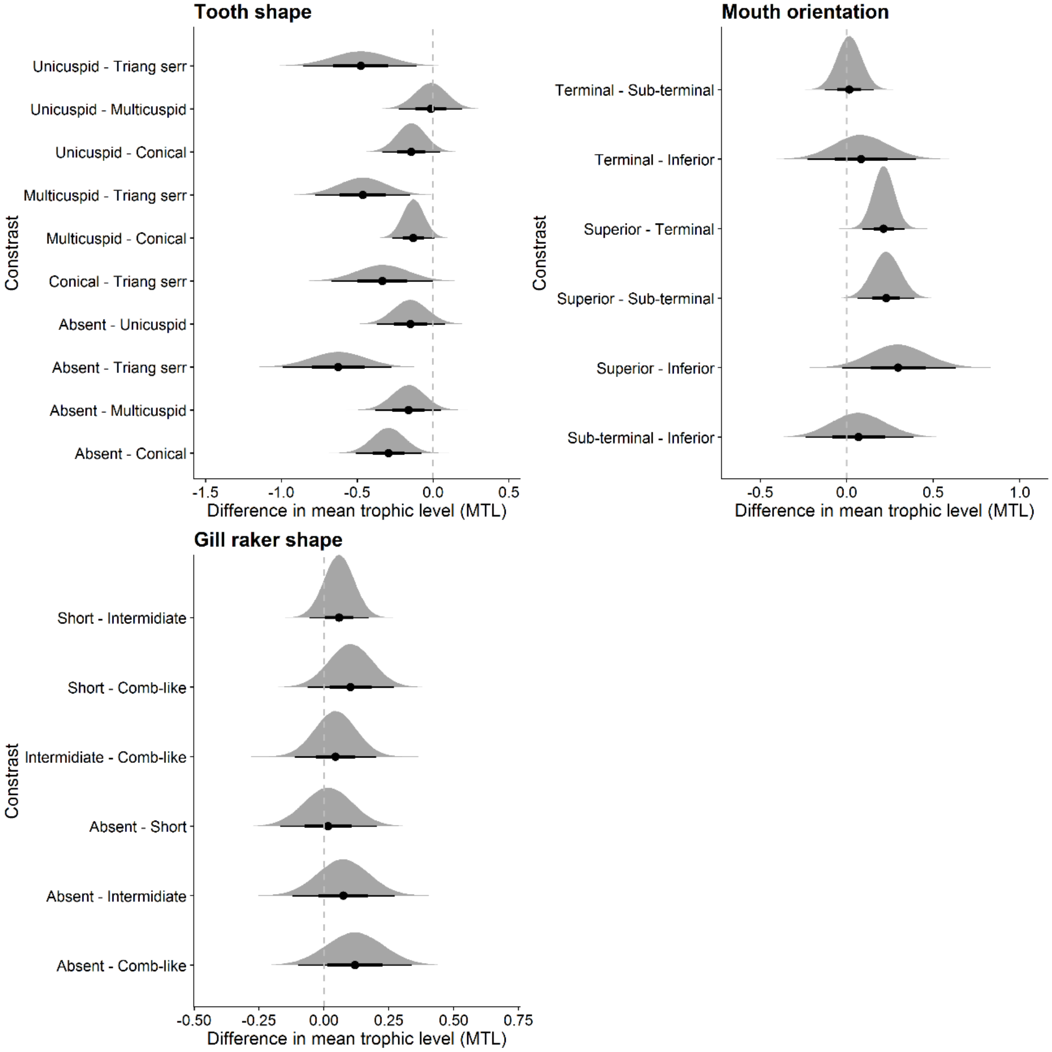


Figure A.1 Posterior distributions of estimated marginal mean differences of MTL among different types of tooth shape, mouth orientation and gill raker shape according to Bayesian phylogenetic linear mixed models performed on 100 different trees. The models were run with standard length as proxy for body size.

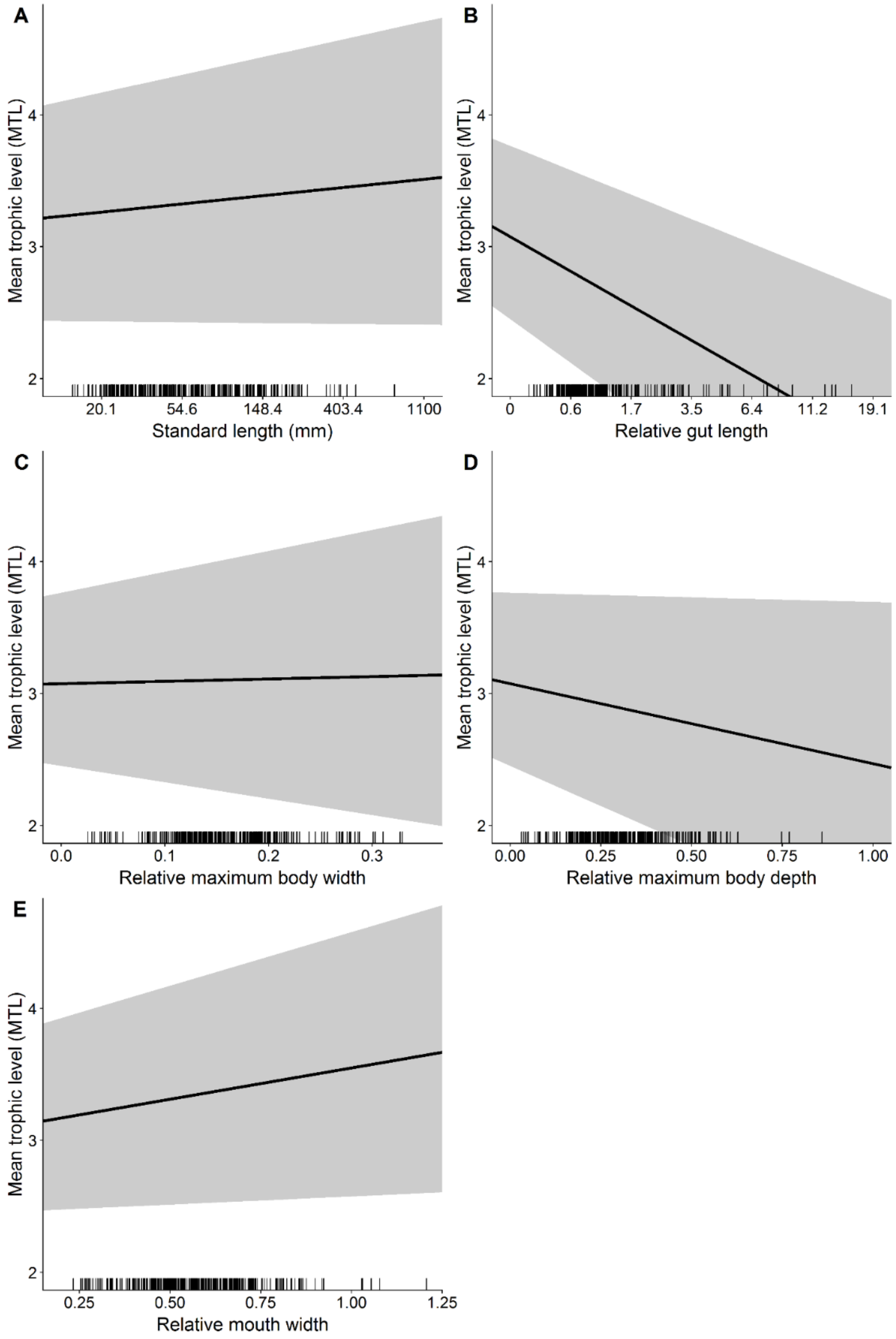


Figure A.2 Marginal effects of standard length (A), relative gut length (B), relative maximum body width (C), relative maximum body depth (D), and relative mouth width (E) on MTL according to Bayesian phylogenetic linear mixed models performed on 100 different trees. Tick marks represent the position of the species according to the x variables. 95% credible intervals of slopes are shown as gray ribbons. The models were run with standard length as proxy for body size.

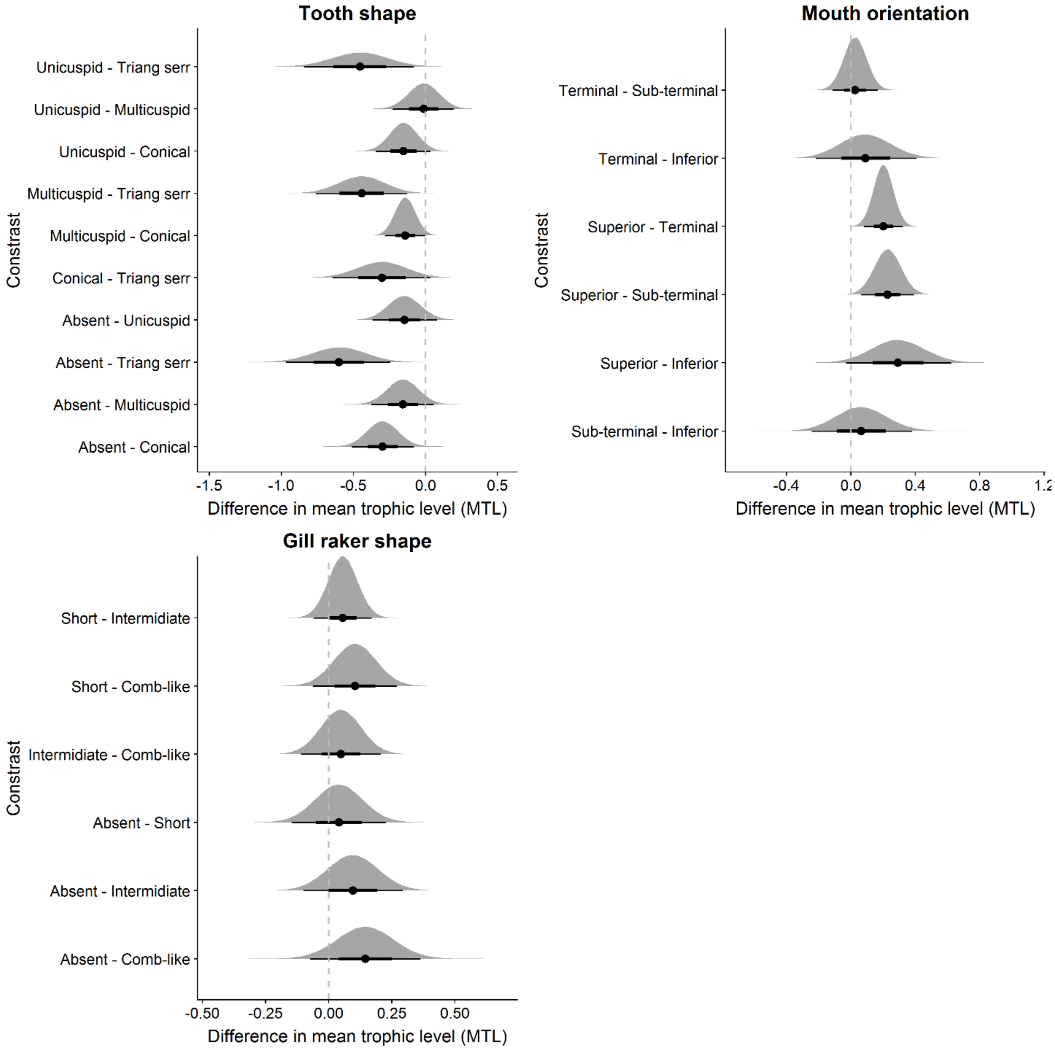


Figure A.3 Posterior distributions of estimated marginal mean differences of MTL among different types of tooth shape, mouth orientation and gill raker shape according to Bayesian phylogenetic linear mixed models performed on 100 different trees. The models were run with body mass as proxy for body size.

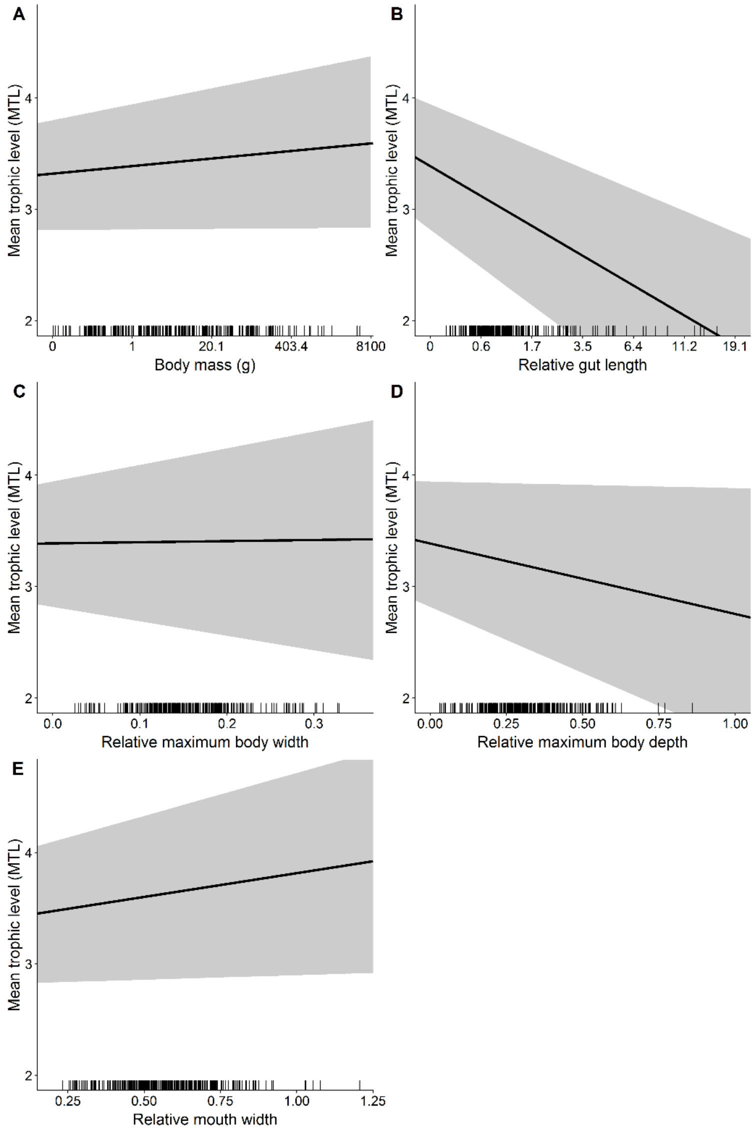


Figure A.4 Marginal effects of body mass (A), relative gut length (B), relative maximum body width (C), relative maximum body depth (D), and relative mouth width (E) on MTL according to Bayesian phylogenetic linear mixed models performed on 100 different trees. Tick marks represent the position of the species according to the x variables. 95% credible intervals of slopes are shown as gray ribbons. The models were run with body mass as proxy for body size.

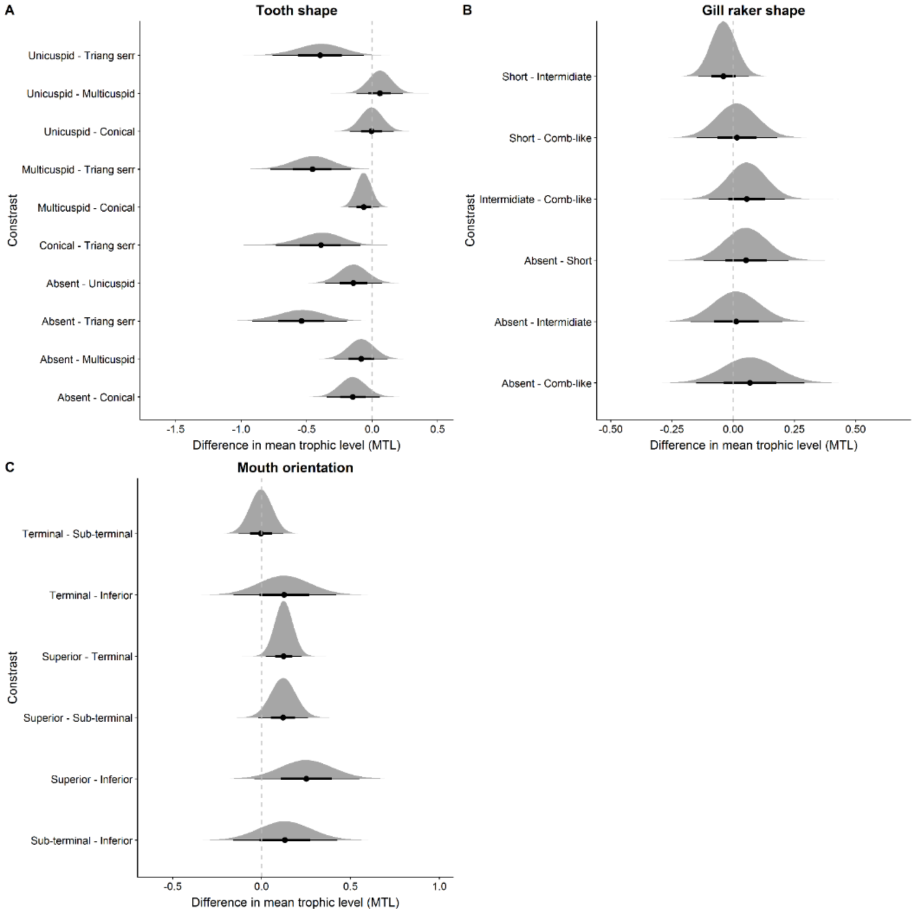


Figure A.5 Posterior distributions of estimated marginal mean differences of mean trophic level (MTL) among different types of tooth shape, mouth orientation and gill raker shape of carnivorous fishes according to Bayesian phylogenetic linear mixed models performed on 100 different trees. The models were run with standard length as proxy for body size.

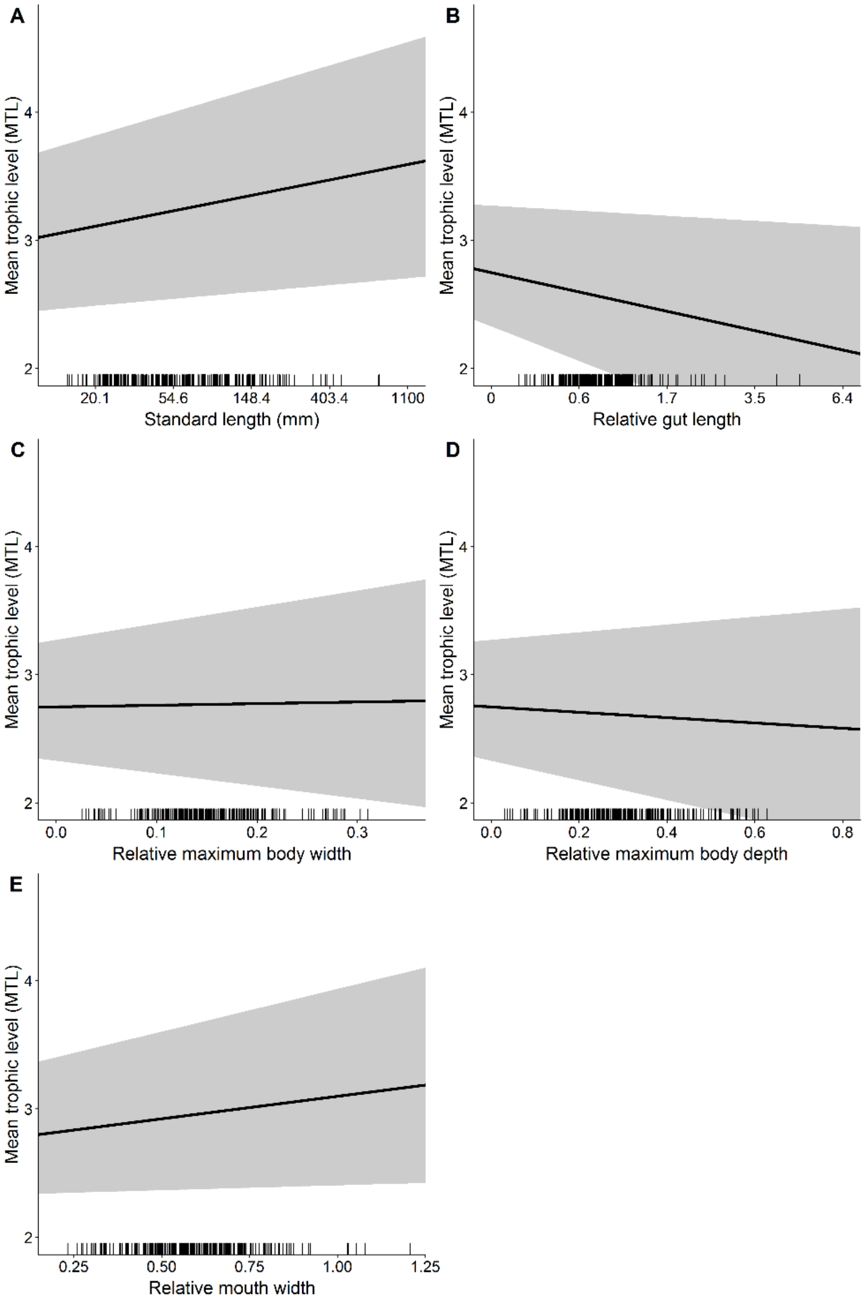


Figure A.6 Marginal effects of standard length (A), relative gut length (B), relative maximum body width (C), relative maximum body depth (D), and relative mouth width on the mean trophic level (MTL) of carnivorous fishes according to Bayesian phylogenetic linear mixed models performed on 100 different trees. Tick marks represent the position of the species according to the x axis. 95% credible intervals of slopes are shown as gray ribbons. The models were run with standard length as proxy for body size.

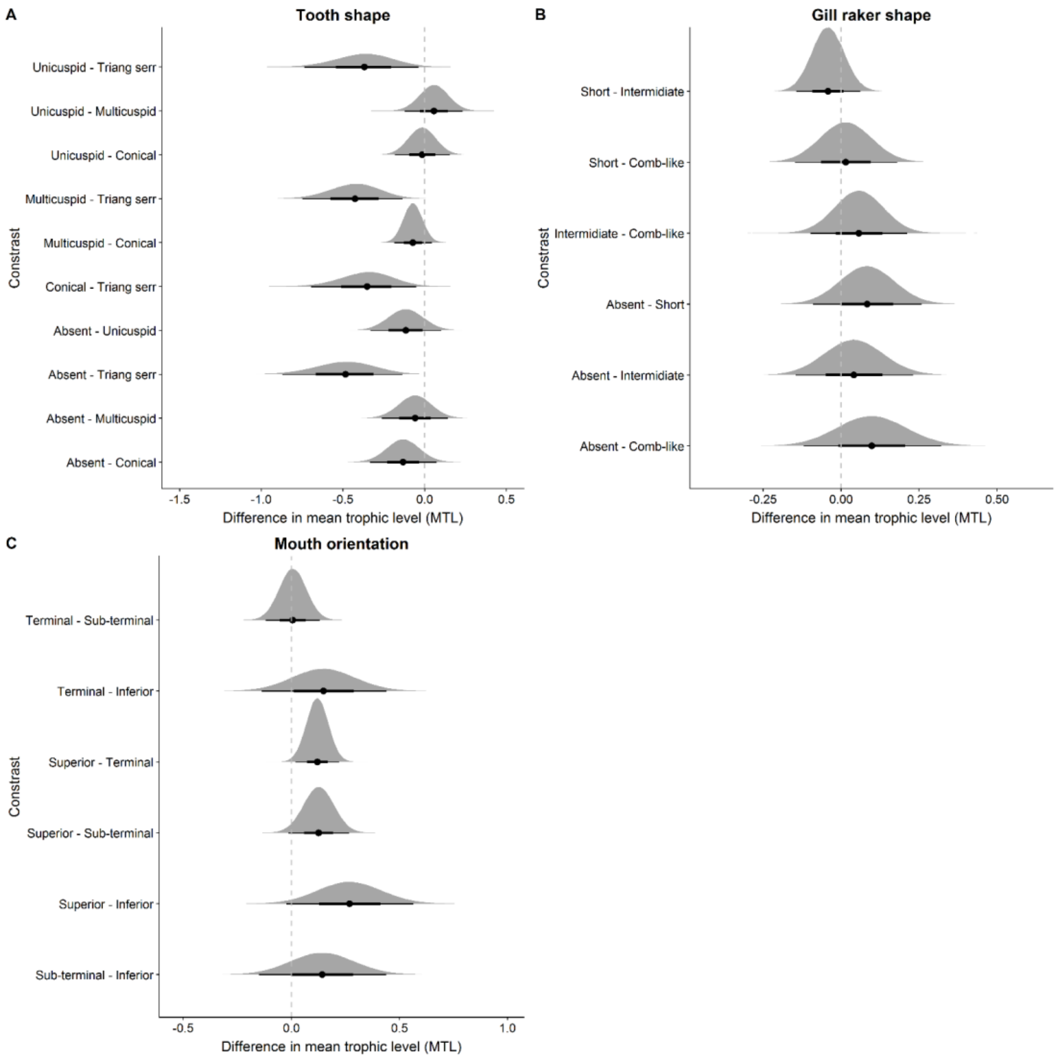


Figure A.7 Posterior distributions of estimated marginal mean differences of the mean trophic level (MTL) among different types of tooth shape, mouth orientation and gill raker shape of carnivorous fishes according to Bayesian phylogenetic linear mixed models performed on 100 different trees. The models were run with body mass as proxy for body size.

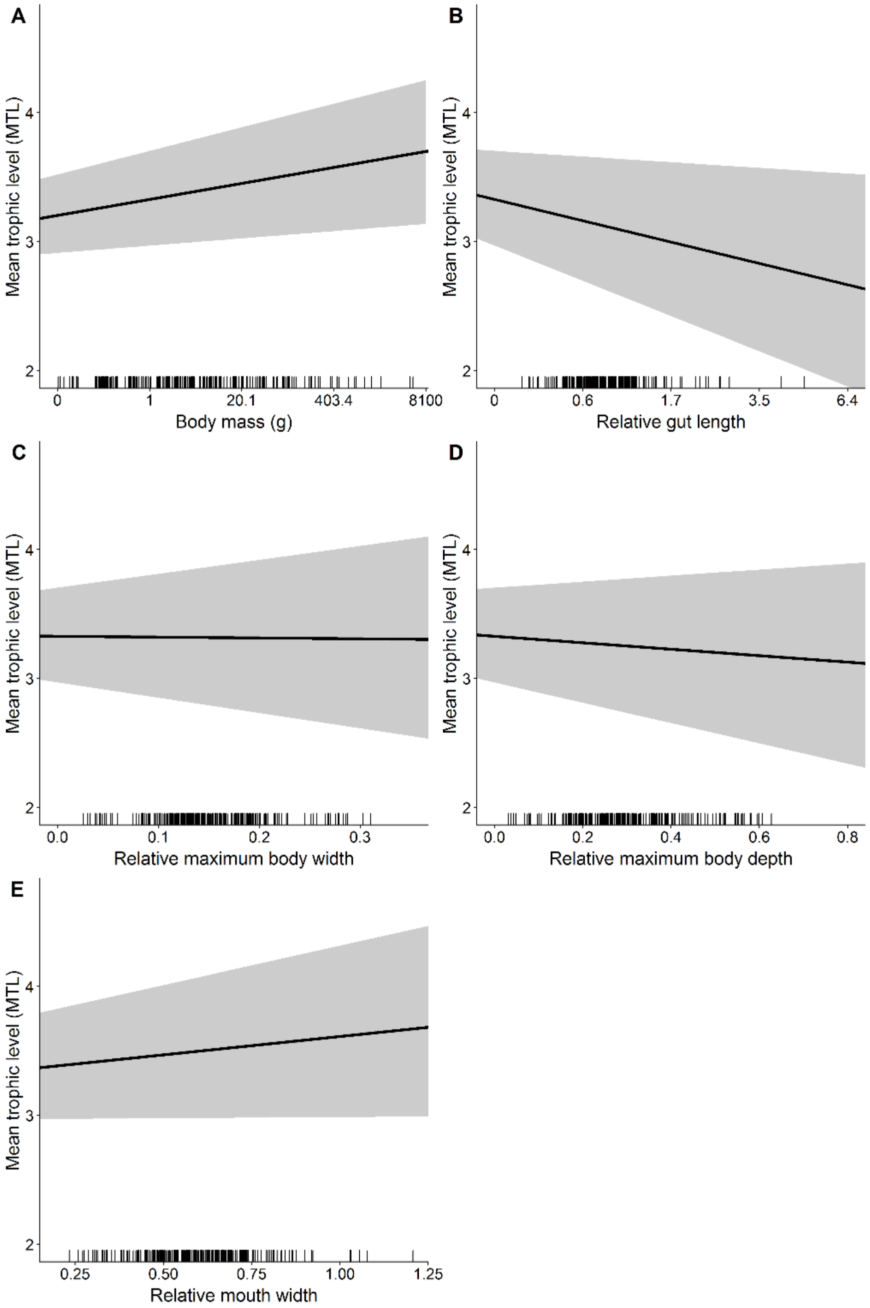


Figure A.8 Marginal effects of body mass (A), relative gut length (B), relative maximum body width (C), relative maximum body depth (D), and relative mouth width on the mean trophic level (MTL) of carnivorous fishes according to Bayesian phylogenetic linear mixed models performed on 100 different trees. Tick marks represent the position of the species according to the x axis. 95% credible intervals of slopes are shown as gray ribbons. The models were run with body mass as proxy for body size.

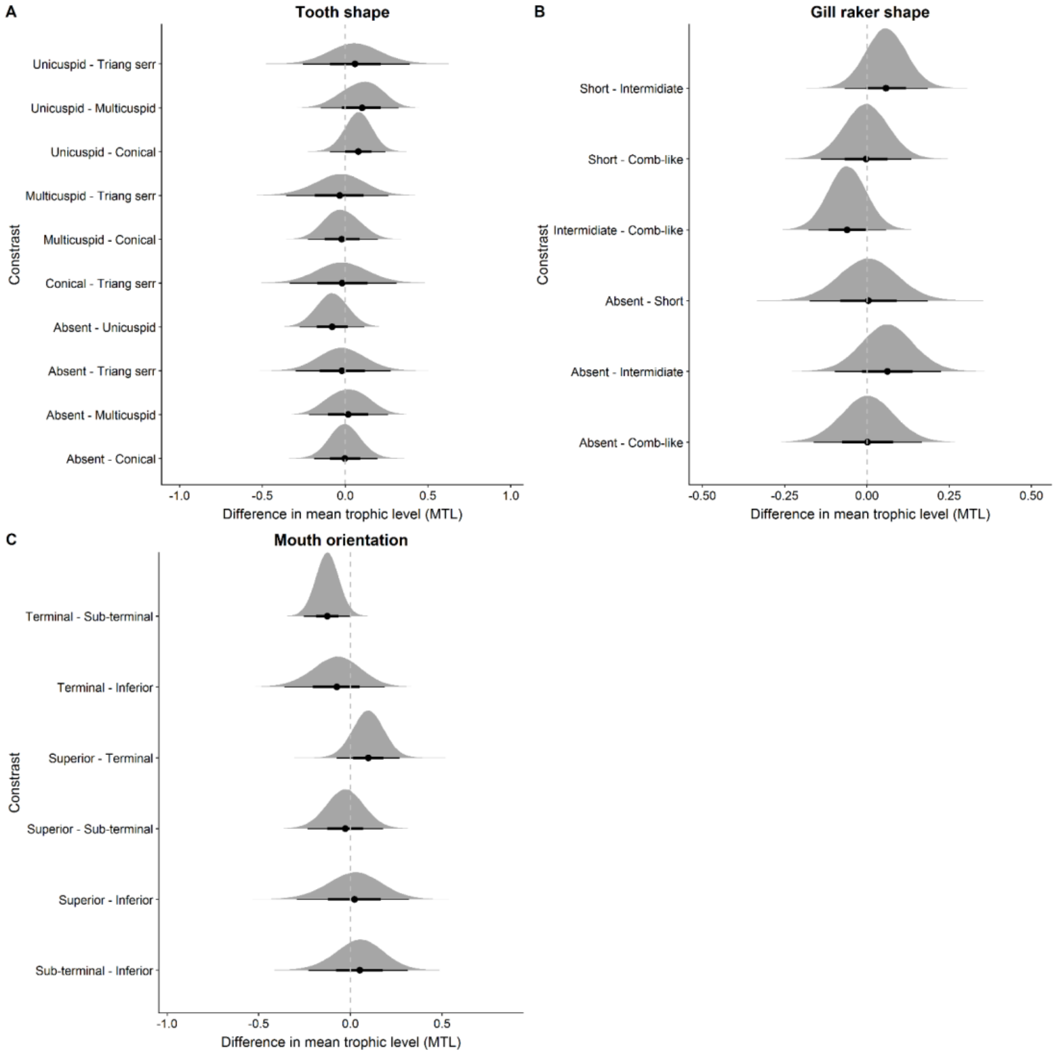


Figure A.9 Posterior distributions of estimated marginal mean differences of the mean trophic level (MTL) among different types of tooth shape, mouth orientation and gill raker shape of non-carnivorous fishes according to Bayesian phylogenetic linear mixed models performed on 100 different trees. The models were run with standard length as proxy for body size.

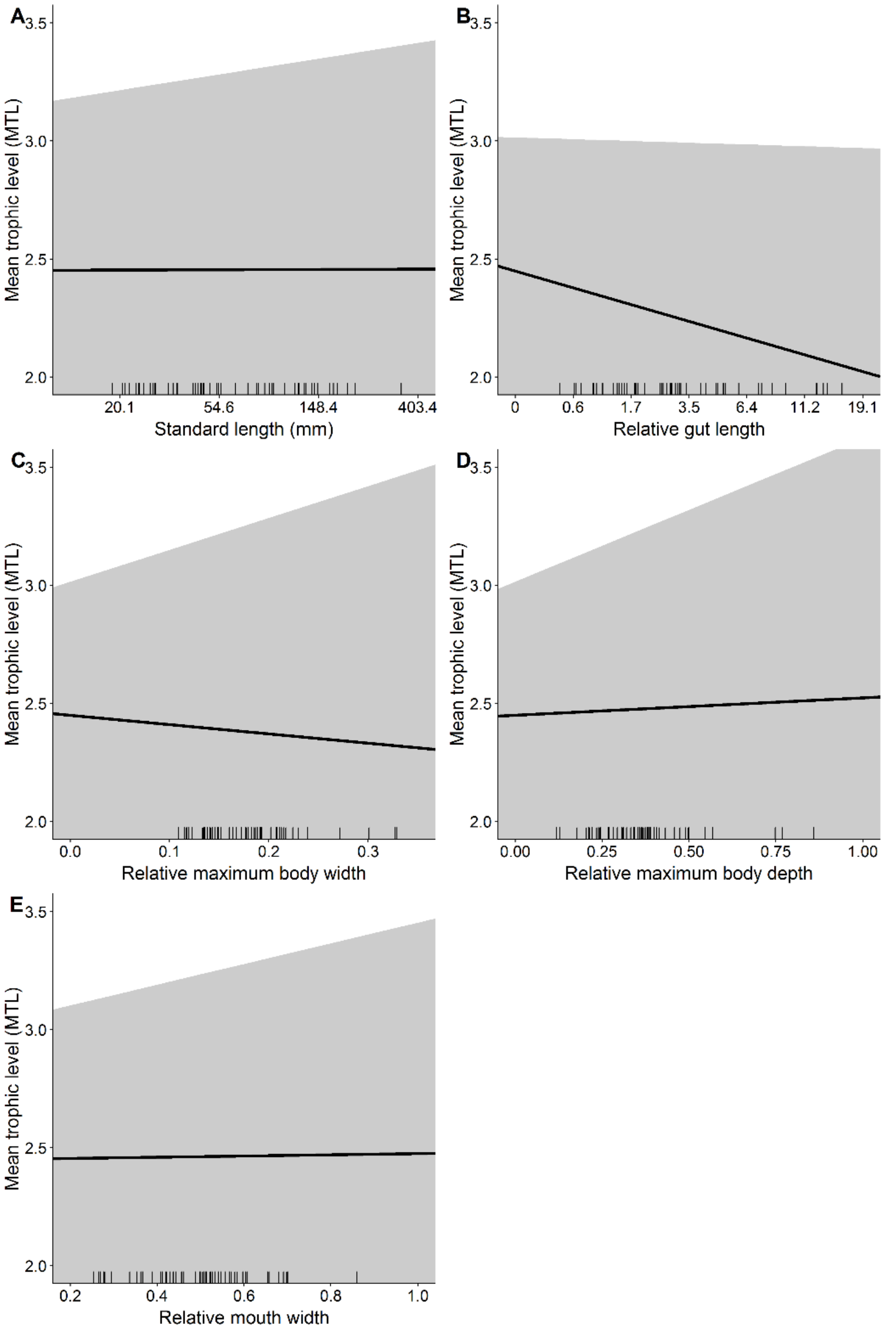


Figure A.10 Marginal effects of standard length (A), relative gut length (B), relative maximum body width (C), relative maximum body depth (D), and relative mouth width on the mean trophic level (MTL) of non-carnivorous fishes according to Bayesian phylogenetic linear mixed models performed on 100 different trees. Tick marks represent the position of the species according to the x axis. 95% credible intervals of slopes are shown as gray ribbons. The models were run with standard length as proxy for body size.

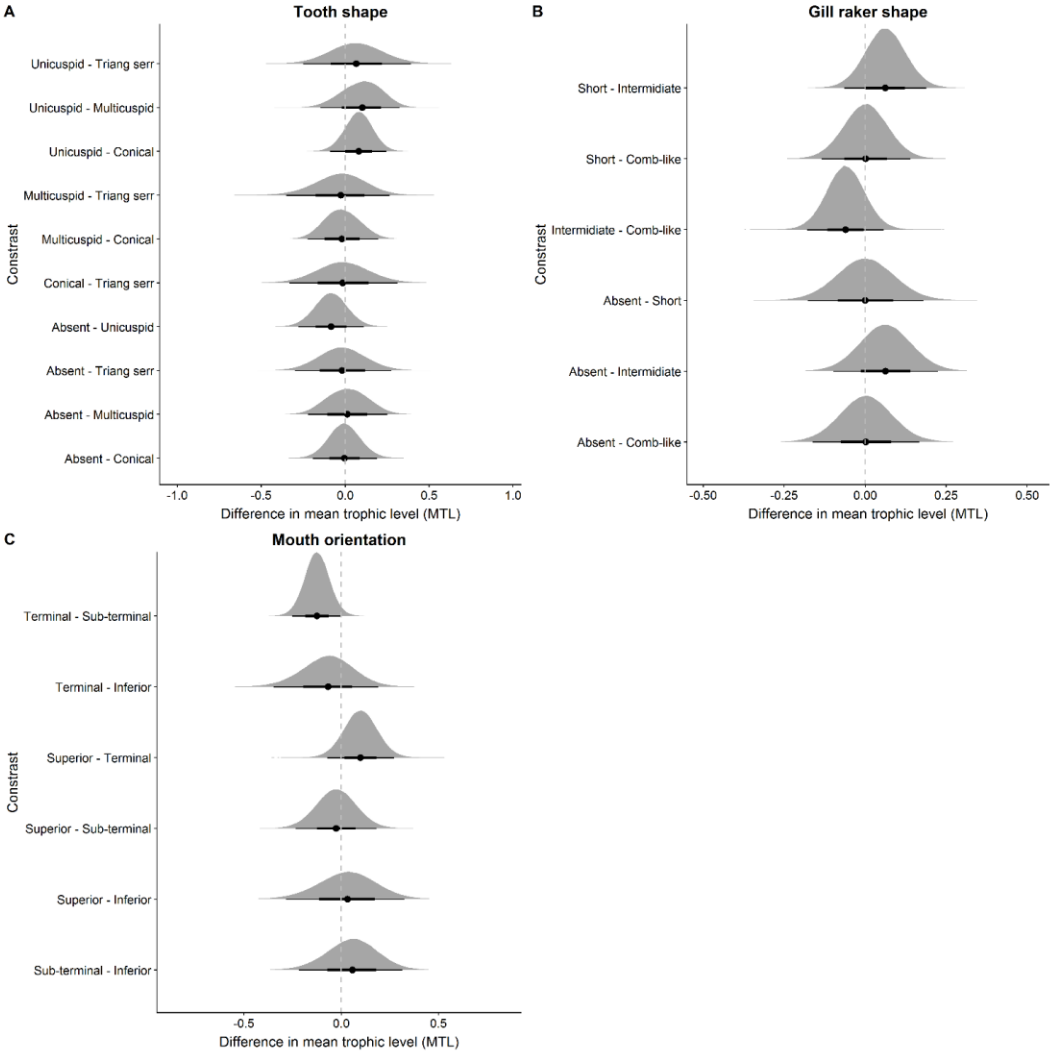


Figure A.11 Posterior distributions of estimated marginal mean differences of the mean trophic level (MTL) among different types of tooth shape, mouth orientation and gill raker shape of non-carnivorous fishes according to Bayesian phylogenetic linear mixed models performed on 100 different trees. The models were run with body mass as proxy for body size.

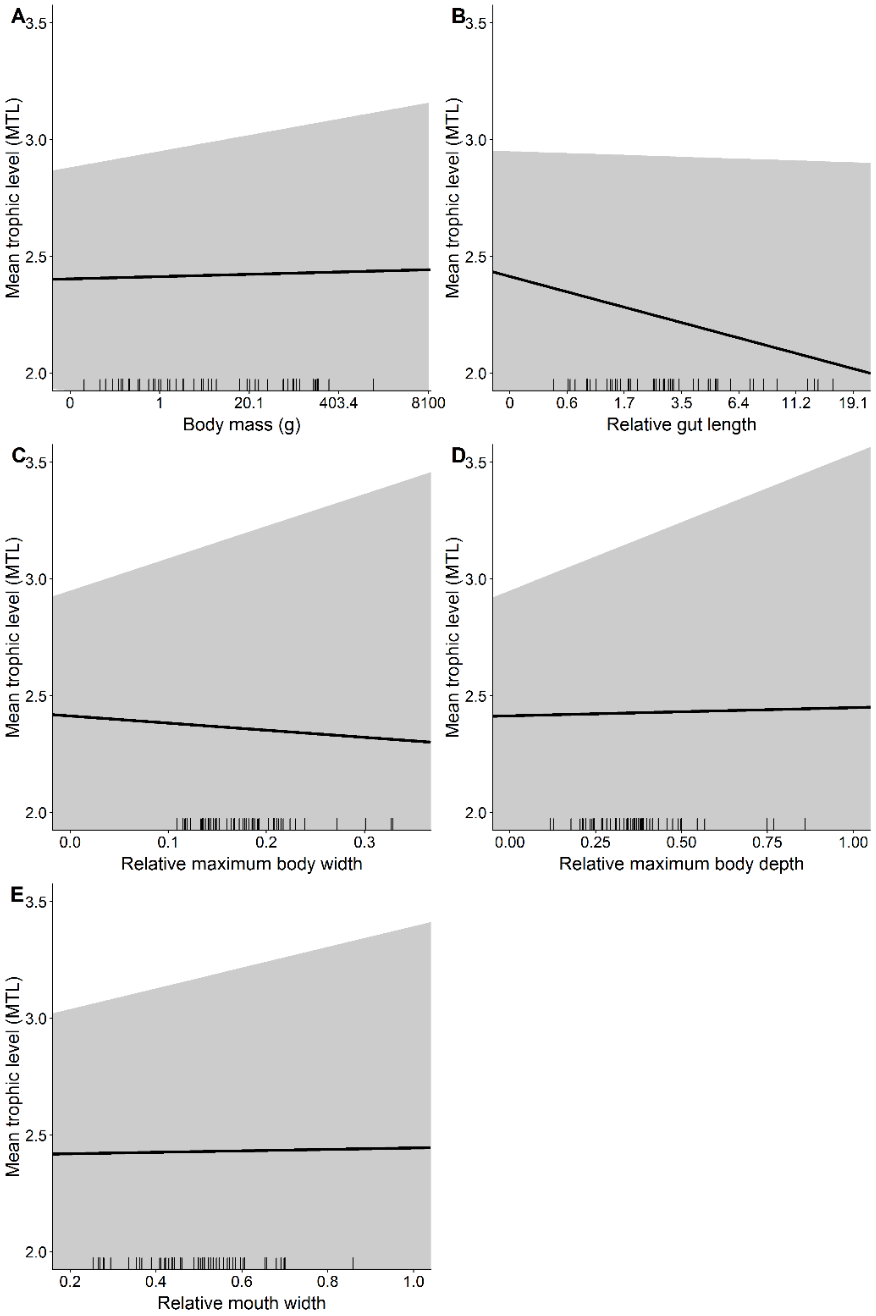


Figure A.12 Marginal effects of body mass (A), relative gut length (B), relative maximum body width (C), relative maximum body depth (D), and relative mouth width on the mean trophic level (MTL) of non-carnivorous fishes according to Bayesian phylogenetic linear mixed models performed on 100 different trees. Tick marks represent the position of the species according to the x axis. 95% credible intervals of slopes are shown as gray ribbons. The models were run with body mass as proxy for body size.

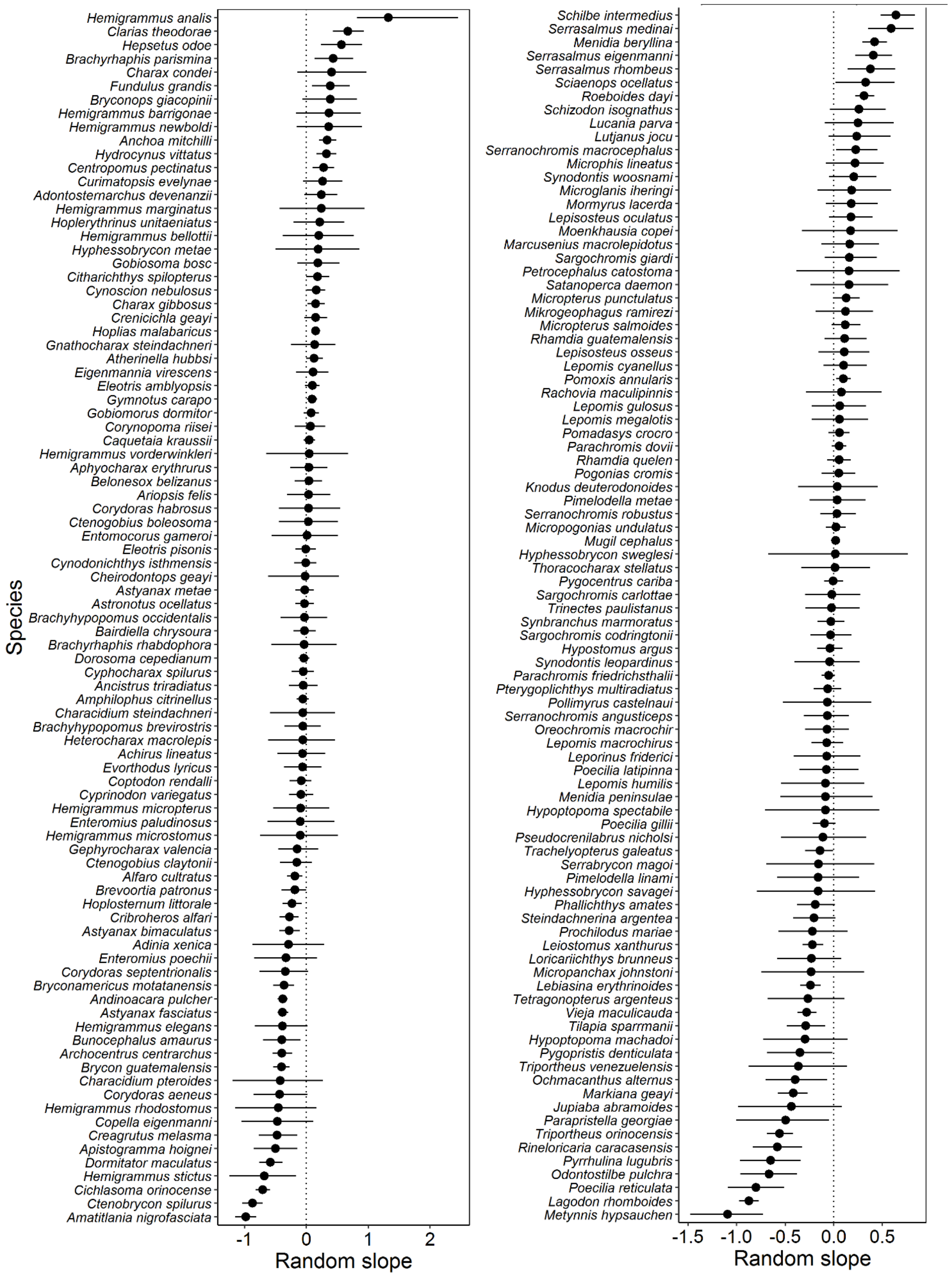


Figure A.13 Slopes for the trophic level (TL)-standard length relationship generated by a semi-parametric mixed model for all species with more than 30 individuals dissected.

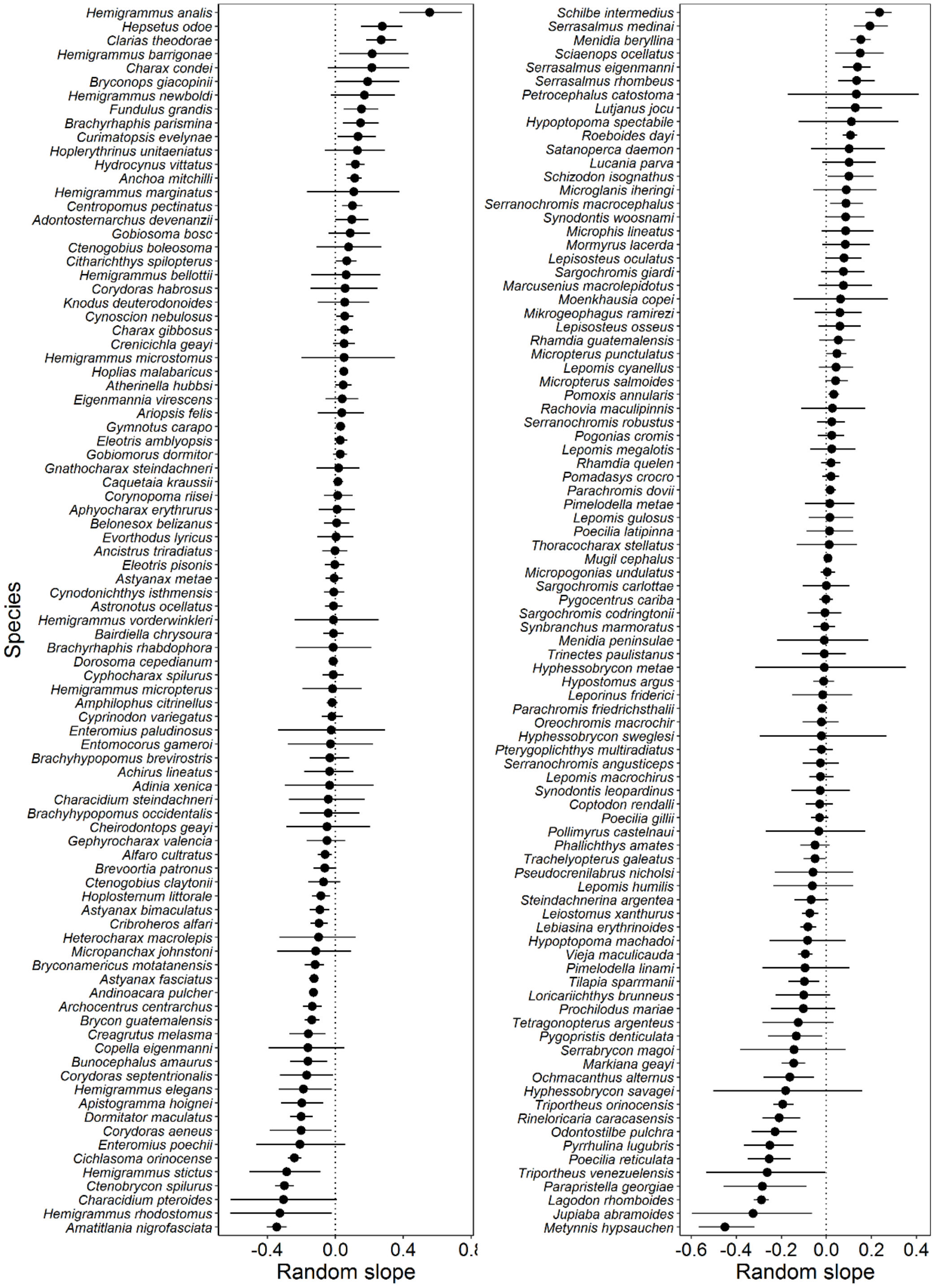


Figure A.14 Slopes for the trophic level (TL)-body mass relationship generated by a semi-parametric mixed model for all species with more than 30 individuals dissected.

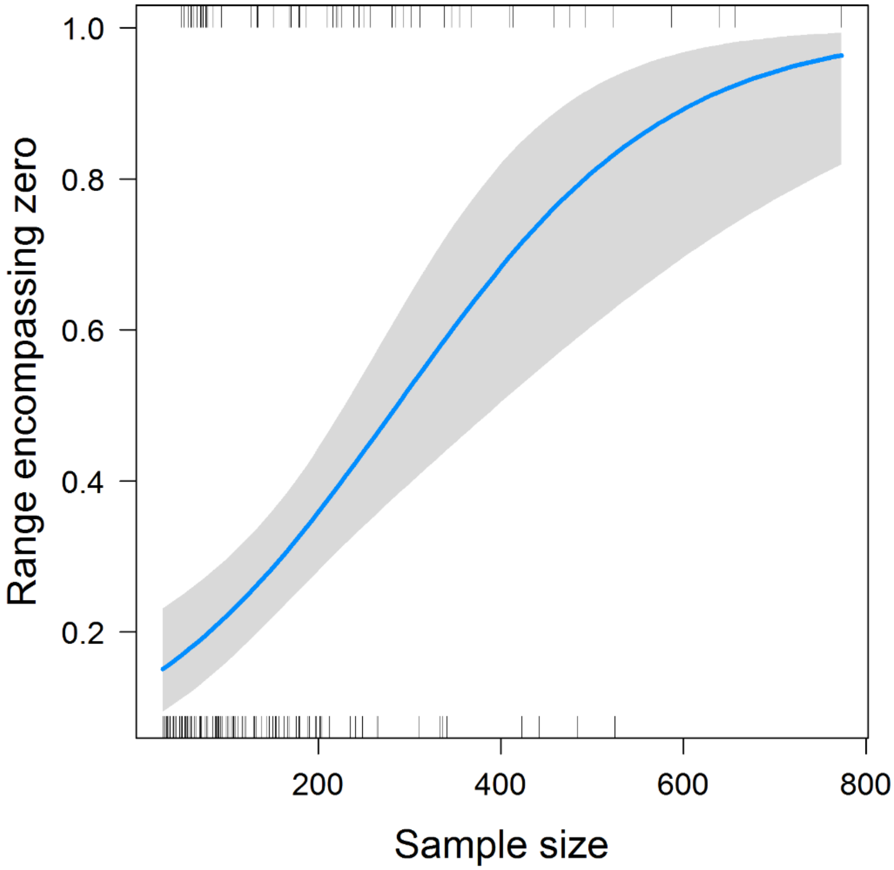


Figure A.15 Relationship between sample size and the occurrence of species with credible intervals (CI) of the TL-standard length slopes not encompassing zero. 0= CI encompassing zero 1= CI not encompassing zero.

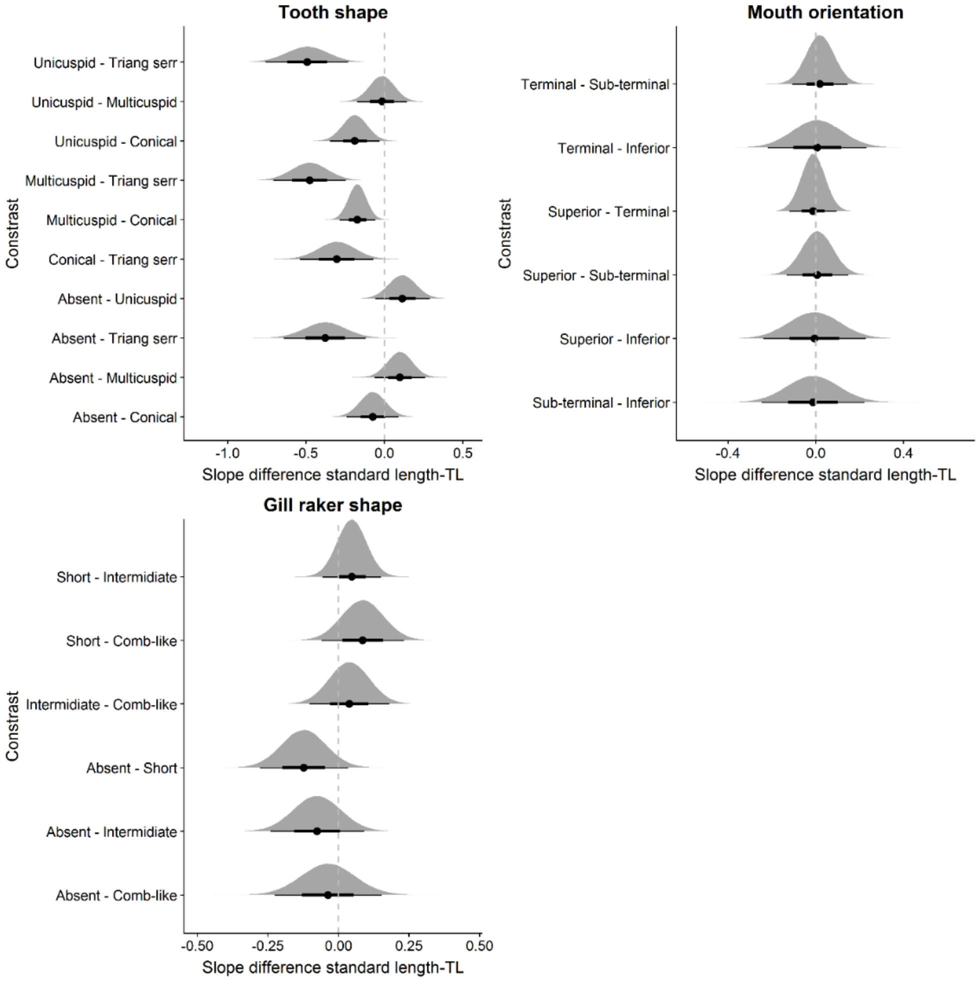


Figure A.16 Posterior distributions of estimated marginal mean differences of the slope of the trophic level (TL)–standard length relationship among different types of tooth shape, mouth orientation and gill raker shape according to Bayesian phylogenetic linear mixed models performed on 100 different trees. The models were run with standard length as proxy for body size.

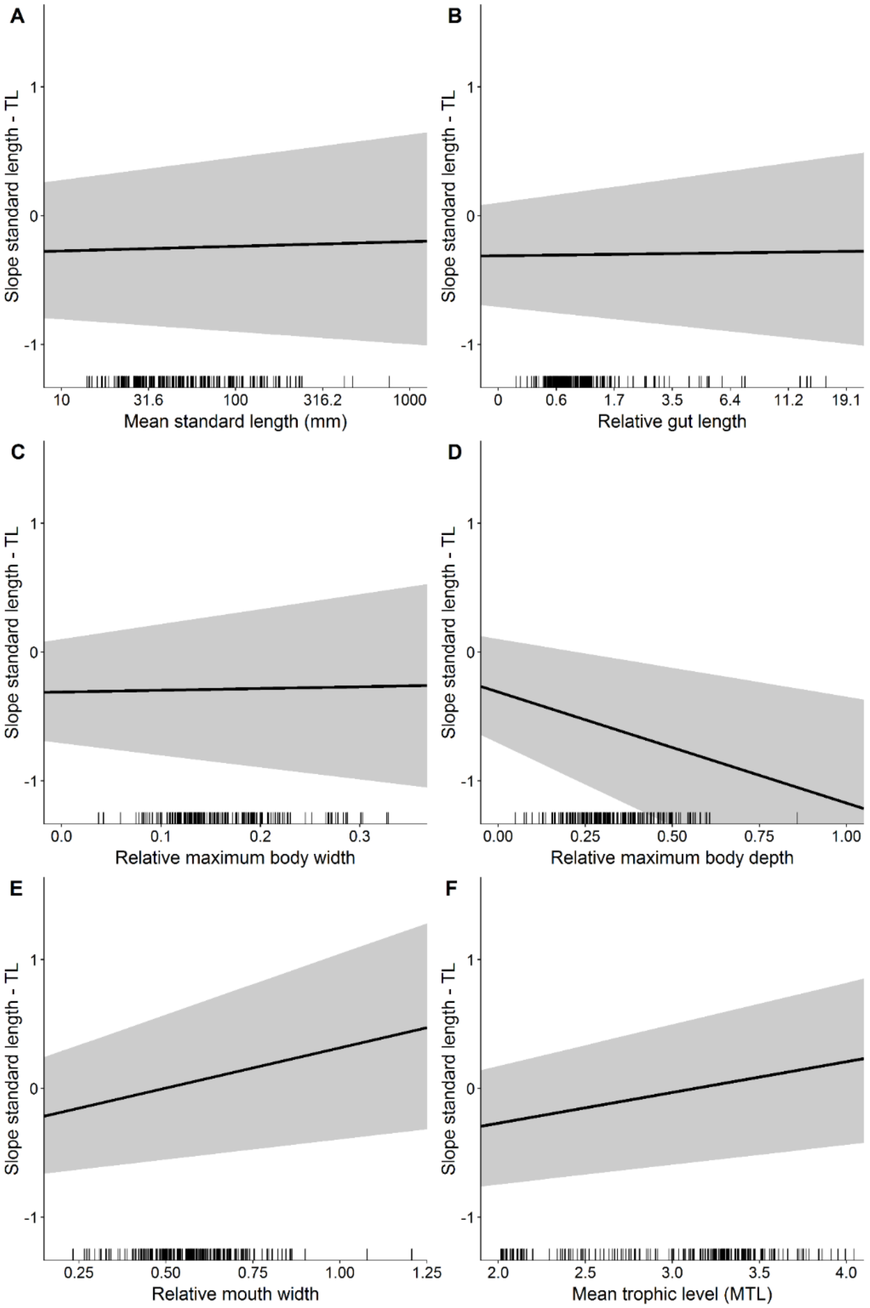


Figure A.17 Marginal effects of standard length (A), relative gut length (B), relative maximum body width (C), relative maximum body depth (D), relative mouth width (E) and mean trophic level (MTL) on the slope of the trophic level (TL)–standard length relationship according to Bayesian phylogenetic linear mixed models performed on 100 different trees. Tick marks represent the position of the species according to the x variables. 95% credible intervals of slopes are shown as gray ribbons. The models were run with standard length as proxy for body size.

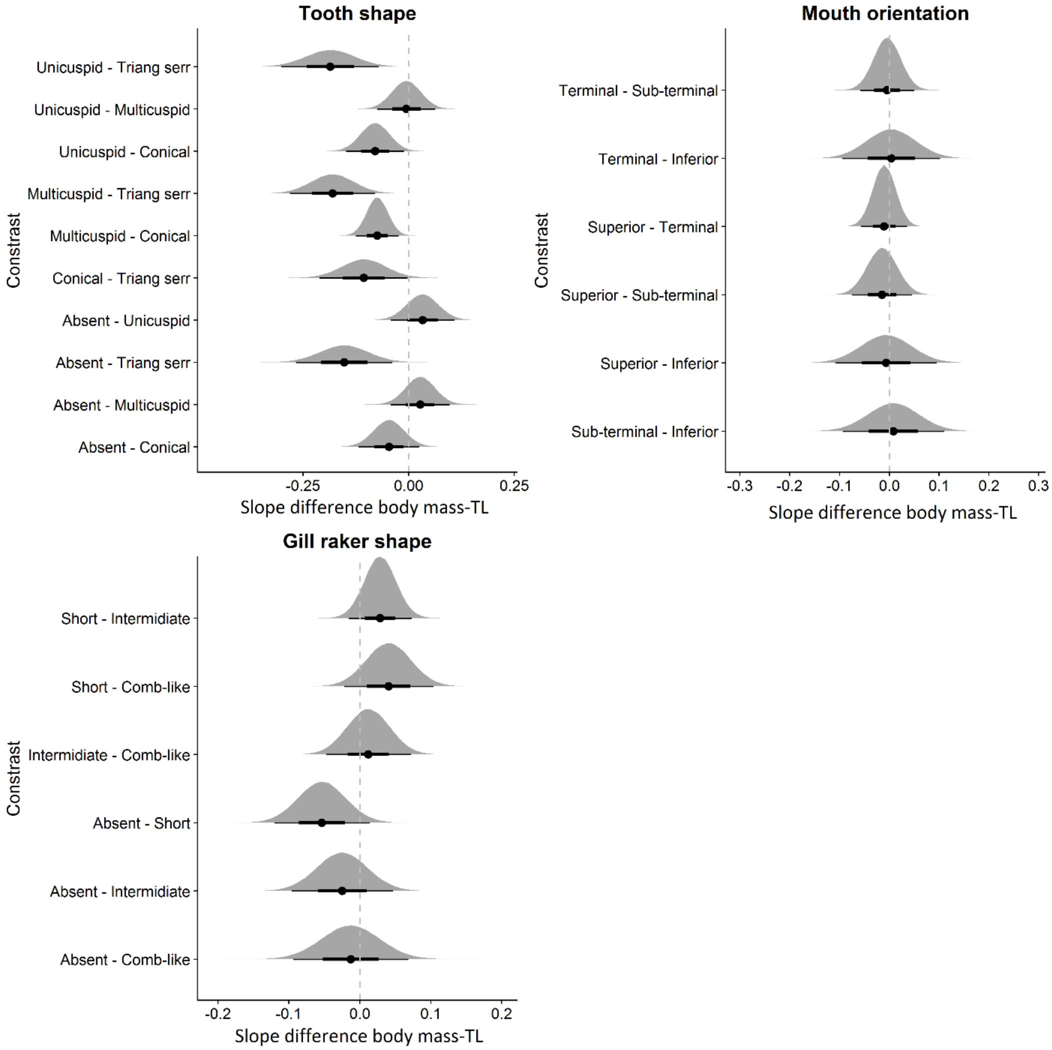


Figure A.18 Posterior distributions of estimated marginal mean differences of the slope of the trophic level (TL)–body mass relationship among different types of tooth shape, mouth orientation and gill raker shape according to Bayesian phylogenetic linear mixed models performed on 100 different trees. The models were run with body mass as proxy for body size.

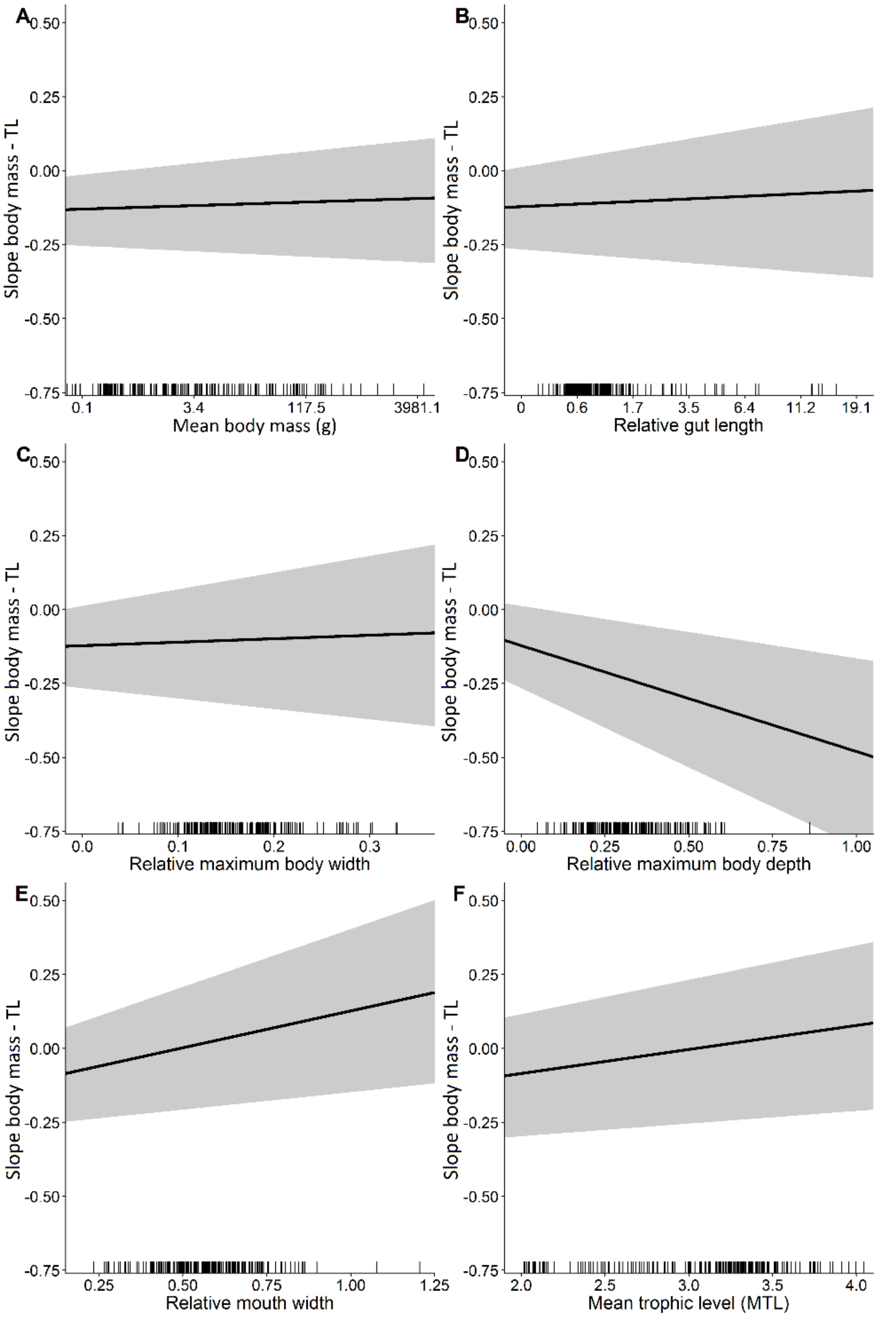


Figure A.19 Marginal effects of body mass (A), relative gut length (B), relative maximum body width (C), relative maximum body depth (D), relative mouth width (E) and mean trophic level (MTL) on the slope of the trophic level (TL)–body mass relationship according to Bayesian phylogenetic linear mixed models performed on 100 different trees. Tick marks represent the position of the species according to the x variables. 95% credible intervals of slopes are shown as gray ribbons. The models were run with body mass as proxy for body size.

APPENDIX B

SUPPORTING INFORMATION FOR THE MANUSCRIPT ENTITLED: INCORPORATING INDIRECT PATHWAYS IN BODY SIZE-TROPHIC POSITION RELATIONSHIPS

Table B.1 Trophic position (TP) estimates for the food items ingested by the fishes used in this study. All basal sources, including autotrophs and detritus, were placed in the TP 1. Primarily herbivorous taxa were considered as TP 2. Secondary and other high-level consumer taxa had TP that vary according to their main food types. For instance, a taxon that ingest primarily plants but eventually eat primary consumers was considered TP 2.25. A taxon that eat both plants and primary consumers at the same rate is considered TP 2.5. On the other hand, if a taxon eats mostly primary consumers but eventually eat plants was considered TP 2.75. References consulted for TP estimates are provided in the end of the document.

Food items	**TP**
Detritus/Sediment	
Coarse detritus	1
Fine detritus	1
Vegetative detritus	1
Miscellaneous detritus	1
Algae	
Chara sp.	1
Filamentous algae	1
Diatoms	1
Golden brown algae	1
Brown algae	1
Blue green algae	1
Polycystis	1
Desmids	1
Miscellaneous algae	1
Plants	
Wolffia sp.	1
Aquatic macrophytes	1
Aquatic vegetation	1
Terrestrial vegetation	1
Leaf litter	1

Table B.1 Continued.

Food items	**TP**
Seeds	1
Fruits (soft tissues) and flowers	1
Miscellaneous vegetation	1
Protozoans	
Miscellaneous protozoans	2
Tubulinea	
Difflugiid	2.25
Bryozoa	
Miscellaneous Bryozoa	2.25
Rotifers	
Miscellaneous Rotifers	2.5
Sponge	
Miscellaneous sponge	2
Platyhelminthes	
Turbellaria	3
Nematoda	
Nematods (non-parasitic forms)	2.75
Nematophora	
Horsehair	3
Miscellaneous Nematophora	2.75
Annelids	
Oligochaeta	2.25
Polychaeta	2.5
Hirudinea (Leeches)	3.5
Molluscs	
Bivalvia	2
Clams	2
Gastropoda	2
Miscellaneous molluscs	2
Microcrustaceans	
Miscellaneous Copepoda	2.5
Ostracoda	2
Cladocera	2.25
Anostraca	2
Branchiopoda	2.25
Miscellaneous microcrustacea	2.25
Crustacea	

Table B.1 Continued.

Food items	**TP**
Miscellaneous Amphipoda	2.5
Thoracica	2
Decapoda	2.5
Palaemonidae	2.5
Dendrobranchiata (shrimps)	2.25
Astacoidea (crayfish)	2.5
Miscellaneous Crustacea	2.5
Chilopoda	
Miscellaneous Chilopoda	3.5
Arachnids	
Hydracarina	3.25
Acarina terrestrial	3
Miscellaneous Acarina	3
Araneae	3.5
Hexapods	
Collembola	2
Coleoptera (Elmidae)	2
Coleoptera (Psephenidae)	2
Coleoptera (Hydrophilidae)	2.75
Coleoptera (Carabidae)	3.5
Coleoptera (Dysticidae)	3.5
Miscellaneous aquatic Coleoptera (adult)	2.5
Miscellaneous aquatic Coleoptera (larvae)	2.5
Miscellaneous terrestrial Coleoptera (adult)	2.5
Ephemeroptera (Ephemeridae)	2
Ephemeroptera (Heptageniidae)	2
Ephemeroptera (Leptophlebidae)	2
Ephemeroptera (Polymitarcidae)	2
Ephemeroptera (Baetidae)	2
Miscellaneous Ephemeroptera (nymph)	2
Miscellaneous Ephemeroptera (adult)	2
Diptera (Psychodidae)	2
Diptera (Ephydridae)	2.25
Diptera (Tipulidae)	2.25
Diptera (Ceratopogonidae)	2.75
Diptera (Tanypodinae)	2.75
Diptera (Chaboridae)	3

Table B.1 Continued.

Food items	**TP**
Diptera pupe (Chaboridae)	3
Diptera (Tabanidae)	3
Diptera (Chironomidae - larvae)	2.5
Diptera (Chironomidae - pupae)	2.5
Miscellaneous Diptera (larvae)	2.5
Miscellaneous Diptera (pupae)	2.5
Miscellaneous Diptera (adult)	2.5
Lepidoptera (adult)	2
Lepidoptera (larvae)	2
Orthoptera (Gryllidae)	2.25
Miscellaneous Orthoptera	2
Isoptera	2
Trichoptera (Calamoceratidae)	2
Trichoptera (Limnephilidae)	2
Trichoptera (Hydropsychidae)	2.25
Trichoptera (Leptoceridae)	2.25
Trichoptera (Heptageniidae)	2.25
Miscellaneous Trichiptera (nymph)	2.25
Blattodea	2.25
Isopoda	2.25
Thysanoptera	2.25
Plecoptera	2.25
Hymenoptera (Formicidae)	2.5
Hymenoptera (Pteromalidae)	3
Miscellaneous Hymenoptera	2.5
Hemiptera (Corixidae)	2.5
Hemiptera (Naucoridae)	3.5
Hemiptera (Gerridae)	3.5
Hemiptera (Notonectidae)	3.5
Miscellaneous terrestrial Hemiptera	2.5
Miscellaneous aquatic Hemiptera	2.75
Odonata (Coenagrionidae)	3.5
Odonata (Cordullidae)	3.5
Odonata (Gomphidae)	3.5
Odonata (Libellulidae)	3.5
Odonata (Adult)	3.5
Odonata (Nymphs)	3.5

Table B.1 Continued.

Food items	**TP**
Odonata (Zygoptera)	3.5
Miscellaneous Odonata	3.5
Neuroptera	3.25
Aquatic Neuroptera (Larvae)	3.25
Miscellaneous terrestrial insects	2.5
Miscellaneous aquatic insects	2.5
Miscellaneous insects (adult)	2.5
Miscellaneous insects (larvae)	2.5
Miscellaneous insects	2.5
Unidentified invertebrates	
Miscellaneous terrestrial invertebrates	2.5
Miscellaneous aquatic invertebrates	2.5
Miscellaneous invertebrates	2.5
Chitin fragments	2.5
Miscellaneous Arthropoda	2.5
Miscellaneous worms	2.5
Non-fish Vertebrates	
Tadpoles	2.25
Frogs	3.5
Adult anurans	3.5
Amphibia Anura	3.5
Bird feather	2.5
Non-fish flesh	2.5
Lizard	2.75
Eggs	
Invertebrate eggs	2.5
Fish eggs	3.1
Miscellaneous eggs	2.5

References

Arcifa M.S. (2000) Feeding habits of Chaoboridae larvae in a tropical brasilian journal. *Revista Brasileira de Biologia,* 60, 591–597.

Arnett Jr.R.H. (2000) *American insects: a handbook of the insects of America North of Mexico*. CRC Press, Boca Raton.

Baker A. & McLachlan A. (1979) Food preferences of Tanypodinae larvae (Diptera: Chironomidae). *Hydrobiologia*, 62, 283–288.

Barnes R. (2003) *Invertebrate zoology*. Cengage Learning, Boston.

Brusca R. & Brusca G. (2003) *Invertebrates*. Sinauer Associates, Sunderland.

Castaño-Meneses G., Palacios-Vargas J.G. & Cutz-Pool. L.Q. (2004) Feeding habits of Collembola and their ecological niche. *Anales del Instituto de Biologia, Universidad Nacional Autonoma de Mexico, Serie Zoologia*, 75, 135–142.

Checon H.H., Pardo E.V. & Amaral A.C.Z. (2017) Breadth and composition of polychaete diets and the importance of diatoms to species and trophic guilds. *Helgoland Marine Research*, 70, 19.

Joern A. (1979) Feeding patterns in grasshoppers (Orthoptera: Acrididae): factors influencing diet specialization. *Oecologia*, 38, 325–347.

De Jong H., Oosterbroek P., Gelhaus J., Reusch H. & Young C. (2008) Global diversity of craneflies (Insecta, Diptera: Tipulidea or Tipulidae sensu lato) in freshwater. *Hydrobiologia*, 595, 457–467.

Jumars P.A., Dorgan K.M. & Lindsay S.M. (2015) Diet of worms emended: an update of Polychaete feeding guilds. Annual Review of Marine Science, 7, 497–520.

Keiper J.B., Walton W.E. & Foote B.A. (2002) Biology and ecology of higher diptera from freshwater wetlands. *Annual Review of Entomology*, 47, 207–232.

Kiφrboe T. & Titelman J. (1998) Feeding, prey selection and prey encounter mechanisms in the heterotrophic dinoflagellate Noctiluca scintillans. *Journal of Plankton Research*, 20, 1615–1636.

Lima J.F., Garcia J.S. & da Silva T.C. (2014) Natural diet and feeding habits of a freshwater prawn (Macrobrachium carcinus: Crustacea, Decapoda) in the estuary of the Amazon River. *Acta Amazonica*, 44, 235–244.

McDiarmid R.W. & Altig R. (1999) *Tadpoles: the biology of anuran larvae*. The University of Chicago Press, Chicago.

Merrit R.W., Cummins K.W. & Berg M.B. (2008) An introduction to aquatic insects of North America. Kendall Hunt Publishers, Dubuque.

Morgan M.D. (1980) Grazing and predation of the grass shrimp Palaemonetes pugio. *Limnology and Oceanography*, 25, 896–902.

Rossa-Feres D.C., Jim J. & Fonseca M.G. (2004) Diets of tadpoles from a temporary pond in southeastern Brazil (Amphibia, Anura). *Revista Brasileira de Zoologia*, 21, 745–754.

Thorp J. & Covich A. (2009) Ecology and classification of North American freshwater invertebrates. Academic Press, Boston.

Winemiller K.O. (1990) Spatial and temporal variation in tropical fish trophic networks. Ecological Monographs, 60, 331–367.

Table B.2 Comparison of species mean body size (standard length, mm) based on specimens that were measured for gape size and gut length, based on the mode approach (specimens comprising the largest mode within the body size distribution of each species) and based on the largest 10% approach (specimens larger than the 90th percentile of the size distribution for each species). Values in parentheses are standard deviations of the mean.

Species	**Body size of fishes measured for mouth gape and gut length**	**Body size of fishes dissected for diet analysis (mode approach)**	**Body size of fishes dissected for diet analysis (largest 10% approach)**
Achirus lineatus	65.1 (18.8)	35.2 (35.2)	54.1 (54.1)
Adontosternarchus devenanzii	119.9 (20.1)	100.3 (100.3)	113.9 (113.9)
Ageneiosus inermis	127.1 (4.3)	121.9 (121.9)	125.8 (125.8)
Alfaro cultratus	51.8 (6.2)	32.5 (32.5)	54.9 (54.9)
Amatitlania nigrofasciata	60.6 (11.9)	37 (37)	60.6 (60.6)
Amphilophus alfari	109.7 (19.9)	17.3 (17.3)	108.2 (108.2)
Amphilophus citrinellus	109.7 (22)	143.6 (143.6)	193.1 (193.1)
Amphilophus rostratus	117 (43)	135.4 (135.4)	150.6 (150.6)
Ancistrus triradiatus	69.6 (9.6)	45.4 (45.4)	68.9 (68.9)
Andinoacara pulcher	61.5 (9.1)	41.4 (41.4)	71.4 (71.4)
Anguilla rostrate	139 (43.3)	79.9 (79.9)	119.4 (119.4)
Aphyocharax erythrurus	32.5 (4.1)	30.4 (30.4)	35.9 (35.9)
Apistogramma hoignei	26.1 (1.7)	22.5 (22.5)	30 (30)
Archocentrus centrarchus	67 (9.6)	24.6 (24.6)	66.1 (66.1)
Archocentrus multispinosus	62.6 (4.6)	54 (54)	75.3 (75.3)
Astronotus ocellatus	152.7 (36.9)	127.6 (127.6)	187.7 (187.7)
Astyanax bimaculatus	45.7 (8.8)	39.8 (39.8)	66 (66)
Astyanax fasciatus	62.1 (12.1)	61.8 (61.8)	81 (81)
Astyanax maximus	70 (19.3)	29.8 (29.8)	84.1 (84.1)
Astyanax superbus	46.4 (13.9)	57.7 (57.7)	59.3 (59.3)
Atherinella hubbsi	67 (10.4)	58.9 (58.9)	76.5 (76.5)
Awaous tajasica	97.2 (NA)	-	96.3 (96.3)
Belonesox belizanus	114.7 (9.8)	59 (59)	113.9 (113.9)
Brachychalcinus orbicularis	55.4 (5.2)	33.3 (33.3)	39.6 (39.6)
Brachyhypopomus brevirostris	192.2 (16.6)	46.1 (46.1)	57.7 (57.7)
Brachyrhaphis parismina	27.2 (7.7)	22.9 (22.9)	36 (36)
Brycon guatemalensis	165.6 (56.6)	199 (199)	341.8 (341.8)
Brycon whitei	185.8 (35.7)	208.6 (208.6)	254.7 (254.7)
Bryconamericus deuterodonoides	33.4 (2.3)	24.1 (24.1)	31.7 (31.7)
Bryconamericus motatanensis	40.6 (0.5)	32.8 (32.8)	40.4 (40.4)

Table B.2 Continued.

Species	**Body size of fishes measured for mouth gape and gut length**	**Body size of fishes dissected for diet analysis (mode approach)**	**Body size of fishes dissected for diet analysis (largest 10% approach)**
Bunocephalus amaurus	53.5 (2.4)	39.5 (39.5)	52.2 (52.2)
Caquetaia kraussii	145.2 (38.4)	39 (39)	139.3 (139.3)
Carlana eigenmanni	47.9 (3.1)	47.1 (47.1)	50.1 (50.1)
Centropomus pectinatus	126.8 (11.6)	189.3 (189.3)	249.7 (249.7)
Characidium pellucidum	33.3 (9.7)	17.1 (17.1)	17.4 (17.4)
Characidium steindachneri	18.6 (2.2)	24.3 (24.3)	27.4 (27.4)
Charax gibbosus	69.8 (12.7)	54 (54)	86.3 (86.3)
Cheirodontops geayi	27 (2.8)	23.1 (23.1)	26.7 (26.7)
Cichlasoma orinocense	79.8 (18.8)	49.3 (49.3)	90.1 (90.1)
Citharichthys spilopterus	74.8 (27.6)	66.5 (66.5)	79.3 (79.3)
Corydoras aeneus	34.9 (3.7)	33.8 (33.8)	42.3 (42.3)
Corydoras habrosus	19.2 (0.8)	16.8 (16.8)	21.7 (21.7)
Corydoras septentrionalis	39.2 (1.7)	33.4 (33.4)	41.9 (41.9)
Corynopoma riisei	36.2 (0.7)	31.7 (31.7)	36.7 (36.7)
Creagrutus melasma	30.4 (2.2)	23.8 (23.8)	28.9 (28.9)
Crenicichla geayi	96.4 (22.6)	73.2 (73.2)	103.5 (103.5)
Crenicichla saxatilis	120.7 (6.6)	61 (61)	81.3 (81.3)
Cryptoheros septemfasciatus	67 (10.3)	25.7 (25.7)	33.4 (33.4)
Ctenobrycon spilurus	38.3 (2.9)	37.7 (37.7)	44.2 (44.2)
Ctenogobius claytonia	52.2 (5.7)	34 (34)	58 (58)
Curimata cyprinoides	99.3 (8.7)	130.4 (130.4)	165.4 (165.4)
Cynodonichthys isthmensis	35.3 (2)	27.6 (27.6)	39.7 (39.7)
Dormitator maculatus	62.1 (3.3)	45.5 (45.5)	68 (68)
Eigenmannia virescens	112.7 (6.5)	92.5 (92.5)	157 (157)
Eleotris amblyopsis	71.2 (7.2)	43.6 (43.6)	71.8 (71.8)
Eleotris Pisonis	97.7 (14.3)	94.3 (94.3)	115.3 (115.3)
Entomocorus gameroi	39.2 (5.2)	33.8 (33.8)	39.3 (39.3)
Evorthodus lyricus	42.9 (9.8)	25.4 (25.4)	47.3 (47.3)
Gephyrocharax valencia	30.2 (1.4)	28.5 (28.5)	35 (35)
Gobiomorus dormitory	176.7 (26.6)	42.1 (42.1)	143.5 (143.5)
Gobiosoma spes	24.3 (4.9)	25.3 (25.3)	25.9 (25.9)
Gymnotus carapo	162.5 (11.5)	164.9 (164.9)	262.8 (262.8)
Gymnotus cylindricus	139.6 (47.9)	108.1 (108.1)	142.9 (142.9)
Hemigrammus elegans	25.3 (4.7)	21.2 (21.2)	29.6 (29.6)

Table B.2 Continued.

Species	**Body size of fishes measured for mouth gape and gut length**	**Body size of fishes dissected for diet analysis (mode approach)**	**Body size of fishes dissected for diet analysis (largest 10% approach)**
Hoplerythrinus unitaeniatus	88.8 (10.1)	39.3 (39.3)	190.4 (190.4)
Hoplias malabaricus	166.7 (32.8)	28.8 (28.8)	195.6 (195.6)
Hoplosternum littorale	105.9 (11.6)	106 (106)	155.6 (155.6)
Hyphessobrycon tortuguerae	38.5 (4.3)	33.5 (33.5)	33.6 (33.6)
Hypopomus sp	132.8 (5.3)	118.2 (118.2)	157.3 (157.3)
Hypostomus argus	132 (39.1)	46.2 (46.2)	166.7 (166.7)
Jupiaba abramoides	28.4 (7.6)	72.6 (72.6)	89.8 (89.8)
Leporinus friderici	94.7 (2.8)	83.1 (83.1)	130.1 (130.1)
Loricariichthys brunneus	163.5 (42.4)	198.2 (198.2)	209.7 (209.7)
Lutjanus jocu	120.4 (9.6)	132.5 (132.5)	225.3 (225.3)
Markiana geayi	65.6 (2.8)	59.6 (59.6)	75.7 (75.7)
Microglanis iheringi	27 (2.1)	26.6 (26.6)	34.4 (34.4)
Microphis lineatus	133 (26.1)	99.5 (99.5)	139.7 (139.7)
Mylossoma duriventre	96 (2)	116.8 (116.8)	117.1 (117.1)
Ochmacanthus alternus	33.9 (1.5)	29.5 (29.5)	35.6 (35.6)
Odontostilbe pulchra	27.5 (1.8)	24.5 (24.5)	30.4 (30.4)
Otocinclus sp	24.7 (0.7)	20.4 (20.4)	25.1 (25.1)
Parachromis dovii	158.5 (19.6)	23.6 (23.6)	177.7 (177.7)
Parachromis friedrichsthalii	114.4 (26.6)	31.9 (31.9)	123 (123)
Paraneetroplus maculicauda	137 (12.5)	150.7 (150.7)	212.7 (212.7)
Phallichthys amates	49.5 (4.4)	32.3 (32.3)	48.3 (48.3)
Piabucina erythrinoides	85.8 (47.9)	44.8 (44.8)	120.9 (120.9)
Pimelodella linami	71.4 (6.1)	64.3 (64.3)	75.9 (75.9)
Pimelodella metae	46.5 (0.8)	46 (46)	58.8 (58.8)
Pimelodus blochii	147.9 (3.4)	128 (128)	128 (128)
Poecilia gillii	70.9 (6.8)	28.9 (28.9)	76.4 (76.4)
Poecilia reticulata	20.4 (1.6)	19 (19)	25 (25)
Pomadasys crocro	106.8 (59.9)	50.1 (50.1)	281.5 (281.5)
Prochilodus mariae	109.7 (7.1)	136 (136)	222.7 (222.7)
Pseudophallus mindii	111.3 (7.6)	99 (99)	98.7 (98.7)
Pterygoplichthys multiradiatus	117 (41.9)	168.5 (168.5)	224.9 (224.9)
Pygocentrus cariba	103.2 (8.6)	92.4 (92.4)	221.1 (221.1)
Pyrrhulina lugubris	35.3 (2.3)	32 (32)	36.1 (36.1)
Rachovia maculipinnis	28.3 (2.5)	21 (21)	28.8 (28.8)
Rhamdia nicaraguensis	115.6 (31.6)	78.2 (78.2)	126.3 (126.3)

Table B.2 Continued.

Species	**Body size of fishes measured for mouth gape and gut length**	**Body size of fishes dissected for diet analysis (mode approach)**	**Body size of fishes dissected for diet analysis (largest 10% approach)**
Rhamdia quelen	100.5 (13.1)	34 (34)	93.5 (93.5)
Rhamdia sp2	176.9 (37.2)	96 (96)	161.6 (161.6)
Rhamphichthys marmoratus	290 (85.4)	230.6 (230.6)	243.3 (243.3)
Rineloricaria caracasensis	104.1 (0.4)	63.3 (63.3)	112.3 (112.3)
Roeboides dayi	51.4 (7.3)	39.3 (39.3)	68.6 (68.6)
Roeboides guatemalensis	69.4 (3.4)	63 (63)	68.9 (68.9)
Schizodon isognathus	147.1 (8.3)	91.9 (91.9)	187.3 (187.3)
Serrasalmus eigenmanni	92 (26.5)	30.5 (30.5)	96 (96)
Serrasalmus medinai	59.1 (11.8)	20.2 (20.2)	67.7 (67.7)
Serrasalmus rhombeus	88.8 (30.9)	37.5 (37.5)	79 (79)
Steindachnerina argentea	61.4 (7.3)	55.7 (55.7)	76 (76)
Sternopygus macrurus	138.4 (32)	-	149.6 (149.6)
Synbranchus marmoratus	330.7 (120.1)	279 (279)	284.7 (284.7)
Tetragonopterus argenteus	45.2 (2.3)	43.1 (43.1)	74.7 (74.7)
Thoracocharax stellatus	32.6 (1.9)	29.5 (29.5)	35.1 (35.1)
Trachelyopterus galeatus	69.2 (3.2)	70.7 (70.7)	96.6 (96.6)
Trinectes paulistanus	54.3 (3.2)	23 (23)	49.8 (49.8)
Triportheus orinocensis	89 (37.3)	60.9 (60.9)	90.9 (90.9)
Triportheus venezuelensis	103.3 (4)	94.7 (94.7)	103.7 (103.7)
Xenagoniates bondi	41.4 (2.1)	38.3 (38.3)	40.3 (40.3)

Table B.3 Direct, indirect, and net effects from each predictor variable to each dependent variable in the piecewise confirmatory path analysis (CPA) built using the dataset containing only specimens larger than the 90th percentile of the size distribution for each species (largest 10% approach). Dashes indicate the absence of an effect.

		Not controlling for phylogeny			**Controlling for phylogeny**		
		Effects			**Effects**		
From	**On**	**Direct**	**Indirect**	**Net**	**Direct**	**Indirect**	**Net**
Consumer size	Gut length	0.79	-	0.79	0.70	-	0.70
Consumer size	Mouth gape	0.90	-	0.90	0.88	-	0.88
Consumer size	Food size	0.72	-0.09	0.63	0.63	0.07	0.70
Consumer size	Food size variation	0.68	-0.40	0.28	0.68	-0.35	0.33
Consumer size	Trophic position	0.21	-0.19	0.02	0.15	-0.06	0.09
Gut length	Food size	-0.70	-	-0.70	-0.61	-	-0.61
Gut length	Food size variation	-0.54	-	-0.54	-0.54	-	-0.54
Gut length	Trophic position	-0.71	-0.29	-1.00	-0.76	-0.25	-1.01
Mouth gape	Food size	0.51	-	0.51	0.56	-	0.56
Mouth gape	Food size variation	0.03	-	0.03	0.03	-	0.03
Mouth gape	Trophic position	0.11	0.23	0.34	0.21	0.24	0.45
Food size	Trophic position	0.45	-	0.45	0.43	-	0.43
Food size variation	Trophic position	-0.05	-	-0.05	-0.03	-	-0.03

Table B.4 Phylogenetic signal, measured via the Pagel’s lambda statistic (Pagel 1999), and its significance for all variables analyzed in this study. The phylogenetic signal was calculated using two different approaches: one in which I excluded outliers and maintain only the main mode of the body size distribution of each species (mode approach), and the other where I kept only specimens larger than the 90th percentile of the size distribution for each species in the dataset (largest 10% approach). Lambda values close to one indicate that the attributes evolved according to Brownian motion, whereas values near zero suggest that the attribute is evolving independently of the phylogeny. Significant phylogenetic signals are showed in bold.

	Mode approach		**Largest individuals approach**	
Variable	Lambda	*p* value	Lambda	*p* value
Consumer size	0.45	> 0.050	0.89	**< 0.001**
Mouth gape	0.98	**< 0.001**	0.99	**< 0.001**
Gut length	0.96	**< 0.001**	0.97	**< 0.001**
Food size	0.00	>0.050	0.63	**=0.019**
Food size variation	0.14	> 0.050	0.00	> 0.050
Trophic position	0.82	**< 0.001**	0.83	**< 0.001**

Table B.5 List of species that were not present in the super tree published by Rabosky et al. (2018). I included these unsampled species in the tree based on the position of related species or genus (right-side column).

Species	**Position in the phylogenetic tree**
Triportheus venezuelensis	*Triportheus angulatus*
Synbranchus marmoratus	*Monopterus fossorius*
Steindachnerina argentea	*Steindachnerina elegans*
Schizodon scotorhabdotus	*Schizodon fasciatus*
Roeboides dayi	*Roeboides xenodon*
Rineloricaria caracasensis	*Rineloricaria parva*
Pyrrhulina lugubris	*Pyrrhulina australis*
Pseudophallus mindii	*Syngnathus californiensis*
Piabucina erythrinoides	*Copella nattereri*
Otocinclus sp	*Otocinclus flexilis*
Microphis lineatus	*Microphis brachyurus*
Markiana geayi	*Markiana nigripinnis*
Loricariichthys brunneus	*Loricariichthys anus*
Jupiaba abramoides	*Jupiaba anteroides*
Hypostomus argus	*Hypostomus plecostomoides*
Hemigrammus elegans	*Hemigrammus rodwayi*
Hyphessobrycon tortuguerae	*Hyphessobrycon eques*
Hypopomus sp	*Hypopomus artedi*
Gobiosoma spes	*Gobiosoma bosc*
Entomocorus gameroi	*Auchenipterus nigripinnis*
Gephyrocharax valencia	*Gephyrocharax atracaudatus*
Curimata cyprinoides	*Potamorhina latior*
Ctenogobius claytonii	*Ctenogobius boleosoma*
Crenicichla sveni	*Crenicichla lepidota*
Ctenobrycon spilurus	*Ctenobrycon hauxwellianus*
Creagrutus melasma	*Creagrutus peruanus*
Cheirodontops geayi	*Cheirodon ibicuhiensis*
Charax gibbosus	*Charax leticiae*
Characidium steindachneri	*Characidium pterostictum*
Characidium pellucidum	*Characidium vidali*
Bunocephalus amaurus	*Bunocephalus coracoideus*
Bryconamericus deuterodonoides	*Bryconamericus iheringii*
Bryconamericus motatanensis	*Bryconamericus diaphanus*
Brycon guatemalensis	*Brycon hilarii*
Brycon whitei	*Brycon amazonicus*

Table B.5 Continued.

Species	**Position in the phylogenetic tree**
Brachychalcinus orbicularis	*Brachychalcinus copei*
Adontosternarchus devenanzii	*Adontosternarchus clarkae*
Ancistrus triradiatus	*Ancistrus multispinis*
Aphyocharax erythrurus	*Aphyocharax alburnus*
Astyanax maximus	*Astyanax microlepis*
Astyanax superbus	*Astyanax magdalenae*
Pimelodella linami	*Pimelodella lateristriga*
Pimelodella metae	*Pimelodella cristata*
Rhamdia sp2	*Rhamdia laticauda*

Table B.6 Direct, indirect, and net effects from each predictor variable to each dependent variable in the piecewise confirmatory path analysis (CPA) built using the dataset containing only specimens comprising the main mode of the body size distribution of each species. Dashes indicate the absence of an effect.

		Not controlling for phylogeny			**Controlling for phylogeny**		
		Effects			**Effects**		
From	**On**	**Direct**	**Indirect**	**Net**	**Direct**	**Indirect**	**Net**
Consumer size	Gut length	0.78	-	0.78	0.71	-	0.71
Consumer size	Mouth gape	0.87	-	0.87	0.89	-	0.89
Consumer size	Food size	0.6	-0.04	0.56	0.59	0.03	0.62
Consumer size	Food size variation	0.5	-0.37	0.13	0.52	-0.36	0.16
Consumer size	Trophic position	0.16	-0.31	-0.15	0.10	-0.19	-0.09
Gut length	Food size	-0.65	-	-0.65	-0.64	-	-0.64
Gut length	Food size variation	-0.74	-	-0.74	-0.73	-	-0.73
Gut length	Trophic position	-0.8	-0.24	-1.04	-0.85	-0.23	-1.08
Mouth gape	Food size	0.54	-	0.54	0.54	-	0.54
Mouth gape	Food size variation	0.19	-	0.19	0.18	-	0.18
Mouth gape	Trophic position	0.18	0.15	0.33	0.23	0.18	0.41
Food size	Trophic position	0.14	-	0.14	0.33	-	0.33
Food size variation	Trophic position	0.02	-	0.02	0.02	-	0.02

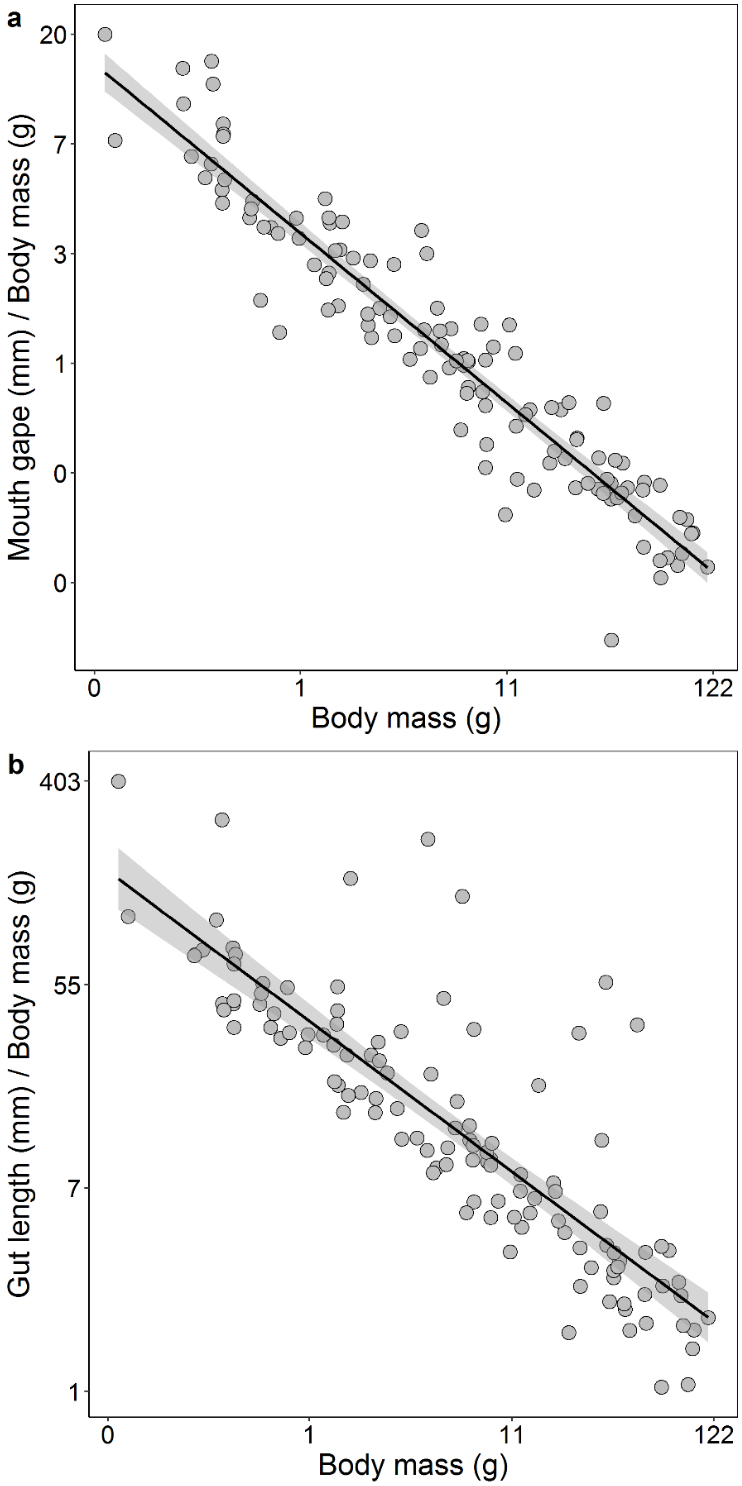


Figure B.1 Relationship between body mass and mouth gape/body mass ratio (a), and between body mass and gut length/body mass ratio.

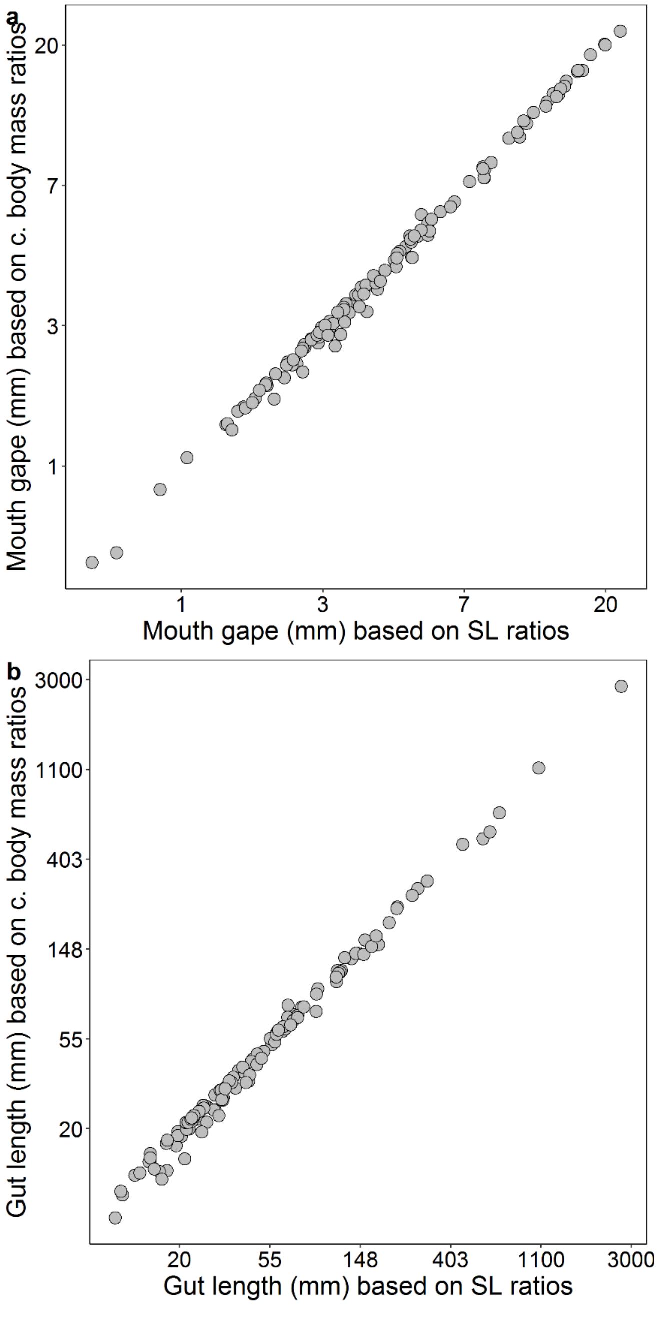


Figure B.2 Relationship between mouth gape estimation based on the standard length (SL) ratio and mouth gape estimation based on the corrected (c.) body mass ratio (a), and between gut length estimation based on SL ratio and gut length estimation based on the c. body mass ratio.

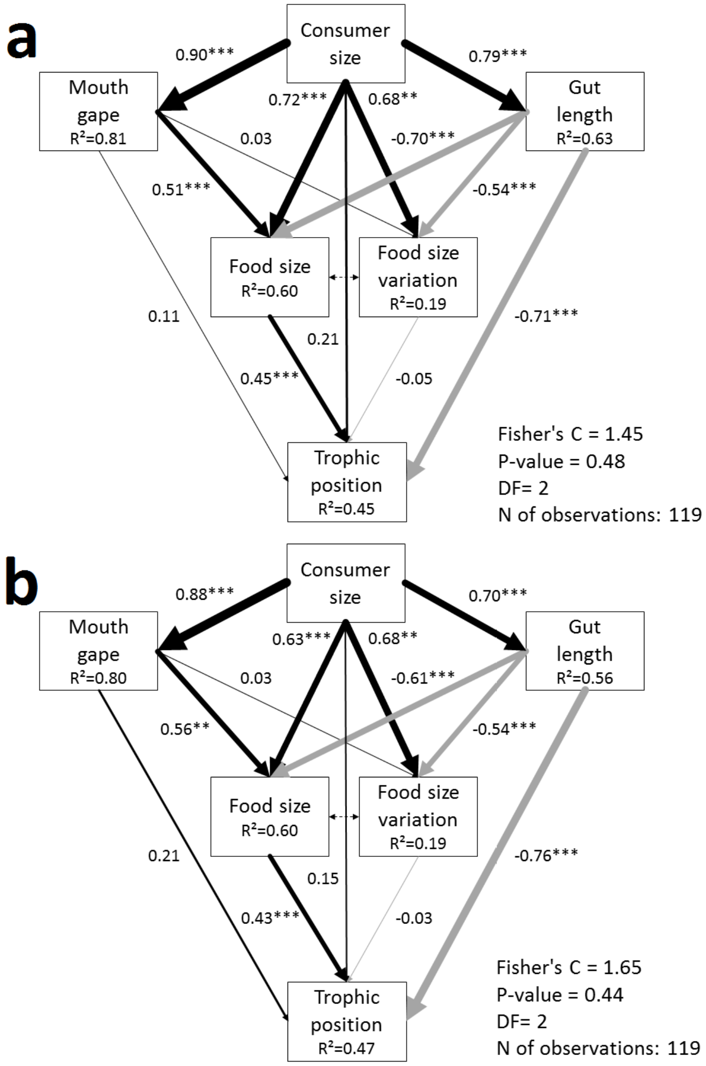


Figure B.3 Piecewise confirmatory path analysis (CPA) for the variables consumer body size, consumer mouth gape, consumer gut length, maximum food item size (Food size), coefficient of variation of food item size (Food size variation), and trophic position. The dataset used for these models were based on the largest individual approach (i.e., largest 10% of specimens dissected for dietary analysis). Compartments of the Piecewise CPA consist either of linear regressions (a) or phylogenetic generalized least squared models (PGLS; b) that account for shared species ancestry. Black and gray arrows represent positive and negative relationships, respectively. Arrow size is proportional to the strength of the relationship. Double-headed arrows with dash lines indicate correlated errors between the variables. Direct path coefficients are shown next to their respective arrows. Asterisks indicate significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Coefficients of determination (R^2) are shown for each response variable. P-values associated with Fisher's C score that are larger than 0.05 indicate consistent CPA models.

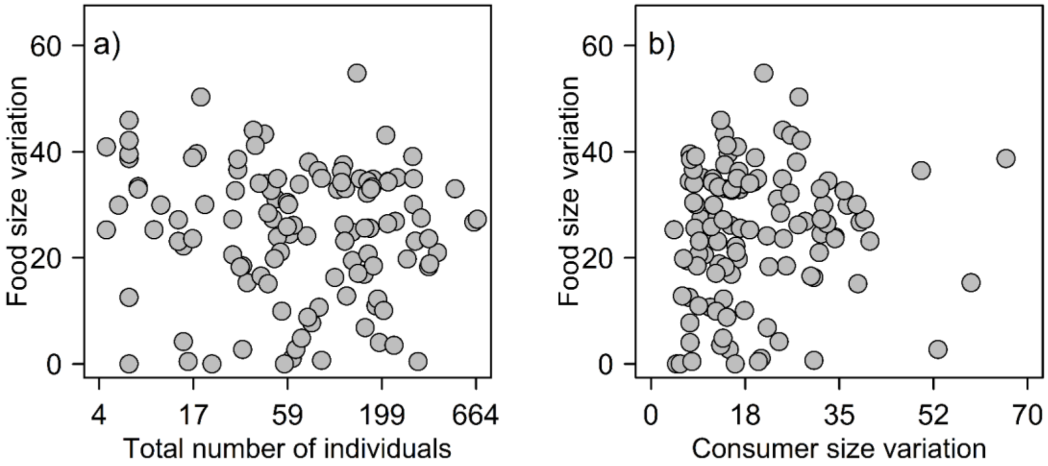


Figure B.4 Relationship of coefficient of variance of food item size (Food size variation) with the total number of specimens (a) and the coefficient of variance of consumer body size (Consumer size variation) (b). Variables were calculated using the dataset based on the mode approach. In both cases, the relationship between the variables was not significant (*p* > 0.05). Food size variation for each consumer species was calculated as the average of 1000 sub-samples of 5 specimens. Food size was based on size intervals of 10 mm. Total number of individuals is shown in a log-scale.

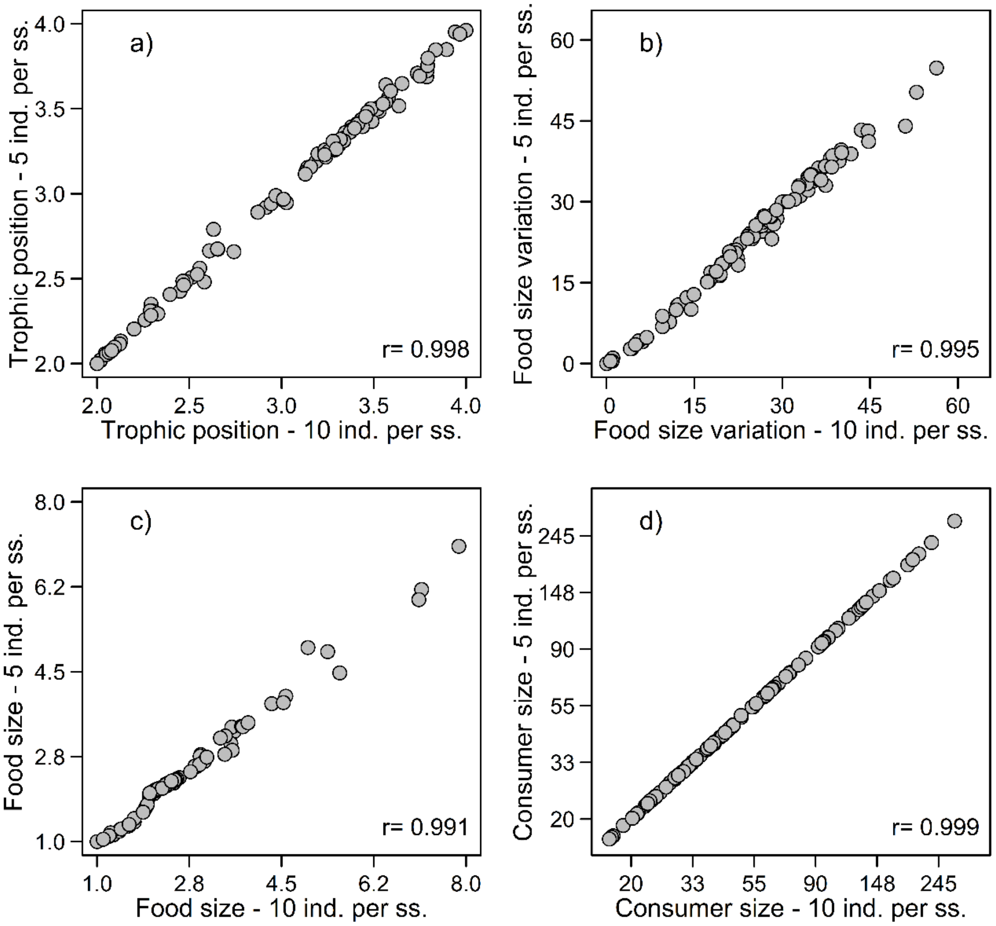


Figure B.5 Correlation between estimates of trophic position (a), coefficient of variation of food item size (food size variation) (b), maximum food item size (food size) (c), and consumer body size (d) with 5 and 10 individuals per sub-sample. The estimates were based on the average of 1000 sub-samples. This use of fix sub-groups was necessary to create species estimates that were comparable in terms of sample size (i.e., N of individual per sample). Food size was based on size intervals of 10 mm. Consumer size is shown in a log-scale. These four variables were generated using the dataset based on the mode approach. ss.=sub-samples, ind.=individuals.

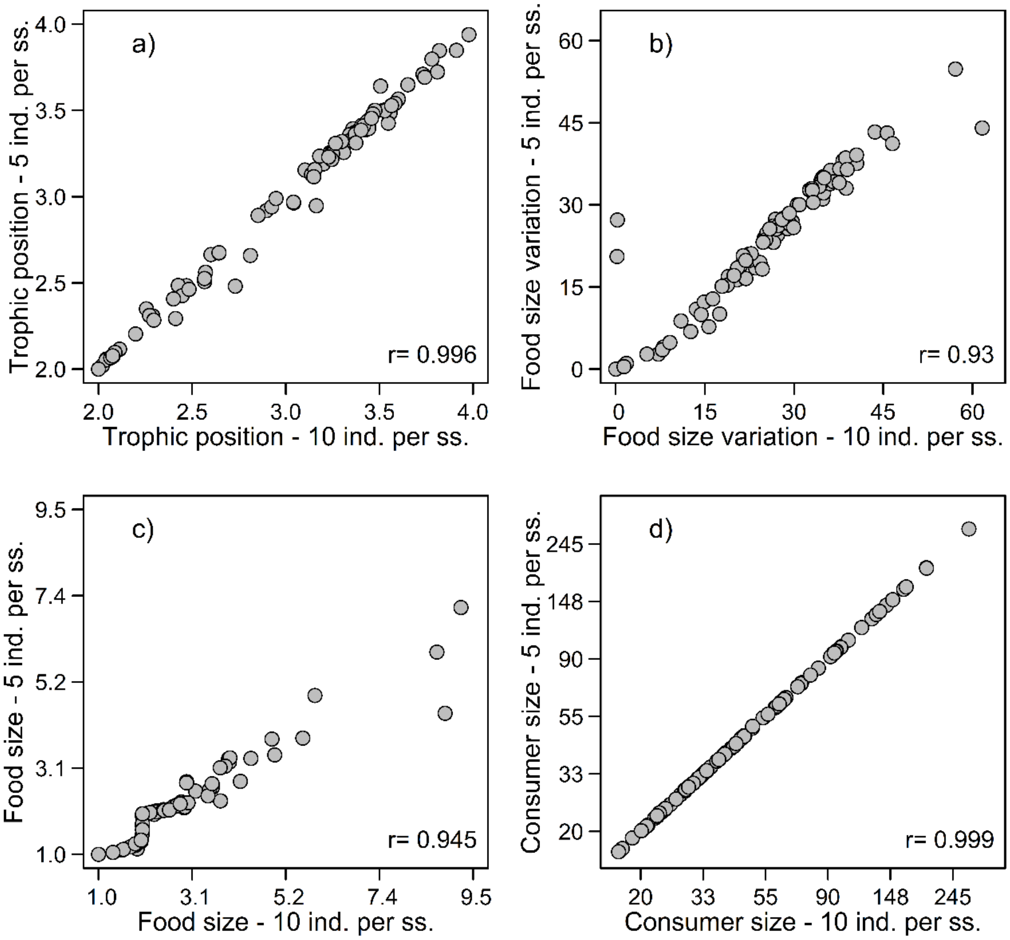


Figure B.6 Correlation between estimates of trophic position (a), coefficient of variation of food item size (food size variation) (b), maximum food item size (food size) (c), and consumer body size (d) with 5 and 30 individuals per sub-sample. The estimates were based on the average of 1000 sub-samples. This use of fix sub-groups was necessary to create species estimates that were comparable in terms of sample size (i.e., N of individual per sample). Food size was based on size intervals of 10 mm. Consumer size is shown in a log-scale. All of these four variables were generated using the dataset based on the mode approach. ss.=sub-samples, ind.=individuals, Cons.=consumer.

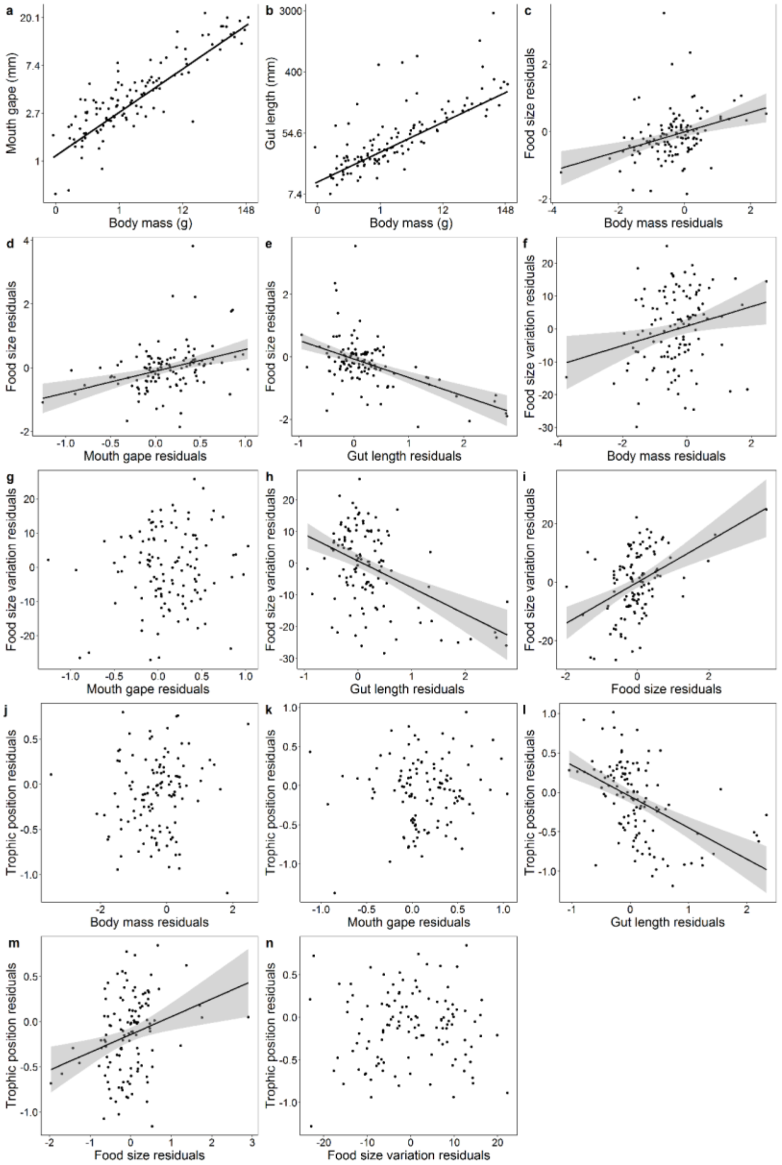


Figure B.7 The estimated relationship between body mass and mouth gape (a), body mass and gut length (b), body mass and maximum food item size (food size) (c), mouth gape food size (d), gut length and food size (e), body size and coefficient of variation of food item size (food size variation) (f), mouth gape and food size variation (g), gut length and food size variation (h), food size and food size variation (i), body mass and trophic position (TP) (j), mouth gape and TP (k), gut length and TP (l), food size and TP (m), food size variation and TP (n). Excepting panels “a” and “b” that are based on simple Phylogenetic Generalized Least Squares models (single explanatory variable), the estimated relationships are based on partial residuals Trend lines provided for significant relationships ($P<0.05$). All variables were generated using the dataset based on the mode approach.

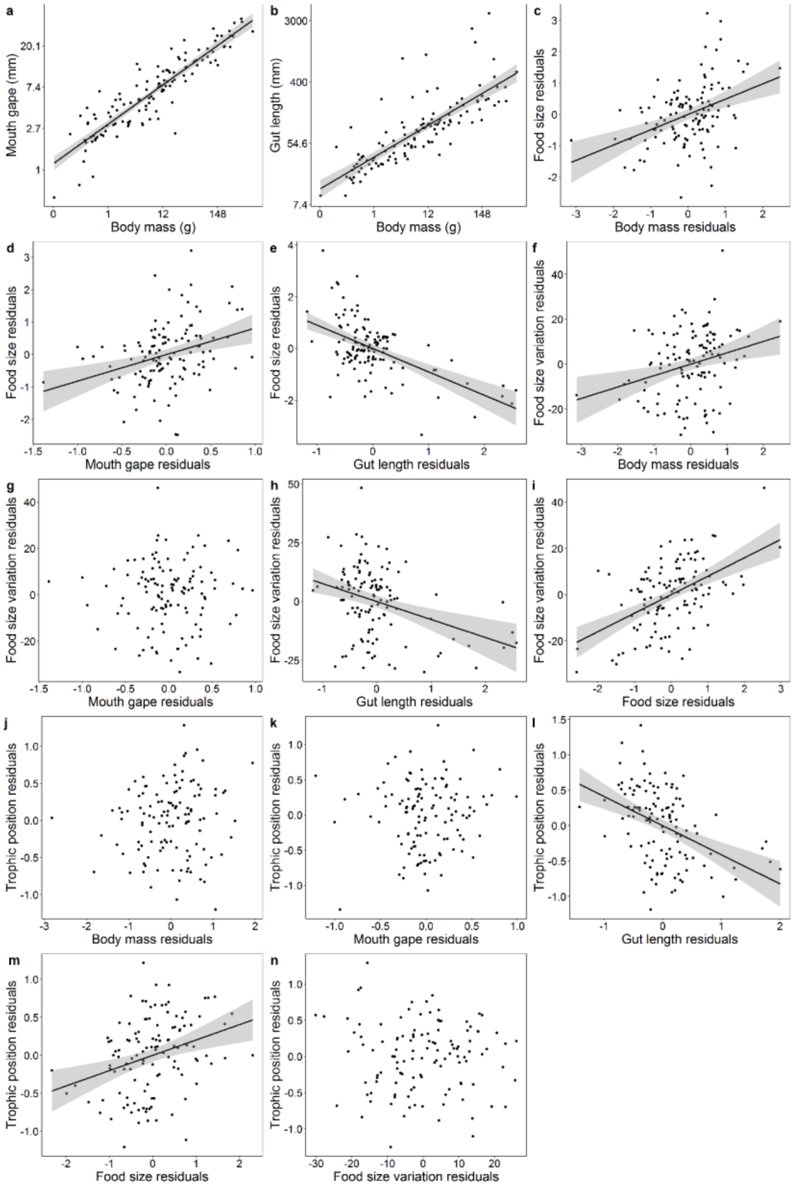


Figure B.8 The estimated relationship between body mass and mouth gape (a), body mass and gut length (b), body mass and maximum food item size (food size) (c), mouth gape and food size (d), gut length and food size (e), body size and coefficient of variation of food item size (food size variation) (f), mouth gape and food size variation (g), gut length and food size variation (h), food size and food size variation (i), body mass and trophic position (TP) (j), mouth gape and TP (k), gut length and TP (l), food size and TP (m), food size variation and TP (n). Excepting panels “a” and “b” that are based on simple linear regressions (single explanatory variable), the estimated relationships are based on partial residuals. Trend lines are provided for significant relationships ($P<0.05$). All variables were generated using the dataset based on the largest 10% approach.

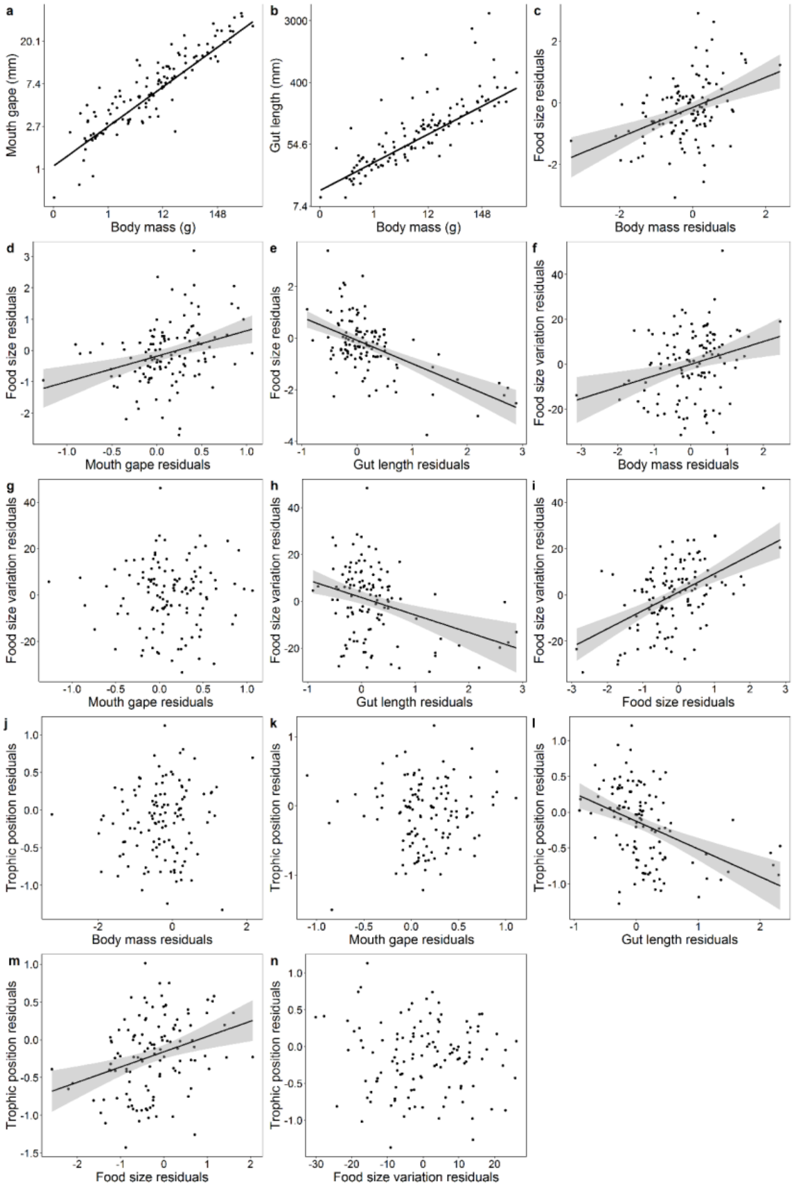


Figure B.9 The estimated relationship between body mass and mouth gape (a), body mass and gut length (b), body mass and maximum food item size (food size) (c), mouth gape and food size (d), gut length and food size (e), body size and coefficient of variation of food item size (food size variation) (f), mouth gape and food size variation (g), gut length and food size variation (h), food size and food size variation (i), body mass and trophic position (TP)(j), mouth gape and TP (k), gut length and TP (l), food size and TP (m), food size variation and TP (n). Excepting panels "a" and "b" that are based on simple Phylogenetic Generalized Least Squares models (single explanatory variable), the estimated relationships are based on partial residuals. Trend lines are provided for significant relationships ($P<0.05$). All variables were generated using the dataset based on the largest 10% approach.

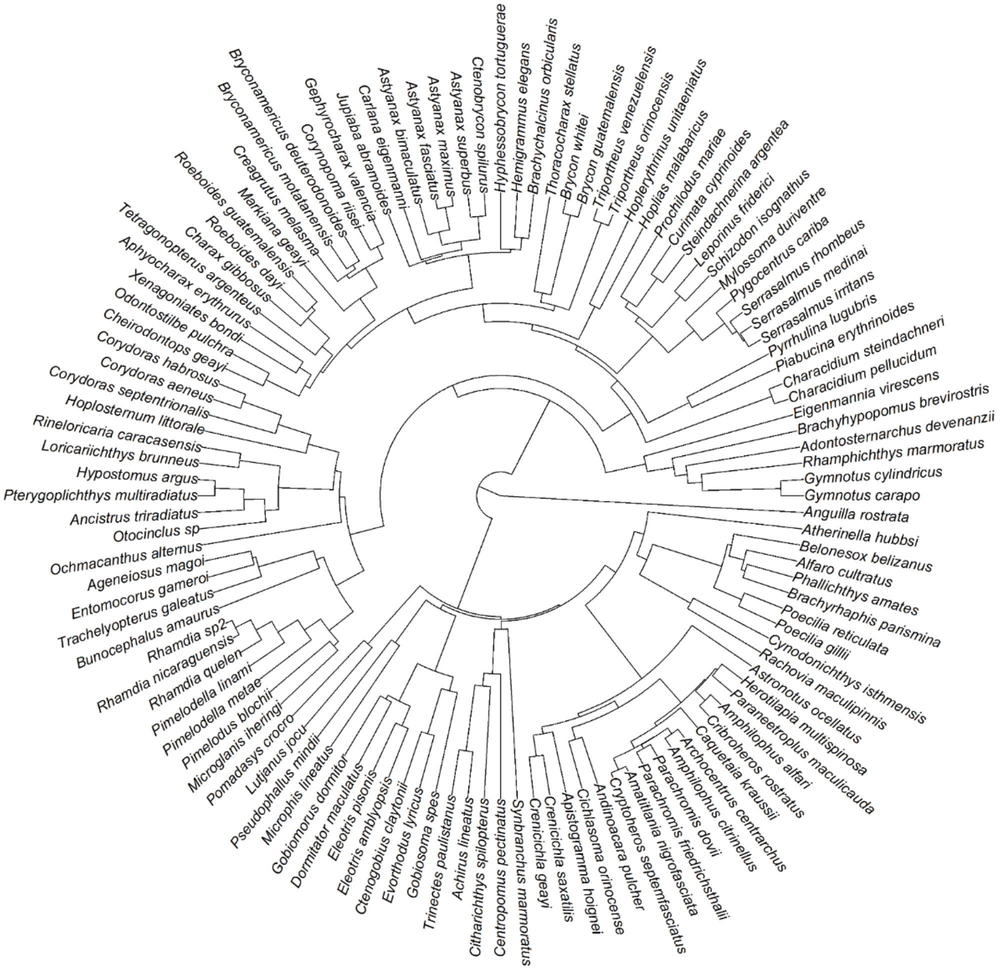


Figure B.10 Phylogenetic tree used in the phylogenetic generalized least squares models (PGLS) to account for the lack of independence among species due to shared ancestry. The tree is based on the super tree published by Rabosky et al. (2018).

APPENDIX C

SUPPORTING INFORMATION FOR THE MANUSCRIPT ENTITLED: CAN ANCESTRY AND MORPHOLOGY BE USED AS SURROGATES FOR SPECIES NICHE RELATIONSHIPS?

Table C.1 List of the fish species collected in Caño Maraca and Caño Agra Fría Viejo that were used for comparisons between phylogenic, morphological traits, dietary, and stable-isotope ratios datasets. Body size (mean and associated standard deviation) and number of individuals for diet, isotopic ratios and morphological traits are provided for each species.

Species	**Site**	**N. of ind. analyzed for diet**	**N. of ind. analyzed for stable isotopes**	**N. of ind. analyzed for morphological traits**	**Size and SD of ind. analysed for diet**	**Size and SD of ind. analysed for stable isotopes**	**Size and SD of ind. analysed for morphological traits**
Achirus lineatus	Agua Fría Viejo	17	4	9	42.42 (11.16)	42.12 (1.82)	65.13 (18.77)
Alfaro cultratus	Agua Fría Viejo	262	3	3	34.08 (10.46)	35.73 (1.63)	51.83 (6.24)
Amphilophus citrinellus	Agua Fría Viejo	45	3	3	71.62 (68.27)	44 (25.64)	109.73 (22.03)
Ancistrus triradiatus	Maraca	68	4	3	44.78 (13.72)	61.52 (6.47)	69.63 (9.55)
Andinoacara pulcher	Maraca	396	3	5	44.08 (17.22)	23.17 (3.34)	61.54 (9.08)
Aphyocharax erythrurus	Maraca	192	3	3	30.27 (3.11)	33.6 (0.7)	32.53 (4.05)
Apistogramma hoignei	Maraca	163	3	3	22.24 (3.84)	26.5 (2.43)	26.07 (1.75)
Archocentrus centrarchus	Agua Fría Viejo	82	3	3	29.09 (16.37)	20.83 (0.84)	67 (9.6)
Astronotus ocellatus	Maraca	53	2	3	130.41 (34.71)	167.5 (4.95)	152.67 (36.94)
Astyanax bimaculatus	Maraca	203	3	6	45.17 (9.34)	49.1 (0.95)	45.68 (8.82)
Astyanax fasciatus	Agua Fría Viejo	275	3	3	47.02 (18.63)	46.4 (1.68)	62.13 (12.11)
Belonesox belizanus	Agua Fría Viejo	40	4	3	64.53 (32.34)	70.58 (5.94)	114.67 (9.83)
Brachyhypopomus brevirostris	Maraca	30	3	3	44.31 (8.17)	54.93 (3.56)	192.17 (16.65)

Table C.1 Continued.

Species	Site	N. of ind. analyzed for diet	N. of ind. analyzed for stable isotopes	N. of ind. analyzed for morphological traits	Size and SD of ind. analysed for diet	Size and SD of ind. analysed for stable isotopes	Size and SD of ind. analysed for morphological traits
Brachyrhaphis parismina	Agua Fría Viejo	35	2	3	22.12 (6.26)	28.9 (2.26)	27.2 (7.71)
Brycon guatemalensis	Agua Fría Viejo	60	3	3	156.52 (75.19)	82.3 (10.65)	165.6 (56.63)
Bunocephalus amaurus	Maraca	109	3	5	38.4 (6.82)	44.67 (2.72)	53.52 (2.42)
Caquetaia kraussii	Maraca	255	3	6	47.94 (25.56)	34.1 (7.46)	145.18 (38.39)
Characidium steindachneri	Maraca	172	2	2	24.21 (2.06)	26 (1.41)	18.65 (2.19)
Charax gibbosus	Maraca	149	3	3	56.87 (16.81)	107.7 (16.37)	69.77 (12.74)
Cheirodontops geayi	Maraca	88	3	6	23.03 (2.34)	27.33 (0.61)	27.02 (2.78)
Cichlasoma orinocense	Maraca	131	4	3	53.94 (20.77)	59.85 (14.06)	79.8 (18.8)
Corydoras aeneus	Maraca	128	3	3	34.39 (3.45)	37.63 (3.99)	34.9 (3.7)
Corydoras habrosus	Maraca	174	3	3	17.17 (2)	17.4 (0.36)	19.2 (0.8)
Corydoras septentrionalis	Maraca	112	3	3	33.4 (4.73)	39.5 (2.17)	39.2 (1.71)
Cribroheros alfari	Agua Fría Viejo	16	2	3	43.91 (35.34)	94.85 (9.97)	109.73 (19.86)
Ctenobrycon spilurus	Maraca	233	3	3	37.43 (3.31)	38.8 (2.29)	38.3 (2.93)
Dormitator maculatus	Agua Fría Viejo	107	3	3	45.77 (12.95)	41.83 (0.99)	62.1 (3.31)
Eigenmannia virescens	Maraca	115	6	3	98.51 (21.01)	154.6 (10.71)	112.67 (6.51)
Eleotris amblyopsis	Agua Fría Viejo	263	3	3	44.94 (14.4)	71.4 (7.31)	71.17 (7.24)
Eleotris pisonis	Agua Fría Viejo	30	3	3	79.03 (32.92)	101.43 (16.07)	97.73 (14.32)
Evorthodus lyricus	Agua Fría Viejo	23	7	3	32.31 (10.28)	31.47 (12.17)	42.9 (9.76)
Gobiomorus dormitor	Agua Fría Viejo	77	6	3	59.11 (41.31)	69.25 (40.57)	176.73 (26.6)
Gymnotus carapo	Maraca	195	5	3	166.32 (61.27)	167.32 (26.64)	162.5 (11.46)
Hemigrammus elegans	Maraca	98	3	6	21.13 (3.03)	23.83 (4.2)	25.32 (4.71)
Hoplias malabaricus	Maraca	191	3	3	77.63 (61.8)	140.3 (12.92)	166.67 (32.81)

Table C.1 Continued.

Species	**Site**	**N. of ind. analyzed for diet**	**N. of ind. analyzed for stable isotopes**	**N. of ind. analyzed for morphological traits**	**Size and SD of ind. analysed for diet**	**Size and SD of ind. analysed for stable isotopes**	**Size and SD of ind. analysed for morphological traits**
Hoplosternum littorale	Maraca	26	3	3	116.2 (24.51)	92.13 (3.76)	105.87 (11.57)
Hypoptopoma spectabile	Maraca	71	3	4	21.2 (2.4)	25.87 (1.53)	45.12 (7.78)
Hypostomus argus	Maraca	53	3	3	104.69 (43.41)	65.13 (4.37)	132 (39.13)
Loricariichthys brunneus	Maraca	39	2	3	169.12 (43.7)	186.5 (13.44)	163.5 (42.39)
Lutjanus jocu	Agua Fría Viejo	21	2	3	145.49 (37.26)	102.95 (6.29)	120.43 (9.58)
Markiana geayi	Maraca	148	3	5	61.81 (7.79)	68.73 (1.6)	65.56 (2.78)
Microglanis iheringi	Maraca	111	3	3	26.66 (3.43)	35.07 (2.21)	27.03 (2.06)
Microphis lineatus	Agua Fría Viejo	72	3	3	100.59 (20.54)	122.53 (2.2)	133 (26.06)
Ochmacanthus alternus	Maraca	193	3	3	29.55 (3.7)	33.87 (3.27)	33.93 (1.52)
Odontostilbe pulchra	Maraca	228	3	3	24.68 (2.26)	26.2 (1.47)	27.47 (1.85)
Parachromis dovii	Agua Fría Viejo	89	2	3	55.63 (62.93)	99.1 (50.06)	158.47 (19.63)
Parachromis friedrichsthalii	Agua Fría Viejo	232	3	3	49.27 (30.7)	71.97 (25.02)	114.4 (26.61)
Phallichthys amates	Agua Fría Viejo	181	3	3	33.96 (8.3)	44.67 (1.85)	49.53 (4.45)
Pimelodella linami	Maraca	123	3	3	44.2 (6.86)	55.63 (5.95)	71.43 (6.1)
Poecilia gillii	Agua Fría Viejo	143	3	3	48.56 (17.91)	65.23 (2.85)	70.87 (6.79)
Poecilia reticulata	Maraca	145	3	3	18.71 (3.68)	17.37 (1.25)	20.4 (1.57)
Pomadasys crocro	Agua Fría Viejo	54	3	3	125.15 (100.16)	66.1 (14.82)	106.8 (59.94)
Prochilodus mariae	Maraca	49	3	3	147.39 (38.13)	104 (3.52)	109.7 (7.1)
Pterygoplichthys multiradiatus	Maraca	34	3	3	167.53 (50.3)	83.67 (0.45)	117 (41.94)
Pygocentrus cariba	Maraca	143	3	3	92.43 (20.18)	102.87 (4.86)	103.17 (8.56)
Pyrrhulina lugubris	Maraca	154	3	5	32.17 (2.9)	30.97 (0.25)	35.34 (2.32)

Table C.1 Continued.

Species	**Site**	**N. of ind. analyzed for diet**	**N. of ind. analyzed for stable isotopes**	**N. of ind. analyzed for morphological traits**	**Size and SD of ind. analysed for diet**	**Size and SD of ind. analysed for stable isotopes**	**Size and SD of ind. analysed for morphological traits**
Rhamdia quelen	Maraca	86	3	3	100.32 (17.35)	93.6 (6.32)	100.47 (13.15)
Rineloricaria caracasensis	Maraca	41	3	3	82.4 (18.59)	77.83 (2.23)	104.1 (0.36)
Roeboides guatemalensis	Agua Fría Viejo	69	3	3	63.6 (13.49)	72.13 (4.3)	69.4 (3.41)
Steindachnerina argentea	Maraca	64	3	3	51.09 (9.45)	54.7 (4.37)	61.43 (7.31)
Thoracocharax stellatus	Maraca	177	3	3	29.72 (3.47)	30.27 (1.8)	32.6 (1.85)
Trachelyopterus galeatus	Maraca	147	3	3	72.72 (11.84)	92.6 (8.11)	69.23 (3.16)
Trinectes paulistanus	Agua Fría Viejo	18	3	3	32.04 (12.79)	46.6 (9.81)	54.3 (3.21)
Triportheus orinocensis	Maraca	157	3	3	62.27 (13.85)	78.6 (9.8)	88.97 (37.27)
Vieja maculicauda	Agua Fría Viejo	65	3	3	118.06 (62.76)	116.83 (38.98)	137 (12.53)

Table C.2 Food item categories organized in seven hierarchical levels, from course (Level 1) to fine taxonomic resolution (Level 7). Number of categories per level is provided in parenthesis.

Level 1 (# Cat: 3)	**Level 2 (# Cat: 7)**	**Level 3 (# Cat: 16)**	**Level 4 (# Cat: 30)**	**Level 5 (# Cat: 66)**	**Level 6 (# Cat: 90)**	**Level 7 (# Cat: 126)**
Autotrophs	Plants	Veg. plant structures	Veg. aquatic structures	Veg. aquatic structures	Veg. aquatic structures	Veg. aquatic structures
Autotrophs	Plants	Veg. plant structures	Veg. terrestrial structures	Veg. terrestrial structures	Veg. terrestrial structures	Veg. terrestrial structures
Autotrophs	Plants	Soft flowers and fruits	Soft flowers and fruits	Soft flowers and fruits	Soft flowers and fruits	Soft flowers and fruits
Autotrophs	Plants	Hard fruits and seeds	Hard fruits and seeds	Hard fruits and seeds	Hard fruits and seeds	Hard fruits and seeds
Autotrophs	Plants	Plant spores	Plant Spores	Plant Spores	Plant Spores	Plant Spores
Autotrophs	Algae	Multicelular algae	Chara	Chara	Chara	Chara
Autotrophs	Algae	Multicelular algae	Filamentous algae	Filamentous algae	Filamentous algae	Filamentous algae
Autotrophs	Algae	Diatoms	Diatoms	Diatoms	Diatoms	Diatoms
Autotrophs	Algae	Desmids	Desmids	Desmids	Desmids	Desmids
Detritus	Fine detritus	Fine detritus	Fine detritus	Fine detritus	Fine detritus	Fine detritus
Detritus	Vegetative detritus	Vegetative detritus	Vegetative detritus	Vegetative detritus	Vegetative detritus	Vegetative detritus
Detritus	Coarse detritus	Coarse detritus	Coarse detritus	Coarse detritus	Coarse detritus	Coarse detritus
Heterotrophs	Invertebrates	Invertebrate eggs	Invertebrate eggs	Invertebrate eggs	Invertebrate eggs	Invertebrate eggs
Heterotrophs	Invertebrates	Microinvertebrates	Protozoa	Protozoa	Protozoa	Protozoa
Heterotrophs	Invertebrates	Microinvertebrates	Rotifers	Rotifers	Rotifers	Rotifers
Heterotrophs	Invertebrates	Microinvertebrates	Rotifers	Diflugiids	Diflugiids	Diflugiids
Heterotrophs	Invertebrates	Microinvertebrates	Microcrustacea	Copepoda	Copepoda	Copepoda
Heterotrophs	Invertebrates	Microinvertebrates	Microcrustacea	Cladocera	Cladocera	Cladocera
Heterotrophs	Invertebrates	Microinvertebrates	Microcrustacea	Ostracoda	Ostracoda	Ostracoda
Heterotrophs	Invertebrates	Macroinvertebrates	Nematoda	Nematoda	Nematoda	Nematoda
Heterotrophs	Invertebrates	Macroinvertebrates	Nematophora	Nematophora	Nematophora	Nematophora

Table C.2 Continued.

Level 1 (# Cat: 3)	**Level 2 (# Cat: 7)**	**Level 3 (# Cat: 16)**	**Level 4 (# Cat: 30)**	**Level 5 (# Cat: 66)**	**Level 6 (# Cat: 90)**	**Level 7 (# Cat: 126)**
Heterotrophs	Invertebrates	Macroinvertebrates	Annelida	Oligochaeta	Oligochaeta	Oligochaeta
Heterotrophs	Invertebrates	Macroinvertebrates	Annelida	Hirudinea	Hirudinea	Hirudinea
Heterotrophs	Invertebrates	Macroinvertebrates	Mollusca	Gastropoda	Gastropoda	Gastropoda
Heterotrophs	Invertebrates	Macroinvertebrates	Mollusca	Bivalve	Bivalve	Bivalve
Heterotrophs	Invertebrates	Macroinvertebrates	Macrocrustaceans	Anostraca (fairy shrimp)	Anostraca (fairy shrimp)	Anostraca (fairy shrimp)
Heterotrophs	Invertebrates	Macroinvertebrates	Macrocrustaceans	Caridea (shrimps)	Caridea (shrimps)	Caridea (shrimps)
Heterotrophs	Invertebrates	Macroinvertebrates	Macrocrustaceans	Brachyura (crabs)	Brachyura (crabs)	Brachyura (crabs)
Heterotrophs	Invertebrates	Macroinvertebrates	Macrocrustaceans	Isopoda	Isopoda	Isopoda
Heterotrophs	Invertebrates	Macroinvertebrates	Macrocrustaceans	Amphipoda	Amphipoda	Amphipoda
Heterotrophs	Invertebrates	Macroinvertebrates	Collembola	Collembola	Collembola	Collembola
Heterotrophs	Invertebrates	Macroinvertebrates	Chelicerata	Acarina	Acarina	Acarina
Heterotrophs	Invertebrates	Macroinvertebrates	Chelicerata	Araneae	Araneae	Araneae
Heterotrophs	Invertebrates	Macroinvertebrates	Insects	Diptera (larvae)	Chironomidae (larvae)	Chironomidae (larvae)
Heterotrophs	Invertebrates	Macroinvertebrates	Insects	Diptera (larvae)	Other Diptera (larvae)	Other Diptera (larvae)
Heterotrophs	Invertebrates	Macroinvertebrates	Insects	Diptera (larvae)	Mosquito (larvae)	Mosquito (larvae)
Heterotrophs	Invertebrates	Macroinvertebrates	Insects	Diptera (adult)	Diptera (adult)	Diptera (adult)
Heterotrophs	Invertebrates	Macroinvertebrates	Insects	Odonata (nymph)	Odonata (nymph)	Odonata (nymph)
Heterotrophs	Invertebrates	Macroinvertebrates	Insects	Ephemeroptera	Ephemeroptera	Ephemeroptera
Heterotrophs	Invertebrates	Macroinvertebrates	Insects	Coleoptera (aquatic larvae)	Coleoptera (aquatic larvae)	Coleoptera (aquatic larvae)
Heterotrophs	Invertebrates	Macroinvertebrates	Insects	Coleoptera (aquatic adult)	Coleoptera (aquatic adult)	Coleoptera (aquatic adult)
Heterotrophs	Invertebrates	Macroinvertebrates	Insects	Coleoptera (terrestrial adult)	Coleoptera (terrestrial adult)	Coleoptera (terrestrial adult)

Table C.2 Continued.

Level 1 (# Cat: 3)	Level 2 (# Cat: 7)	Level 3 (# Cat: 16)	Level 4 (# Cat: 30)	Level 5 (# Cat: 66)	Level 6 (# Cat: 90)	Level 7 (# Cat: 126)
Heterotrophs	Invertebrates	Macroinvertebrates	Insects	Plecoptera	Plecoptera	Plecoptera
Heterotrophs	Invertebrates	Macroinvertebrates	Insects	Trichoptera	Trichoptera	Trichoptera
Heterotrophs	Invertebrates	Macroinvertebrates	Insects	Neuroptera	Neuroptera	Neuroptera
Heterotrophs	Invertebrates	Macroinvertebrates	Insects	Orthoptera	Orthoptera	Orthoptera
Heterotrophs	Invertebrates	Macroinvertebrates	Insects	Hemiptera (aquatic)	Hemiptera (aquatic)	Hemiptera (aquatic)
Heterotrophs	Invertebrates	Macroinvertebrates	Insects	Hemiptera (aquatic)	Corixidae	Corixidae
Heterotrophs	Invertebrates	Macroinvertebrates	Insects	Hemiptera (aquatic)	Gerridae	Gerridae
Heterotrophs	Invertebrates	Macroinvertebrates	Insects	Hemiptera (terrestrial)	Hemiptera (terrestrial)	Hemiptera (terrestrial)
Heterotrophs	Invertebrates	Macroinvertebrates	Insects	Lepidoptera (larvae)	Lepidoptera (larvae)	Lepidoptera (larvae)
Heterotrophs	Invertebrates	Macroinvertebrates	Insects	Lepidoptera (adult)	Lepidoptera (adult)	Lepidoptera (adult)
Heterotrophs	Invertebrates	Macroinvertebrates	Insects	Hymenoptera	Hymenoptera	Hymenoptera
Heterotrophs	Invertebrates	Macroinvertebrates	Insects	Isoptera	Isoptera	Isoptera
Heterotrophs	Vertebrates	Non-fish vertebrates	Anura	Anura (tadpoles)	Anura (tadpoles)	Anura (tadpoles)
Heterotrophs	Vertebrates	Non-fish vertebrates	Anura	Anura (frogs)	Anura (frogs)	Anura (frogs)
Heterotrophs	Vertebrates	Fish eggs	Fish eggs	Fish eggs	Fish eggs	Fish eggs
Heterotrophs	Vertebrates	Fish	Fish mucus	Fish mucus	Fish mucus	Fish mucus
Heterotrophs	Vertebrates	Fish	Fish scales	Fish scales	Fish scales	Fish scales
Heterotrophs	Vertebrates	Fish	Fish fins	Fish fins	Fish fins	Fish fins
Heterotrophs	Vertebrates	Fish	Fish (whole)	Atheriniformes	Atherinopsidae	Atherinella
Heterotrophs	Vertebrates	Fish	Fish (whole)	Characiformes	Anostomidae	Schizodon
Heterotrophs	Vertebrates	Fish	Fish (whole)	Characiformes	Bryconidae	Brycon
Heterotrophs	Vertebrates	Fish	Fish (whole)	Characiformes	Characidae	Aphyocharax

Table C.2 Continued.

Level 1 (# Cat: 3)	Level 2 (# Cat: 7)	Level 3 (# Cat: 16)	Level 4 (# Cat: 30)	Level 5 (# Cat: 66)	Level 6 (# Cat: 90)	Level 7 (# Cat: 126)
Heterotrophs	Vertebrates	Fish	Fish (whole)	Characiformes	Characidae	Astyanax
Heterotrophs	Vertebrates	Fish	Fish (whole)	Characiformes	Characidae	Bryconamericus
Heterotrophs	Vertebrates	Fish	Fish (whole)	Characiformes	Characidae	Cheirodontops
Heterotrophs	Vertebrates	Fish	Fish (whole)	Characiformes	Characidae	Corynopoma
Heterotrophs	Vertebrates	Fish	Fish (whole)	Characiformes	Characidae	Creagrutus
Heterotrophs	Vertebrates	Fish	Fish (whole)	Characiformes	Characidae	Ctenobrycon
Heterotrophs	Vertebrates	Fish	Fish (whole)	Characiformes	Characidae	Gephyrocharax
Heterotrophs	Vertebrates	Fish	Fish (whole)	Characiformes	Characidae	Hemigrammus
Heterotrophs	Vertebrates	Fish	Fish (whole)	Characiformes	Characidae	Markiana
Heterotrophs	Vertebrates	Fish	Fish (whole)	Characiformes	Characidae	Odontostilbe
Heterotrophs	Vertebrates	Fish	Fish (whole)	Characiformes	Characidae	Poptella
Heterotrophs	Vertebrates	Fish	Fish (whole)	Characiformes	Characidae	Roeboides
Heterotrophs	Vertebrates	Fish	Fish (whole)	Characiformes	Characidae	Tetragonopterus
Heterotrophs	Vertebrates	Fish	Fish (whole)	Characiformes	Crenuchidae	Characidium
Heterotrophs	Vertebrates	Fish	Fish (whole)	Characiformes	Curimatidae	Curimata
Heterotrophs	Vertebrates	Fish	Fish (whole)	Characiformes	Erythrinidae	Hoplias
Heterotrophs	Vertebrates	Fish	Fish (whole)	Characiformes	Gasteropelecidae	Thoracocharax
Heterotrophs	Vertebrates	Fish	Fish (whole)	Characiformes	Lebiasinidae	Pyrrhulina
Heterotrophs	Vertebrates	Fish	Fish (whole)	Characiformes	Prochilodontidae	Prochilodus
Heterotrophs	Vertebrates	Fish	Fish (whole)	Characiformes	Serrasalmidae	Pygocentrus
Heterotrophs	Vertebrates	Fish	Fish (whole)	Characiformes	Triportheidae	Triportheus
Heterotrophs	Vertebrates	Fish	Fish (whole)	Clupeiformes	Engraulidae	Anchoviella
Heterotrophs	Vertebrates	Fish	Fish (whole)	Cyprinodontiformes	Cynolebiidae	Rachovia
Heterotrophs	Vertebrates	Fish	Fish (whole)	Cyprinodontiformes	Cynolebiidae	Rivulus

Table C.2 Continued.

Level 1 (# Cat: 3)	Level 2 (# Cat: 7)	Level 3 (# Cat: 16)	Level 4 (# Cat: 30)	Level 5 (# Cat: 66)	Level 6 (# Cat: 90)	Level 7 (# Cat: 126)
Heterotrophs	Vertebrates	Fish	Fish (whole)	Cyprinodontiformes	Poeciliidae	Alfaro
Heterotrophs	Vertebrates	Fish	Fish (whole)	Cyprinodontiformes	Poeciliidae	Belonesox
Heterotrophs	Vertebrates	Fish	Fish (whole)	Cyprinodontiformes	Poeciliidae	Phallichthys
Heterotrophs	Vertebrates	Fish	Fish (whole)	Cyprinodontiformes	Poeciliidae	Poecilia
Heterotrophs	Vertebrates	Fish	Fish (whole)	Gymnotiformes	Gymnotidae	Gymnotus
Heterotrophs	Vertebrates	Fish	Fish (whole)	Perciformes	Cichlidae	Aequidens
Heterotrophs	Vertebrates	Fish	Fish (whole)	Perciformes	Cichlidae	Amatitlania
Heterotrophs	Vertebrates	Fish	Fish (whole)	Perciformes	Cichlidae	Amphilophus
Heterotrophs	Vertebrates	Fish	Fish (whole)	Perciformes	Cichlidae	Apistogramma
Heterotrophs	Vertebrates	Fish	Fish (whole)	Perciformes	Cichlidae	Archocentrus
Heterotrophs	Vertebrates	Fish	Fish (whole)	Perciformes	Cichlidae	Astronotus
Heterotrophs	Vertebrates	Fish	Fish (whole)	Perciformes	Cichlidae	Caquetaia
Heterotrophs	Vertebrates	Fish	Fish (whole)	Perciformes	Cichlidae	Crenicichla
Heterotrophs	Vertebrates	Fish	Fish (whole)	Perciformes	Cichlidae	Parachromis
Heterotrophs	Vertebrates	Fish	Fish (whole)	Perciformes	Cichlidae	Vieja
Heterotrophs	Vertebrates	Fish	Fish (whole)	Perciformes	Eleotridae	Dormitator
Heterotrophs	Vertebrates	Fish	Fish (whole)	Perciformes	Eleotridae	Eleotris
Heterotrophs	Vertebrates	Fish	Fish (whole)	Perciformes	Eleotridae	Gobiomorus
Heterotrophs	Vertebrates	Fish	Fish (whole)	Perciformes	Gerreidae	Diapterus
Heterotrophs	Vertebrates	Fish	Fish (whole)	Perciformes	Gobiidae	Ctenogobius
Heterotrophs	Vertebrates	Fish	Fish (whole)	Perciformes	Haemulidae	Pomadasys
Heterotrophs	Vertebrates	Fish	Fish (whole)	Siluriformes	Aspredinidae	Bunocephalus
Heterotrophs	Vertebrates	Fish	Fish (whole)	Siluriformes	Auchenipteridae	Ageneiosus
Heterotrophs	Vertebrates	Fish	Fish (whole)	Siluriformes	Auchenipteridae	Entomocorus

Table C.2 Continued.

Level 1 (# Cat: 3)	Level 2 (# Cat: 7)	Level 3 (# Cat: 16)	Level 4 (# Cat: 30)	Level 5 (# Cat: 66)	Level 6 (# Cat: 90)	Level 7 (# Cat: 126)
Heterotrophs	Vertebrates	Fish	Fish (whole)	Siluriformes	Auchenipteridae	Parauchenipterus
Heterotrophs	Vertebrates	Fish	Fish (whole)	Siluriformes	Callichthyidae	Corydoras
Heterotrophs	Vertebrates	Fish	Fish (whole)	Siluriformes	Callichthyidae	Hoplosternum
Heterotrophs	Vertebrates	Fish	Fish (whole)	Siluriformes	Heptapteridae	Pimelodella
Heterotrophs	Vertebrates	Fish	Fish (whole)	Siluriformes	Heptapteridae	Rhamdia
Heterotrophs	Vertebrates	Fish	Fish (whole)	Siluriformes	Loricariidae	Ancistrus
Heterotrophs	Vertebrates	Fish	Fish (whole)	Siluriformes	Loricariidae	Hypostomus
Heterotrophs	Vertebrates	Fish	Fish (whole)	Siluriformes	Loricariidae	Loricarichthys
Heterotrophs	Vertebrates	Fish	Fish (whole)	Siluriformes	Loricariidae	Otocinclus
Heterotrophs	Vertebrates	Fish	Fish (whole)	Siluriformes	Loricariidae	Rineloricaria
Heterotrophs	Vertebrates	Fish	Fish (whole)	Siluriformes	Trichomycteridae	Ochmacanthus
Heterotrophs	Vertebrates	Fish	Fish (whole)	Synbranchiformes	Synbranchidae	Synbranchus
Heterotrophs	Vertebrates	Fish	Fish (whole)	Syngnathiformes	Syngnathidae	Oostethus

Table C.3 Species that were not present in the super tree published by Rabosky et al. (2018). I included these unsampled species in the tree based on the position of related species or genus (right-side column).

Species	**Position in the phylogenetic tree**
Ancistrus triradiatus	*Ancistrus multispinis*
Aphyocharax erythrurus	*Aphyocharax alburnus*
Bunocephalus amaurus	*Bunocephalus coracoideus*
Characidium steindachneri	*Characidium pterostictum*
Charax gibbosus	*Charax leticiae*
Cheirodontops geayi	*Cheirodon ibicuhiensis*
Ctenobrycon spilurus	*Ctenobrycon hauxwellianus*
Hemigrammus elegans	*Hemigrammus rodwayi*
Hypostomus argus	*Hypostomus plecostomoides*
Lebiasina erythrinoides	*Copella nattereri*
Loricariichthys brunneus	*Loricariichthys anus*
Markiana geayi	*Markiana nigripinnis*
Pimelodella linami	*Pimelodella lateristriga*
Pyrrhulina lugubris	*Pyrrhulina australis*
Rineloricaria caracasensis	*Rineloricaria parva*
Steindachnerina argentea	*Steindachnerina elegans*
Brycon guatemalensis	*Brycon hilarii*
Microphis lineatus	*Microphis brachyurus*
Vieja maculicauda	*Paraneetroplus maculicauda*
Cribroheros alfari	*Amphilophus alfari*
Amatitlania septemfasciata	*Cryptoheros septemfasciatus*

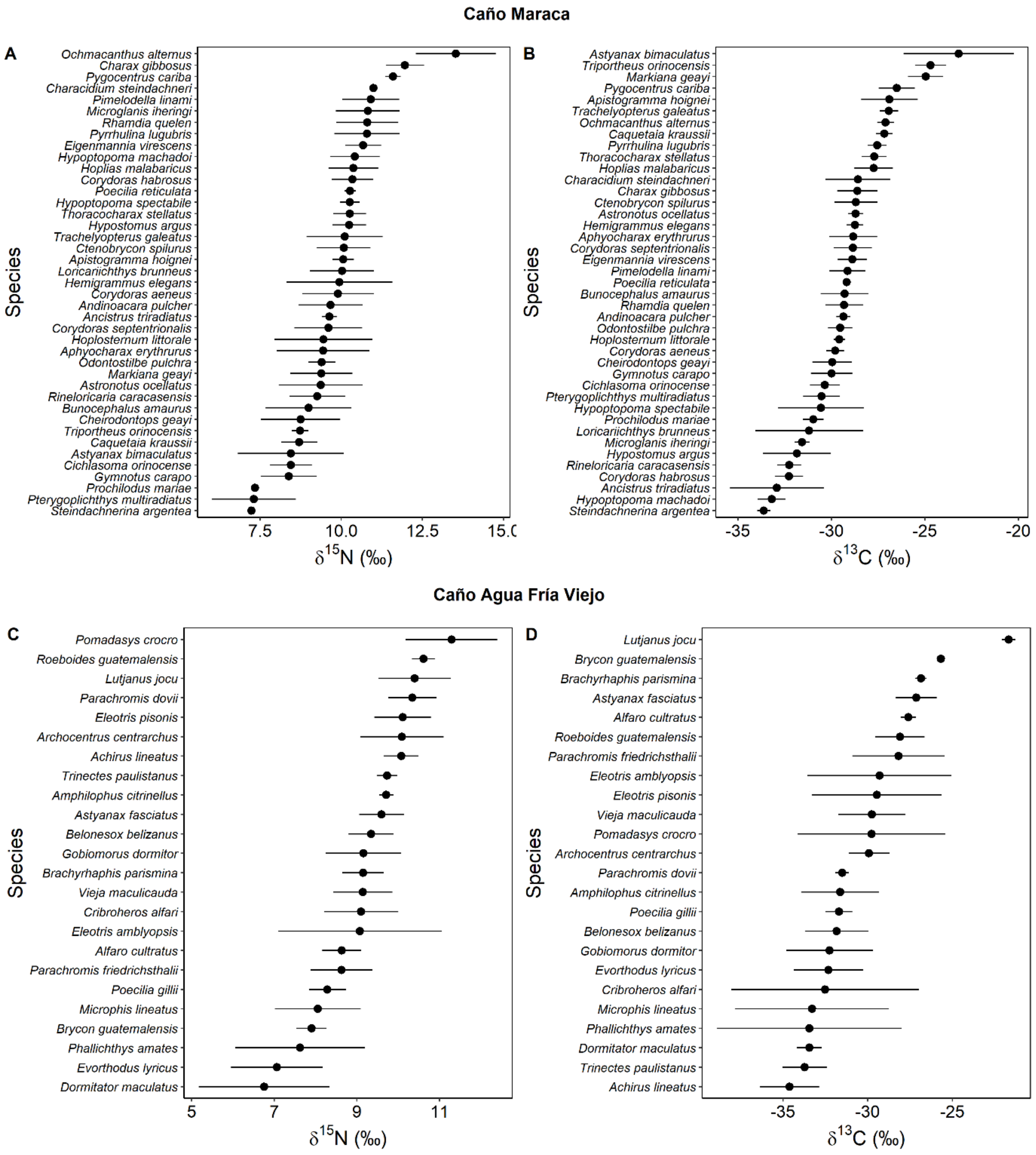
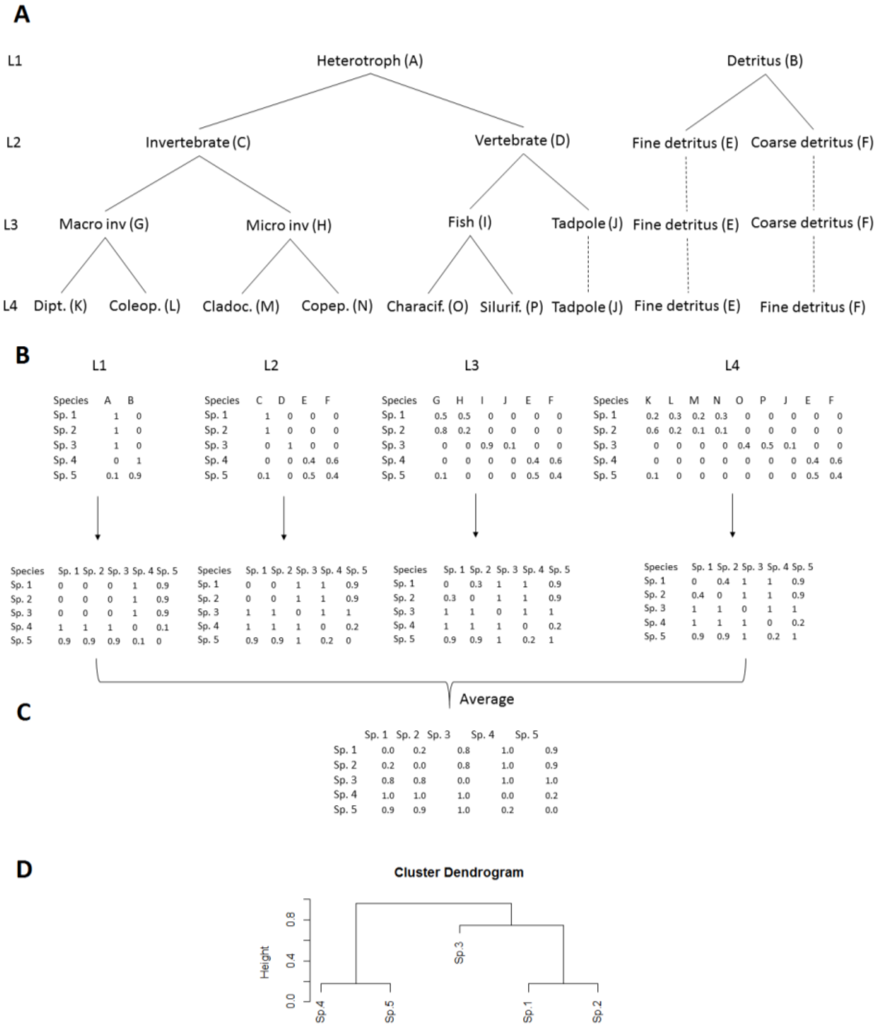


Figure C.1 Average and standard deviation of δ^{15}N (A, C) and δ^{13}C (B, D) for each species in each site (Caño Maraca: A, B; Caño Agua Fría Viejo: C, D).



B

L1

Species	A	B
Sp. 1	1	0
Sp. 2	1	0
Sp. 3	1	0
Sp. 4	0	1
Sp. 5	0.1	0.9

Species	Sp. 1	Sp. 2	Sp. 3	Sp. 4	Sp. 5
Sp. 1	0	0	0	1	0.9
Sp. 2	0	0	0	1	0.9
Sp. 3	0	0	0	1	0.9
Sp. 4	1	1	1	0	0.1
Sp. 5	0.9	0.9	0.9	0.1	0

L2

Species	C	D	E	F
Sp. 1	1	0	0	0
Sp. 2	1	0	0	0
Sp. 3	0	1	0	0
Sp. 4	0	0	0.4	0.6
Sp. 5	0.1	0	0.5	0.4

Species	Sp. 1	Sp. 2	Sp. 3	Sp. 4	Sp. 5
Sp. 1	0	0	1	1	0.9
Sp. 2	0	0	1	1	0.9
Sp. 3	1	1	0	1	1
Sp. 4	1	1	1	0	0.2
Sp. 5	0.9	0.9	1	0.2	0

L3

Species	G	H	I	J	E	F
Sp. 1	0.5	0.5	0	0	0	0
Sp. 2	0.8	0.2	0	0	0	0
Sp. 3	0	0	0.9	0.1	0	0
Sp. 4	0	0	0	0	0.4	0.6
Sp. 5	0.1	0	0	0	0.5	0.4

Species	Sp. 1	Sp. 2	Sp. 3	Sp. 4	Sp. 5
Sp. 1	0	0.3	1	1	0.9
Sp. 2	0.3	0	1	1	0.9
Sp. 3	1	1	0	1	1
Sp. 4	1	1	1	0	0.2
Sp. 5	0.9	0.9	1	0.2	1

L4

Species	K	L	M	N	O	P	J	E	F
Sp. 1	0.2	0.3	0.2	0.3	0	0	0	0	0
Sp. 2	0.6	0.2	0.1	0.1	0	0	0	0	0
Sp. 3	0	0	0	0	0.4	0.5	0.1	0	0
Sp. 4	0	0	0	0	0	0	0	0.4	0.6
Sp. 5	0.1	0	0	0	0	0	0	0.5	0.4

Species	Sp. 1	Sp. 2	Sp. 3	Sp. 4	Sp. 5
Sp. 1	0	0.4	1	1	0.9
Sp. 2	0.4	0	1	1	0.9
Sp. 3	1	1	0	1	1
Sp. 4	1	1	1	0	0.2
Sp. 5	0.9	0.9	1	0.2	1

Average

C

	Sp. 1	Sp. 2	Sp. 3	Sp. 4	Sp. 5
Sp. 1	0.0	0.2	0.8	1.0	0.9
Sp. 2	0.2	0.0	0.8	1.0	0.9
Sp. 3	0.8	0.8	0.0	1.0	1.0
Sp. 4	1.0	1.0	1.0	0.0	0.2
Sp. 5	0.9	0.9	1.0	0.2	0.0

Figure C.2 Example of the method used to account for the hierarchy nature of dietary data. The example consists of nine food items that are registered for five fish species. Two fish species are invertivores (Sp1 and Sp2), one is piscivorous (Sp3), and two are detritivores (Sp4 and Sp5). Some food items, such as invertebrates and fishes, are identified at lower taxonomic level, while others, such as detritus, are restricted to more broad categories. First (A), food items are organized according to their similarities into four hierarchical levels (L1, L2, L3, L4). Food item categories that have poor identification resolution and are from distinct clades are kept in levels of lower taxonomic resolution (bottom of the pyramid; A), which is represented by the dotted lines. For each hierarchical level, a diet matrix (consumers in rows and food item categories in columns) is created (B). These diet matrices were transformed into similarity matrices using Bray-Curtis dissimilarity (B) and then averaged, forming a unified similarity matrix that summarize the food overlap among species at the five resolution scales (C). This uniformed matrix can be used in hierarchical cluster analysis (D) or other multivariate analysis to visualize the diet overlap patterns among species.

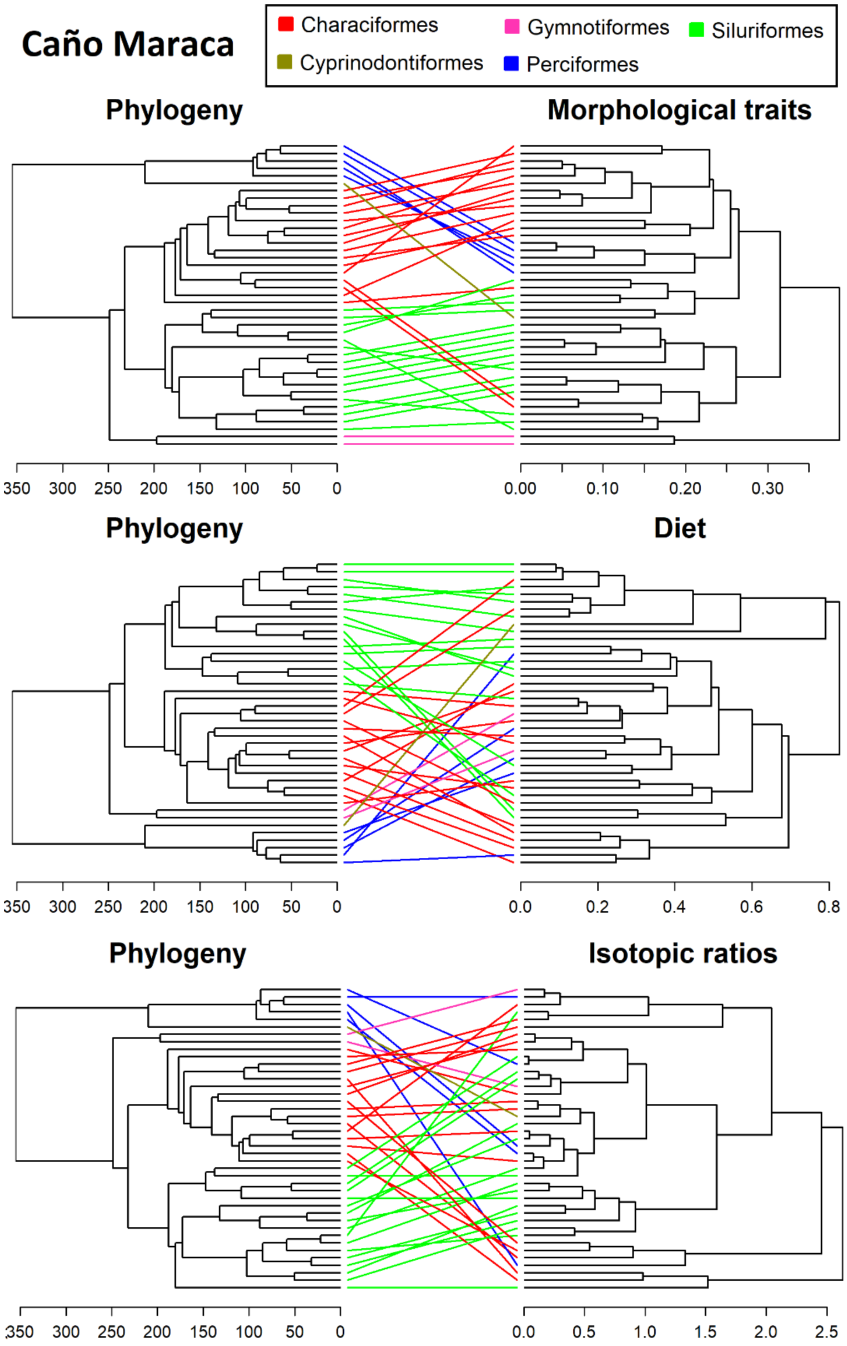


Figure C.3 Tanglegrams constructed for pairwise comparisons of dendrograms based on phylogeny, morphological traits, diet, and stable isotopic ratios. Dendrograms were constructed using the UPGMA algorithm and using different species composition (species from Caño Maraca and species from Caño Agua Fría Viejo). I used an untangle function (algorithm step2side) to improve the visualization of the tanglegrams. Colors represent either different taxonomic orders or trophic groups.

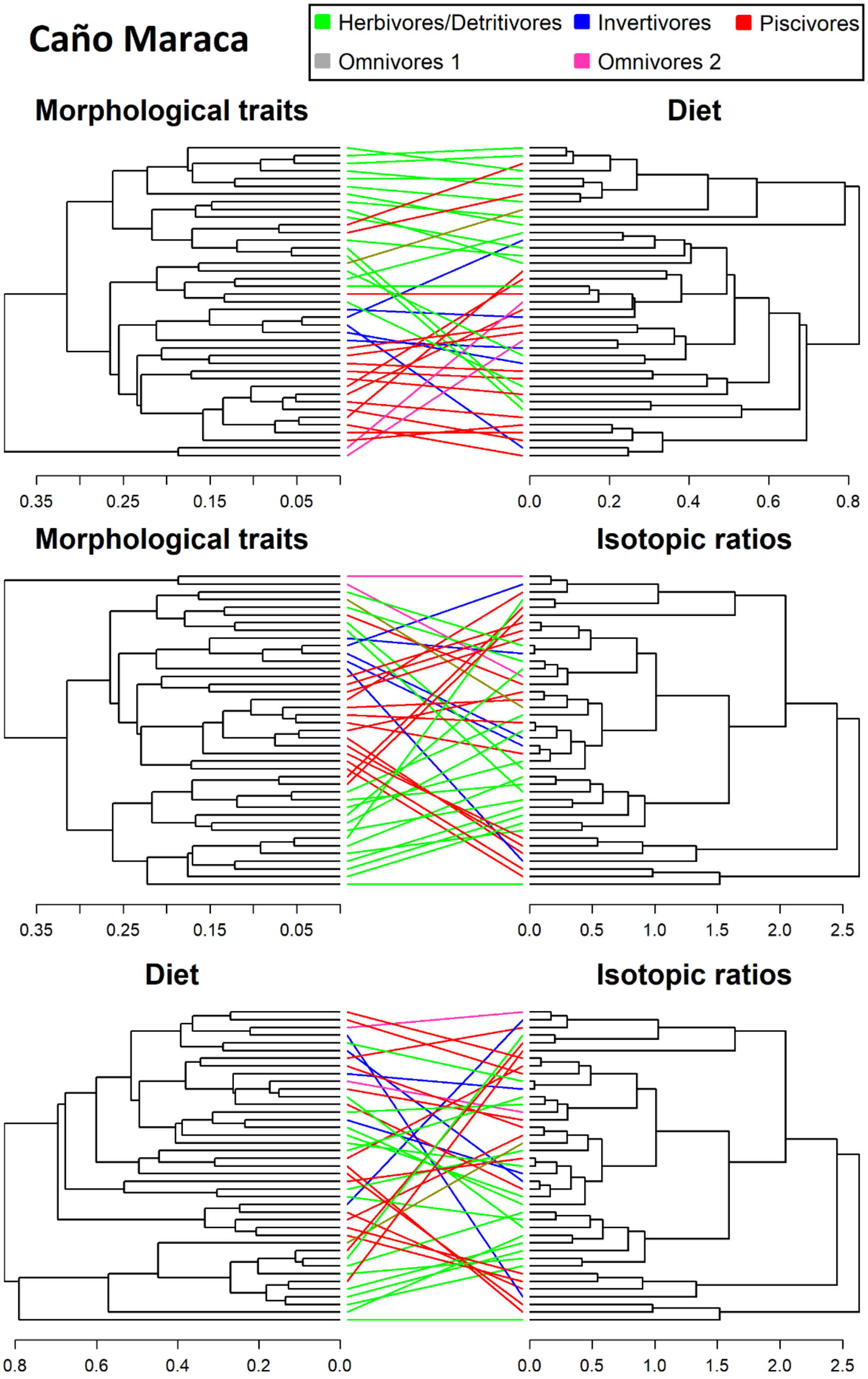


Figure C.3 Continued.

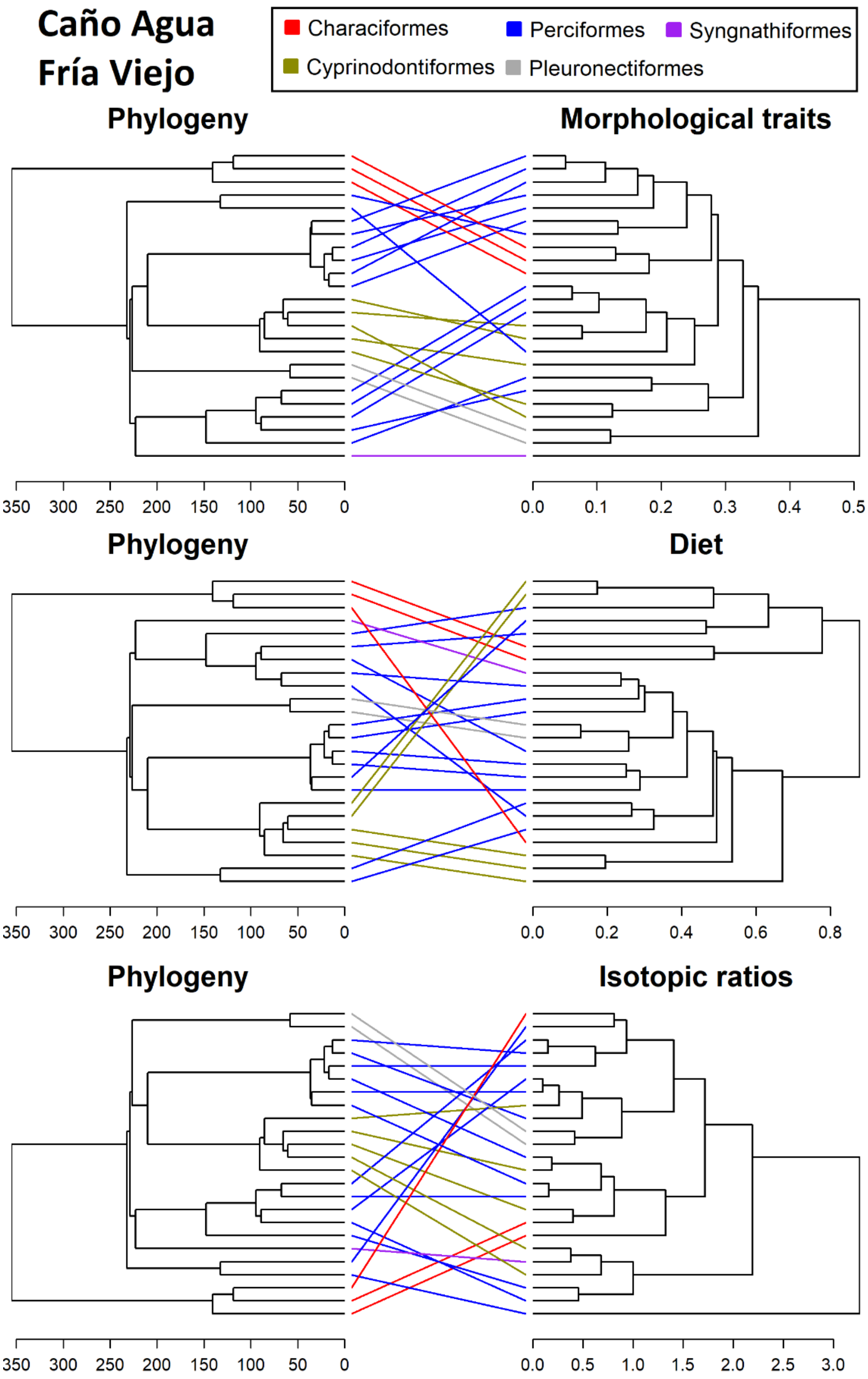


Figure C.3 Continued.

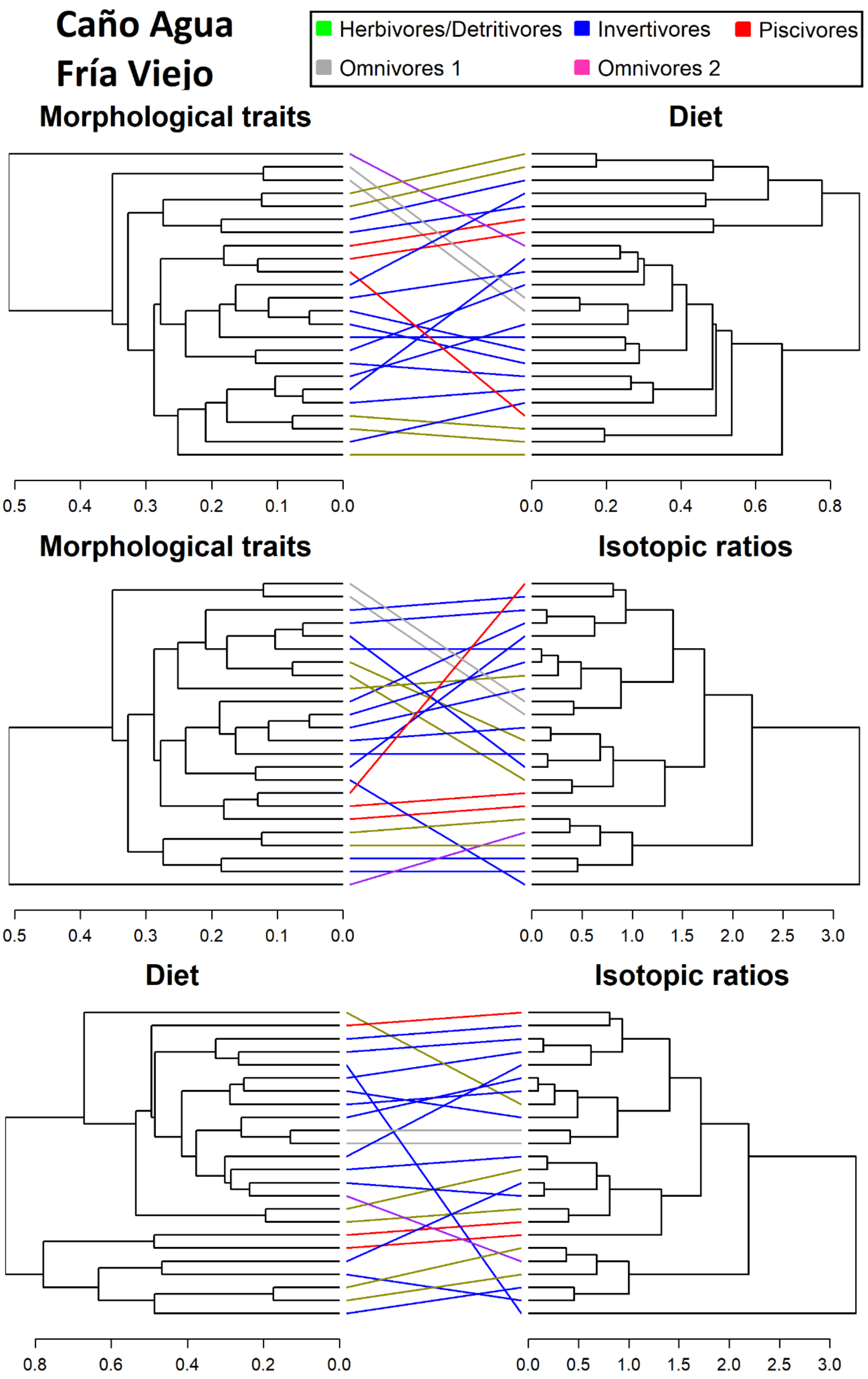


Figure C.3 Continued.

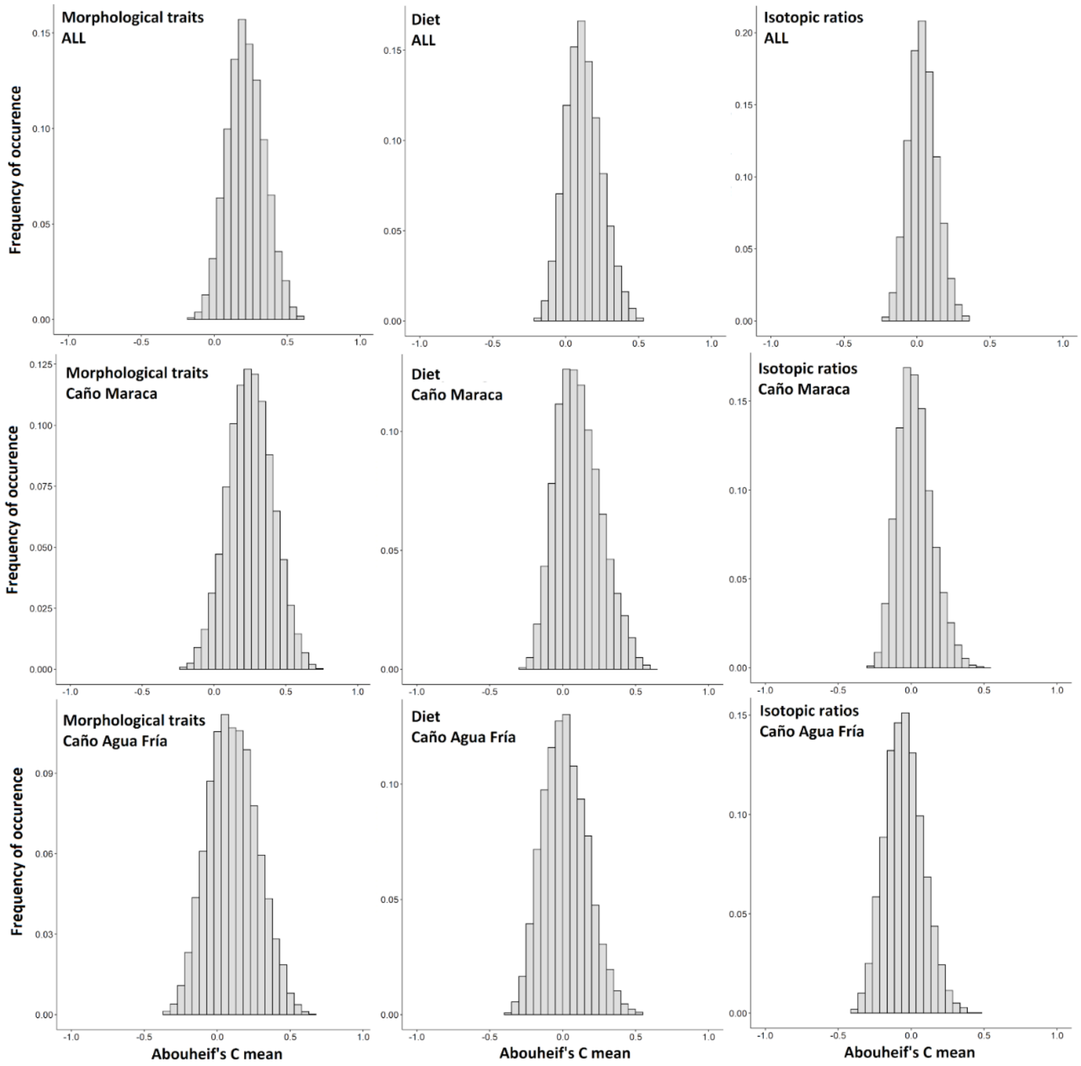


Figure C.4 Phylogenetic signal calculated for morphological, diet, and isotopic dendrograms. Dendograms were constructured using the UPGMA algorithm and using different species composition (species from ALL sites combined; and from Caño Maraca and Caño Agua Fría Viejo separately). The method used to calculate the phylogenetic signals was similar to the one used by Cachera and Le Loc'h (2017), which is based on quantitative states generated for each tip of each dendrogram using Brownian simulations. These quantitative states are then tested for phylogenetic signal using the Abouheif's C mean index. Distribution of phylogenetic signal values for each dendrogram is based on 10,000 Brownian simulations. Abouheif's C_{mean} varies from -1 (no phylogenetic signal) to 1 (complete phylogenetic signal).