Evolutionary convergence in Neotropical cichlids and Nearctic centrarchids: evidence from morphology, diet, and stable isotope analysis

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Despite divergent evolutionary histories, Neotropical cichlids (Cichlidae) and Nearctic sunfishes (Centrarchidae) appear to have similar functional morphotypes and occupy similar ecological niches. We applied an integrative approach analyzing morphological traits, stomach contents, and stable isotope ratios ($\delta^{13}C$, $\delta^{15}N$) to investigate whether local assemblages of cichlids (Venezuela, Peru) and centrarchids (Texas) reveal one-to-one patterns of morphological and ecological convergence. Multivariate ordinations performed on diet and morphology datasets identified a broad overlap between cichlid and centrarchid assemblages. The functional morphology of the two groups has diversified in a convergent manner within the confines of ram-suction modes of prey ingestion. Both groups had the same set of ecomorph types that corresponded to the same trophic niches, including substrate-sifting invertivores, epibenthic invertebrate gleaners, and piscivores; the one exception was a molluscivorous sunfish, comprising a niche that was not represented in the two cichlid assemblages. Estimates of trophic positions based on stable isotope analysis revealed convergent vertical trophic structure; with few exceptions, fishes with similar morphologies had similar trophic positions. Large-bodied piscivores had highest trophic positions, whereas small and medium-bodied generalists and invertivores had low to intermediate trophic positions. Consistent patterns of ecomorphological convergence in these two perciform groups provide strong evidence for adaptation involving constrains in functional morphology associated with feeding. © 2013 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2013, **109**, 146–164.

ADDITIONAL KEYWORDS: adaptation – lowland rivers – North America – Perciformes – phenotypic similarity – South America – trophic morphology.

INTRODUCTION

Morphological and ecological similarity among phylogenetically independent lineages provides compelling evidence of adaptation in response to environmental factors with predictable effects on trait selection (Schluter, 2000; Losos, 2011). Phenotypic similarity normally results from shared common ancestry, although convergent evolution can occur when similar environmental conditions select for restricted sets of functional traits (Blondel *et al.*, 1984; Losos, 1992; Melville, Harmon & Losos, 2006; Hulsey *et al.*, 2008; Young, Sweeney & Badyaev, 2010). Repeated and independent evolution of lizard ecomorphs (*Anolis*) on the Greater Antilles provided evidence for convergent evolution in response to similar environmental conditions (Losos *et al.*, 1998). Stayton (2006) provided support for convergence in the amount of force produced during jaw closure by herbivororus lizards from divergent lineages. The independent evolution of elongate quadrate bones in natricine snakes supported a model of convergent evolution in feeding performance (i.e. piscivory) between European and North American lineages (Vincent *et al.*, 2009).

Ecomorphological patterns among freshwater fish assemblages have provided strong evidence of convergent evolution (Motta, Norton & Lucskovich, 1995a). A recent study of body shapes and trophic morphology (e.g. dentition characters) of eretmodine cichlids in

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Lake Tanganyika revealed morphological convergence in response to selection for similar dietary niches (Ruber & Adams, 2001). Convergence has been observed among fishes possessing highly specialized functional traits (Wainwright *et al.*, 2007). The tube-snouted electric fishes from separated orders (gymnotiforms in South America and mormyriforms in Africa), for example, are adapted to grasp and suck immature aquatic insects that burrow or hide in holes in the river substrate (Marrero & Winemiller, 1993). Research on the evolution of jaw structure of teleost fishes has demonstrated that divergent phenotypes can subsequently converge into the same area of functional space (i.e. many-to-one mapping of morphology to function: Wainwright *et al.*, 2004; Hulsey *et al.*, 2008). For example, in studies of labrid fishes from warm-temperate and tropical reefs, Wainwright *et al.* (2004) and Alfaro, Bolnick & Wainwright (2005) found that different jaw morphologies can produce similar suction force. These findings suggest that organisms need not necessarily show morphological convergence even when challenged with similar functional or ecological demands.

Perciform fishes of the families Cichlidae (cichlids) and Centrarchidae (sunfishes and black basses) are excellent model organisms for research examining evolutionary convergence. These two families evolved independently in different geographical regions, yet their ecological roles in freshwater communities appear to be very similar (Mittelbach, 1984; Layman & Winemiller, 2004). In terms of species richness, Neotropical cichlids exceed centrarchids, with approximately 60 cichlid genera and at least 600 species described for South and Central America (López-Fernández, Winemiller & Honeycutt, 2010). With eight genera and 34 species described, the family Centrarchidae is a relatively young perciform clade endemic to freshwaters of North America (Near, Bolnick & Wainwright, 2005). Cichlids and centrarchids both have parental care (Cook & Phillip, 2009), occupy similar habitat types (Montaña & Winemiller, 2010), and reveal similar patterns of association for functional morphology, feeding mechanics, and diet (e.g. ram-suction feeding modes: Norton & Brainerd, 1993; Galis & Druker, 1996). Both lineages contain a variety of trophic groups including planktivores, benthic invertivores, molluscivores, and piscivores.

Ecomorphology and functional morphology of centrarchids have been extensively studied (Lauder, Wainwright & Findeis, 1986; Winemiller & Taylor, 1987; Caroll *et al.*, 2004; Collar, Near & Wainwright, 2005; Collar & Wainwright, 2006) and similar research has been conducted on cichlids (Meyer, 1987; Winemiller, Kelso-Winemiller & Brenkert, 1995; Waltzek & Wainwright, 2003; Hulsey, 2006; Hulsey *et al.*, 2008; López-Fernández *et al.*, 2012). Norton &

Brainerd (1993) investigated the repeated occurrence of morphological and kinematic traits of ram/suction feeding strategies in piscivorous and invertivorous cichlids and centrarchids. Convergence in ecomorphology and ecological niches of cichlids from three tropical regions (Africa, South, and Central America) was demonstrated by Winemiller *et al.* (1995). In a study examining convergent morphology of molluscivorous and non-molluscivorous heroine cichlids in Central America, Hulsey *et al.* (2008) found that molluscivory has been gained and lost numerous times in this group, but convergence in durophagy (i.e. ability to eat hard prey) was maintained when comparing molluscivores to closely-related species across the Heroini.

In the present study, we examined trophic morphology, stomach contents, and stable isotope ratios in Neotropical cichlid and Nearctic centrarchid fishes from four floodplain rivers to investigate ecomorphological convergence. If cichlids and centrarchids reveal one-to-one patterns of morphological and ecological convergence, we predicted that morphologically similar species would converge in the same areas of the morphological and dietary space. Consequently, morphologically similar species would be expected to occupy similar trophic positions in aquatic food webs. To examine these hypotheses, we used multivariate ordinations to identify patterns of association among morphological traits and diets and overlap among species of cichlids and centrarchids. We examined estimates of trophic positions based on stomach contents and isotopic analysis to evaluate if morphologically similar species displayed similar vertical trophic positions in food webs. Because the two families of perciform fishes included in the present study contain diverse feeding niches, ranging from invertivores, to generalists, to piscivores, we predicted that distributions of trophic positions within species assemblages would be similar if assemblages have convergent trophic structure.

MATERIAL AND METHODS

STUDY AREA AND FIELD SURVEYS

Perciform fishes were collected from four lowland rivers: two Neotropical rivers (the Cinaruco in Venezuela and the Tambopata in Peru) and two temperate rivers (the Neches and the Brazos in Texas, USA). These rivers were chosen for comparison to provide similar environmental conditions in terms of geomorphology, sediments, and water quality. The Cinaruco River (study area centred at approximately 6°32′N, 67°24′W) and the Neches (30°35′N, 94°08′W) have clear, slightly-stained, oligotrophic waters, with sandy substrates, low pH, and high transparency. The

Table 1. Cichlid and centrarchid species surveyed in two tropical and two temperate rivers

Cichlidae species	Tribes	Name abbreviation	Centrarchidae species	Tribes	Name abbreviation
Cinaruco River			Neches River		
Acaronia vultuosa	Cichlasomatini	Avul	*Lepomis cyanellus*	Lepomini	Lc
Aequidens diadema	Cichlasomatini	Ad	*Lepomis gulosus*	Lepomini	Lgu
Apistogramma sp.	Geophagini	Asp1	*Lepomis humilis*	Lepomini	Lhu
Apistogramma hoignei	Geophagini	Ah	*Lepomis macrochirus*	Lepomini	Lma
Biotodoma wavrini	Geophagini	Bw	*Lepomis miniatus*	Lepomini	Lmin
Biotecus dicentrarchus	Geophagini	Bd	*Lepomis megalotis*	Lepomini	Lme
Crenicichla lugubris	Geophagini	Cl	*Lepomis microlophus*	Lepomini	Lmi
Crenicichla aff. *wallacii*	Geophagini	Cw	*Micropterus punctulatus*	Micropterini	Mp
Geophagus abalios	Geophagini	Ga	*Micropterus salmoides*	Micropterini	Ms
Geophagus dicrozoster	Geophagini	Gd	*Pomoxis annularis*	Archoplitini	Pa
Heros sp.	Heroini	Her	*Pomoxis nigromaculatus*	Archoplitini	Pn
Hoplarchus psittacus	Heroini	Hp			
Hypselecara coryphaenoides	Heroini	Hc	Brazos River		
Mesonauta insignis	Heroini	Mi	*Lepomis cyanellus*	Lepomini	Lc
Satanoperca daemon	Geophagini	Sd	*Lepomis gulosus*	Lepomini	Lgu
Satanoperca mapiritensis	Geophagini	Sm	*Lepomis humilis*	Lepomini	Lh
Cichla intermedia	Cichlini	Ci	*Lepomis macrochirus*	Lepomini	Lma
Cichla orinocensis	Cichlini	Co	*Lepomis miniatus*	Lepomini	Lmin
Cichla temensis	Cichlini	Ct	*Lepomis megalotis*	Lepomini	Lme
			Lepomis microlophus	Lepomini	Lmi
Tambopata River			*Micropterus punctulatus*	Micropterini	Mp
Aequidens tetramerus	Cichlasomatini	At	*Micropterus salmoides*	Micropterini	Ms
Apistogramma luelingi	Geophagini	Al	*Pomoxis annularis*	Archoplitini	Pa
Apistogramma urteagai	Geophagini	Au			
Cichlasoma amazonarun	Heroini	Cam			
Crenicichla semicincta	Geophagini	Cs			
Mesonauta festivus	Heroini	Mf			
Satanoperca jurupari	Geophagini	Sjur			

Taxonomic classification for species and tribe within the family Cichlidae follows López-Fernández *et al.* (2010) and, for the family Centrarchidae, follows Near *et al.* (2005). Abbreviations correspond to those shown in Figure 1.

Tambopata River (study area centred at approximately 12°72′N, 69°28′W) and the Brazos River (30°37′N, 96°37′W) are similar to each other, with neutral pH, high loads of suspended sediments of fine grain size, and high turbidity that limits aquatic primary production.

During the low-water period (defined by annual dry season in South America and the summer in Texas), we collected 19 species of cichlids from the Cinaruco River and seven species from the lake Tres Chimbadas in the Tambopata. No cichlid species are shared by these two tropical river systems. Surveys yielded ten centrarchid species that were common to the Brazos and Neches rivers, and one additional species that only was found in the Neches (Table 1). In the Cinaruco River, fishes were collected between December of 2005 and May of 2006; in the Tambopata River, collections were made during June and July of 2009; however, only collections from the connected flood-plain Lake Tres Chimbadas yielded cichlids. In the Texas rivers, collections were conducted during three summers (May to August) from 2009–2011. Surveys employed multiple sampling gears that varied depending on habitat and geographic region. In the Cinaruco and Tambopata rivers, open habitats, such as sand banks and leaf litter, in both the river channel and floodplain lakes were sampled with seines, whereas structured habitats containing rocks and submerged wood were sampled with hooks (# 8) baited with small pieces of fish flesh. Collections in the Neches and Brazos rivers included seines in open areas and electrofishing (pulse DC from a handheld boat unit) for habitats containing rocks and submerged wood.

MORPHOLOGICAL ANALYSIS

Specimens retained for morphological and stomach contents analysis were preserved in 10% formalin

immediately after collection to avoid stomach contents evacuation, and then transported to the laboratory for examination. We measured eleven morphological characters that have been found to be associated with feeding (Gatz, 1979; Motta, 1988; Winemiller, 1991): standard length (SL), body depth, head length, gape width, mouth position, snout length, eye diameter, eye position, interorbital distance, gut length, and gill raker length. Measurements were taken on five adult specimens of each species from each river. Body size is a key variable influencing ecological relationships, and features such as mouth position, gape width (Motta, 1988), and gill raker length (Robinson *et al.*, 1993) are directly associated with modes of feeding and diet (Luczkovich, Norton & Gilmore, 1995). A vernier caliper (precision = 0.1 mm) was used to measure morphometric distances. Linear morphometric distances were transformed into ratios *sensu* Winemiller (1991). In the present study, we used body size (SL) as the denominator for ratios involving head length and body depth. Body width was the denominator for mouth width. Head length was the denominator for the ratio of eye diameter and snout length with mouth closed and open. Head depth was the denominator for eye position. Snout length with the mouth open was divided by the snout length with the mouth closed to provide a measure of relative mouth protrusibility (Gatz, 1979). Ratio transformations remove body size effects and convert linear distances into shape components that have clear functional interpretations. The use of ratios in statistics has been debated extensively because they can introduce allometric bias into shape analysis (Atchley, Gaskin & Anderson, 1976; Corruccini, 1977; Atchley & Anderson, 1978; Dodson, 1978). Early studies by Atchley *et al.* (1976) demonstrated the mathematical properties of ratios, although the problem is not relevant to all biological comparisons (Hill, 1978) as demonstrated by Dodson (1978). Morphometric ratios have some desirable properties, and have been used successfully in bivariate and multivariate analyses (Dodson, 1975, 1978; Winemiller, 1991; Oliveira *et al.*, 2010). Furthermore, allometric influences should be negligible for interspecific comparisons when restricted to limited size interval (e.g. adult size class; Winemiller, 1991). We performed preliminary analysis using three different techniques to remove the effect of body size from components of shape: ratios or proportional standardization based on SL (Gatz, 1979), sheared principal components analysis (PCA) (Bookstein *et al.*, 1985), and residuals from analysis of covariance (McCoy *et al.*, 2006). The results from these methods were virtually identical; therefore, we used SL-standardized values of selected ratios to provide descriptors of shape that have straightforward ecological and functional interpretations (Winemiller, 1991; Winemiller *et al.*, 1995; Cochran-Biederman & Winemiller, 2010).

DIETARY ANALYSIS

Fish specimens were dissected and stomachs were removed for analysis of contents. All food items present in the anterior half of the gut were removed and examined under a microscope (Winemiller, 1990). Prey items from stomachs were identified to the lowest feasible taxonomic level (e.g. fish to species, invertebrates to order). Individuals with empty stomachs were omitted from analyses. When sufficient specimens were available, at least 30 specimens of each fish species were dissected. Overall, species sample sizes for stomach contents analysis ranged from 13 (rare species, e.g. *Satanoperca mapiritensis*) up > 250 individuals (e.g. *Cichla* and *Crenicichla* species; for samples sizes, see the Appendix, Table S1).

To reduce bias from having different specific resources in the two regions, we reduced the number of food categories from approximately 50 taxonomic and functional groups to 24 general categories (Winemiller, 1990; Winemiller *et al.*, 1995): Bryozoa, algae, detritus, terrestrial vegetation, sand, microfauna (including water mites, rotifers, worms), mollusks (snails, bivalves), microcrustacea (Cladocera, Ostracoda, Anostraca, Copepoda, Amphipoda), macrocrustacea (shrimp, crayfish), aquatic insect larvae (Odonata, Trichoptera, Coleoptera, Diptera, Hemiptera, Ephemeroptera, Collembola, Lepidoptera), other aquatic insects, terrestrial insects (Orthoptera, Hymenoptera, unidentified terrestrial insects), fish, and fish scales. We used these categories for interfaunal comparisons. Volumetric proportions of categories from stomach contents were estimated as described by Winemiller (1990).

Tissue samples for stable isotope analysis were taken from three specimens of each species. In addition, tissue samples of macrocrustacea (shrimp only), aquatic invertebrates (Ephemeroptera only, generally grazers and collector/gathers, primarily feeding on algae or other aquatic plant source; Peckarsky *et al.*, 1990), and common primary producers (periphyton, seston, C_3 plants, C_4 plants) were collected from each river. Muscle tissue samples were removed from the dorso-lateral region of fish specimens that had previously been euthanized by immersion in an overdose of anesthesia (tricaine methanesulfonate); for small individuals (< 30 mm SL), the entire specimen (minus the gut) was processed for stable isotope analysis. For macrocrustacea, muscle tissue was obtained from the tail region. Smaller invertebrates were processed whole. Algae and macrophyte tissue samples were

collected by hand; and seston was collected by filtering water through a glass fibre filter. Samples for stable isotope analysis were preserved in salt as described by Arrington & Winemiller (2002). In the laboratory, tissues were soaked and rinsed in distilled water to remove the salt, and then dried at 60 °C for 48 h in a drying oven. Dried samples were ground to a fine powder with a mortar and pestle, and then stored in clean glass vials. Subsamples for each ground sampled were weighed and packaged into an Ultra-Pure tin capsule (Costech) and sent to the Analytical Chemistry Laboratory, Institute of Ecology, University of Georgia, for measurement of stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$).

STATISTICAL ANALYSIS

Morphological and ecological data were used to investigate ecomorphological patterns of convergence between cichlid and centrarchid assemblages. First, we examined interspecific patterns of functional morphological traits in these two perciform groups using a PCA on the correlation matrix of log-transformed morphological traits. This analysis allows comparison of species distributions within a multivariate morphological space and identification of patterns of correlation among morphological variables. To interpret the eigenvalues of each component of the PCA, we followed the approach used by Grossman, Nickerson & Freeman, (1991), which suggests that eigenvalues > 1.0 indicate that the component explains a greater proportion of the variance of the data.

To examine whether cichlids and centrarchids exhibit convergent patterns in their dietary niches, we estimated the volumetric proportions of food items used by each species using the methods of Winemiller (1990) and, subsequently, we calculated the dominance index (IA_i) for diet items proposed by Kawakami & Vazzoler (1980). Volumetric proportions of food items also were used to calculate diet similarities for cichlid and centrarchid species within their respective assemblages using Pianka's (1973) symmetrical measure of niche overlap. Values of this index range from near 0 (no overlap) to 1.0 (complete overlap). We used the analysis of similarity (ANOSIM) to test for significant differences in diets of the two perciform assemblages and assemblages across rivers. Using PRIMER, version 5 (http://www.primer-e.com/), a similarity matrix was generated for the volumetric dietary data using the Bray–Curtis similarity and the observed relationships were compared with random expectations based on 9999 permutations. ANOSIM generates a value of r that is scaled to lie between −1 and +1, with a value of zero representing the null hypothesis that there is no diet

selection. Similarity percentage analysis (SIMPER) was performed to determine which food items were responsible for diet differences among fishes in each river. SIMPER analysis calculates the mean dissimilarities between fish species and how much each diet category contributes to mean diet dissimilarity (Clarke & Warwick, 1994). SIMPER was performed using PRIMER version 5.

To ordinate cichlids and centrarchids according to trophic niches, we performed non-metric multidimensional scaling (NMDS) on arcsine square root-transformed dietary data using mean proportional volumes of the 24 broad diet categories consumed by species from each river. Subsequently, we performed a canonical correspondence analysis (CCA) to examine relationships between morphological gradients and dietary gradients. CCA is a multivariate, direct-gradient analysis technique in which a set of variables (morphology) is related directly to another set of variables (diet) associated with the same set of observations (species). The technique produces linear combinations (canonical variables) between the two datasets (morphology and diet) with the assumption that the two canonical axes are maximally correlated. The analysis was performed on log-transformed morphological data and arcsine square root-transformed dietary data using PC-ORD, version 6 (MJM Software Design).

Finally, we tested whether cichlids and centrarchids converge in their vertical trophic positions within their local food webs. We calculated species trophic positions (TP) based on two kinds of data: stomach contents analysis (SCA) and stable isotope analysis (SIA).

TP_{SCA} was calculated for fish from each river using the formula described in Adams, Kimmel & Ploskey (1983):

$$TP_{SCA} = 1.0 + \sum_{j=1}^{n} TP_j(p_j)$$

where TP_j is the trophic position of the food item j, p_{ij} is the volumetric proportion of food item j, and n is the number of food categories documented for the species. Primary producers were coded as $TP = 1$, primary consumers feeding only on plant material would have $TP = 2$, carnivores feeding on herbivores would be $TP = 3$, etc. Estimates for trophic positions of the prey items (invertebrates and fishes) were based on information obtained from the literature. Vander Zanden & Rasmussen (1999) provided estimations of trophic position values for prey items in North American rivers, and Zeug & Winemiller (2008) provided information on trophic positions of aquatic consumers in the Brazos River, Texas. Jepsen & Winemiller (2002), Layman, Winemiller &

Arrington (2005), and Roach *et al*. (2009) estimated trophic positions of prey taxa from the Cinaruco River. To estimate trophic position for piscivorous fishes, including *Cichla* spp., *Crenicichla lugubris*, *Micropterus* spp., and *Pomoxis* spp., we identified fish components in the diets of these consumers to genus or family and then assigned trophic position values. For example, Layman *et al*. (2005) noted that *Cichla* species from Cinaruco River feed predominantly on fishes at trophic position 2 (herbivore and detritivores).

Trophic position from isotopic data (TP_{SIA}) was estimated based on fractionation of $\delta^{15}N$ between the consumer and basal production sources collected from its locality (Vander Zanden & Rasmussen, 1999; Post, 2002) using the formula:

$$TP_{SIA} = [(\delta^{15}N_{consumer} - \delta^{15}N_{reference})/2.54] + 1$$

where $\delta^{15}N_{reference}$ was the mean $\delta^{15}N$ of basal sources (C3 plants, seston, benthic algae), and 2.54‰ is the mean trophic fractionation (Vanderklift & Ponsard, 2003). Research in large floodplain rivers in North and South America, including the rivers investigated in the present study, has indicated that algae and riparian C_3 plants are the main sources of primary production supporting fish biomass (Hamilton, Lewis & Sippel, 1992; Jepsen & Winemiller, 2007; Zeug & Winemiller, 2008; Roach *et al*., 2009); therefore, we used the mean $\delta^{15}N$ for these sources as a general reference value representing the first trophic level. Reference $\delta^{15}N$ values were based on material obtained from the same river and hydrological season in which a given consumer (fish) sample was taken; therefore, estimates of trophic positions are comparable across the four rivers.

We used the Kolmogorov–Smirnov (K–S) test to compare TP_{SIA} distributions of cichlid and centrarchid assemblages, and to test for differences between TP_{SIA} distributions of centrarchid assemblages from the river channel and floodplain lakes within the Neches and Brazos rivers. For each perciform assemblage, the correlation between TP_{SCA} and TP_{SIA} was evaluated using Pearson's (r) based on species mean values of TP_{SCA} and TP_{SIA}. We only included species having values for both TP_{SCA} and TP_{SIA}. A priori, we tested and confirmed normality of the data. Relationships between trophic position (based on $\delta^{15}N$) and body size (SL in mm) of each consumer were assessed with Spearman's rank correlation.

To test further the null hypothesis of no significant correlation between phylogenetic relationship, morphology, and diet, a Mantel test was performed on the matrix of species stomach contents and matrix of species morphological traits using PC-ORD, version 6. A partial Mantel test was performed to evaluate the effect of phylogeny (Smouse, Long & Sokal, 1986). The partial Mantel test estimates the correlation between morphological and dietary matrices at the same time as controlling for the effect of the phylogeny. For the present study, a matrix of taxonomic distance was constructed by counting the number of nodes that separate each species in the phylogenetic tree (Winemiller *et al*., 1995; Oliveira *et al*., 2010). Species assigned within the same genus were given a distance of 1, species within the same tribe had a distance of 2, species within the same family had a distance of 3, and species in different families had a distance of 4. We used taxonomic levels as proxies for relative degrees of evolutionary divergence for both families. An assumption for the use of taxonomic levels is that rates of evolutionary change are uniform for all branches between a given taxonomic level and the adjacent level, and this assumption would be wrong in most cases. Thus, this method provides a coarse-scale, yet reasonably accurate, assessment of phylogenetic distances between species pairs. Our taxonomic classification and species relationships were based on the most recent phylogenies for the families Cichlidae (López-Fernández *et al*., 2010) and Centrarchidae (Near *et al*., 2005). For their Neotropical cichlid phylogeny derived from molecular data, López-Fernández *et al*. (2010) provided branch lengths only for 17 of 26 cichlid species examined in the present study. The centrarchid phylogeny of Near *et al*. (2005) based on molecular data did not provide branch lengths for the 32 species that they examined. A recent molecular time-calibrated phylogeny of ray-finned fishes by Near *et al*. (2012) provided a hypothesis of evolutionary relationships among higher fish taxa; however, branch lengths were not provided. Thus, our phylogenetic distances are based on the most current topologies, with an assumption of uniform branch length.

RESULTS

MORPHOLOGICAL ANALYSIS

Multivariate ordination of species in morphological trait space revealed high similarity between species from the two major lineages (Fig. 1). The first two PC axes modelled 51.1% of the total variance in morphology of species in the dataset (Table 2). PC1 (29.4% of variance) identified a body-shape gradient contrasting fishes with fusiform bodies versus fishes having discoid, laterally-compressed bodies, with the latter group including the majority of sunfishes (Centrarchidae), heroines (Cichlidae), and cichlasomatines (Cichlidae) (for full list of species and tribe names, see Table 1). Positive values on PC1 also were associated with long gill rakers, large mouth gape, and large
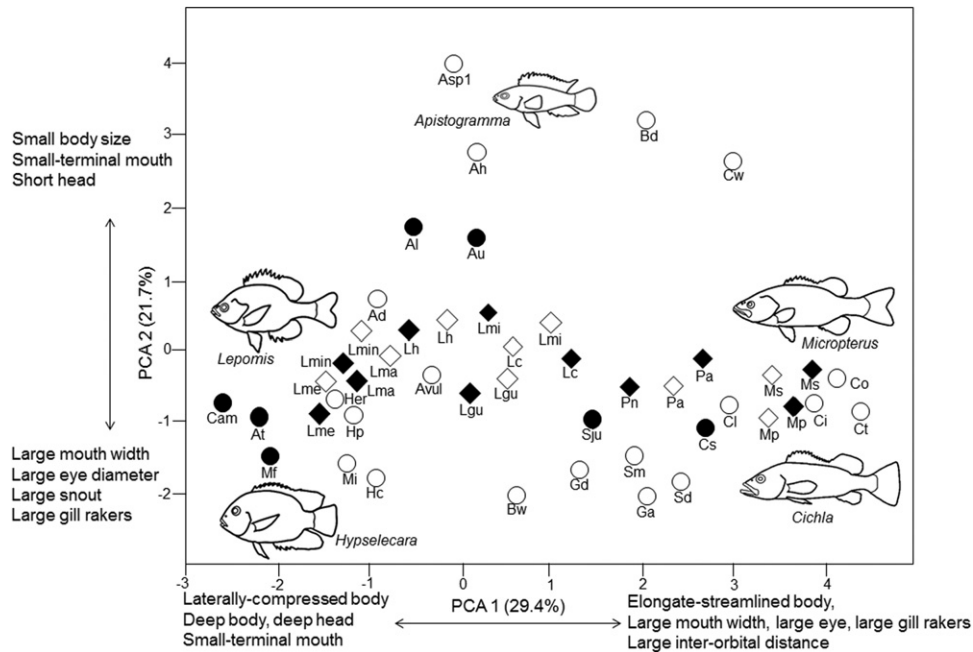
Figure 1. Morphological space occupied by perciform fishes from the Cinaruco, Tambopata, Neches, and Brazos rivers. Principal components analysis (PCAs) were conducted based on the correlation matrix for 11 morphological traits associated with feeding. Circles represent the means for species. Open circles represent cichlid species from Cinaruco River; filled circles represent cichlid species from Lake Tres Chimbadas in Tambopata; open diamonds represent centrarchid species from the Brazos River; and filled diamonds represent centrarchid species from the Neches River. Species abbreviations correspond to those shown in Table 1.

Table 2. Principal components (PC) scores derived from eleven functional morphological traits of cichlid and centrarchid species

	PC1	PC2
Eigenvalues	3.5	2.6
% of variance	29.4	21.7
Morphological traits		
Standard length	0.28	0.46
Head length	−0.22	0.20
Body depth	0.44	−0.21
Inter-orbital distance	0.29	−0.33
Mouth (gape) width	−0.34	−0.17
Mouth position	−0.27	0.12
Snout length, mouth open	0.04	−0.30
Eye position	0.07	−0.26
Eye diameter	0.42	0.18
Gill raker length	0.22	−0.30
Gut length	0.21	0.49

Eigenvalues > 0.1 were used for interpretation.

inter-orbital distance, whereas negative values on PC1 were associated with fishes that have small, relatively terminal mouths and deep heads (Fig. 1, Table 2). PC2 (21.7% of variance) contrasted fishes with small body size, such as the dwarf cichlids *Crenicichla* aff. *wallacii* and *Apistogramma* and *Biotoecus* spp., small terminal mouths, and relatively short guts (large positive scores on PC2) versus those having large mouths, large eyes, and long snouts and gill rakers (e.g. the cichlids *Cichla* spp., *Geophagus* spp., *Satanoperca* spp., and *Crenicichla* spp., and the centrarchids *Micropterus* spp. and *Pomoxis* spp.; all with large negative scores on PC2) (Fig. 1). High morphological overlap occurred between *Cichla* spp. and *Micropterus* spp. as a result of their fusiform bodies, long gill rakers, large mouths, and large eyes.

The first two PC axes showed a gradient that separated five distinctive morphological groups. The first group formed by *Cichla* and *Micropterus* have relatively large heads, large mouths positioned upward, large eyes, and fusiform bodies. A second group included *Biotodoma wavrini* and species of *Satanoperca*, *Geophagus*, and *Pomoxis*, comprising fishes with relatively short heads, long snouts, highly protrusible jaws, and laterally compressed bodies. A third group contained species with short snouts, small mouths, less jaw protrusibility, and laterally-compressed, discoid bodies (e.g. the centrarchids *Lepomis megalotis*, *Lepomis macrochirus*, *Lepomis miniatus*, and the cichlids *Heros* sp. *Hoplarchus psittacus*, *Cichlasoma amazonarum*, *Hypselecara*

coryphaenoide, *Mesonauta insignis*, and *Mesonauta festivus*; Fig. 1). A fourth group contained three sunfishes (*Lepomis cyanellus*, *Lepomis gulosus*, and *Lepomis humilis*) and one cichlasomatine cichlid (*Acaronia vultuosa*). These species have relatively large and terminal mouths, and relatively fusiform bodies respect to other species within their genus or tribe. Despite differences in feeding ecology and possessing hypertrophied pharyngeal jaws that generate strong force to crush mollusk shells, the sunfish *Lepomis microlophus* had morphological traits most similar to the fourth group. *Crenicichla* spp. had no overlap with other genera as a result of their elongate bodies and dorso-ventrally compressed heads; however, the positions of *C. lugubris* and *Crenicichla semicincta* were closer to *Cichla*, *Pomoxis*, and *Micropterus* species, and this can be explained by the large mouths, large eyes, and long gill rakers possessed by these fishes. A fifth group contained only dwarf cichlid species (*Apistogramma*, *Biotoecus*, *Crenicichla* aff. *wallacii*).

DIETARY PATTERNS

A total of 4251 specimens was analyzed for stomach contents (2140 cichlids from the Cinaruco River, 346 cichlids from the Tambopata floodplain lake, 879 centrarchids from the Neches, and 886 centrarchids from the Brazos). ANOSIM did not reveal significant differences in the diets of cichlids and centrarchids overall ($P < 0.06$; $r = 0.14$). ANOSIM revealed dietary differences between cichlids from the Cinaruco and centrarchids from both the Neches ($P < 0.01$; $r = 0.23$) and Brazos rivers ($P < 0.03$; $r = 0.19$). ANOSIM did not reveal significant differences in diets of cichlids from the Cinaruco River and those from the Tambopata floodplain lake ($P < 0.5$; $r = -0.05$), nor in the diets of centrarchids from the Neches and Brazos rivers ($P < 0.60$; $r = -0.02$). There also were no significant differences between cichlids from the Tambopata River and centrarchids from the Neches ($P < 0.35$; $r = 0.03$) and Brazos rivers ($P < 0.62$; $r = -0.07$).

Overall, the dominant food categories found in diets of both cichlid and centrarchid fishes were aquatic insects (larvae of Odonata, Trichoptera, Coleoptera, Diptera, and Ephemeroptera), microcrustacea, macrocrustacea, fish, and fish scales (see Appendix, Table S1). Mollusks (snails, bivalves) and microcrustacea (ostracods) were the main food items identified in the diet of *L. microlophus* in the Neches and Brazos rivers.

NMDS analysis identified two gradients explaining 63.4% of the variance in diet. Axis 1 (43.0% of variance) contrasted the consumption of benthic and epibenthic invertebrates versus piscivory (Fig. 2). Axis 2 (20.4% of variance) was positively correlated with molluscivory (e.g. *L. microlophus*) and negatively correlated with the consumption of other kinds of crustacea, fish, and invertebrates (Fig. 2). NMDS clearly grouped a few piscivorous species, the cichlids *Crenicichla lugubris* and *Cichla* spp., and the centrarchids *Micropterus* spp. and *Pomoxis* spp. Large fractions of benthic macroinvertebrates were consumed by substrate-sifting geophagine cichlids. Benthic and epibenthic invertebrates were consumed in large amounts by nongeophagine cichlids (*Cichlasoma*, *Hoplarchus*, *Heros*, *Hypselecara*, *Mesonauta* spp.) and sunfishes (*L. megalotis*, *L. macrochirus*, *L. humilis*, *L. miniatus*). Generalist species, such as *A. vultuosa*, *L. gulosus*, *L. cyanellus* and *C. semicincta* and *C.* aff. *wallacii*, consumed large amounts of aquatic insects, although their diets also contained large fractions of fish and macrocrustacea (see Appendix, Table S1).

SIMPER analysis identified contributions of individual prey categories to the separation of feeding groups. SIMPER revealed that dietary differences between the two clear-water river assemblages (Cinaruco cichlids and Neches centrarchids) were a result of the differential consumption of aquatic insect larvae (39.6%), microfauna (9%), and microcrustacea (7%). Similarly, differences in diets between the Cinaruco cichlids and Brazos centrarchids (turbid-water river assemblage) were associated with the differential consumption of aquatic insects (24%) and microfauna (8.3%).

Dietary overlap tended to be high among cichlids within the Cinaruco River (0.40) and the Tambopata floodplain lake (0.30), and relatively low among centrarchids within the Neches (0.25) and Brazos (0.13) rivers. Low dietary overlap was observed between geophagine cichlids with laterally-compressed bodies (e.g. *Biotodoma*, *Geophagus* spp., *Satanoperca* spp.) and geophagine cichlids with elongate bodies (e.g. *Crenicichla* spp.). High inter-familial dietary overlap was observed between *Cichla* and *Micropterus* (piscivores), *L. cyanellus*, *L. gulosus*, *A. vultuosa*, *C. semicincta* and *C.* aff. *wallacii* (generalist predators, consuming a mixture of aquatic invertebrates and fish), and among *Cichlasoma*, *Hypselecara*, *Heros*, *Hoplarchus*, *Aequidens* spp., *Mesonauta* spp., *L. miniatus*, *L. megalotis*, *L. humilis*, and *L. macrochirus* (aquatic invertebrate consumers, with detritus also encountered in stomachs).

CCA revealed strong correlation between morphology and diet (Table 3). Positive scores on the first morphological axis (CCA1) were associated with small, terminally-positioned mouths, short snouts, and short to intermediate length gill rakers (e.g. *L. megalotis*, *L. miniatus*, *L. humilis*, *Aequidens diadema*, *Aequidens tetramerus*, *Apistogramma* spp. and *Biotoecus*). This axis was paired with a dietary axis influenced by benthic and epibenthic
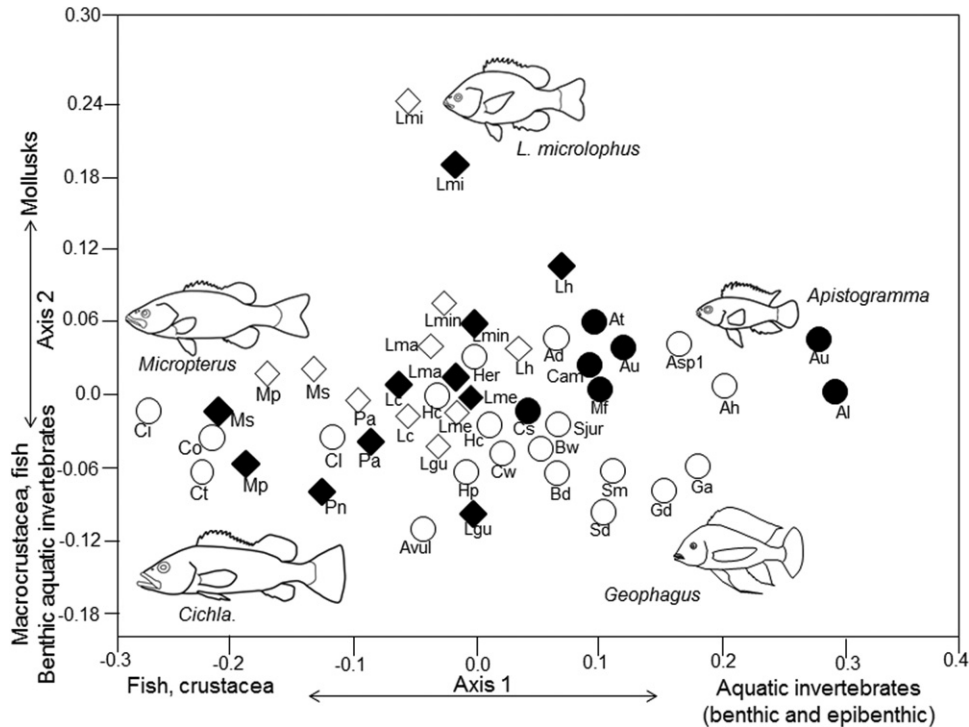
Figure 2. Non-metric multidimensional scaling conducted on dietary data; each circle represents a single species by river observation calculated from the mean volumetric proportions of food categories from stomach contents. Species abbreviations correspond to those shown in Table 1.

invertebrate prey and detritus. Negative scores on CCA1 were associated with long gill rakers, large eyes, large mouths positioned upward, and large fusiform bodies, and these species had positions on a dietary axis that revealed the consumption of fish and macrocrustacea. Piscivorous *Cichla* spp., *Micropterus* spp., *C. lugubris*, and *Pomoxis* spp. had high positive loadings on this pair of axes. Positive scores on the second morphological axis (CCA2) were associated with a long snout and greater jaw protrusion, and were positioned on a dietary axis to indicate the consumption of benthic and epibenthic invertebrates. Geophagine cichlids and sunfishes with laterally-compressed, discoid bodies had high scores on this pair of axes. Negative scores on CCA morphological axis 2 were associated with large eyes, large interorbital distances, and fusiform or elongate bodies (*C. semicincta*, *C.* aff. *wallacii*, *L. cyanellus*, *L. gulosus*, *A. vultuosa*), and high positive scores on CCA diet axis 2 were associated with consumption of fish and macrocrustacea. The third pair of CCA axes was largely influenced by small terminal mouths and short gill rakers in association with feeding on aquatic invertebrates as well as mollusks. In agreement with the CCA results, the Mantel test revealed significant correlations between morphology and diet ($r = 0.29$, $P < 0.0001$). Partial correlations using the

Partial Mantel test confirmed relationships between morphology and diet ($r = 0.14$, $P = 0.01$), with no significant effect of phylogenetic distance ($r = 0.12$, $P = 0.06$).

ISOTOPIC PATTERNS

Cichlid assemblages from Neotropical rivers had greater $\delta^{13}C$ ranges than temperate centrarchid assemblages (Fig. 3A, B). For example, $\delta^{13}C$ for cichlids from the Cinaruco River ranged from –25‰ to –34‰, and $\delta^{13}C$ varied between –29‰ and –36‰ for cichlids from the Tambopata floodplain lake (Fig. 3A, B). For centrarchids in the Neches River, $\delta^{13}C$ ranged from –25.5‰ to –29‰, and between –22‰ and approximately –28‰ for those in the Brazos River (Fig. 3C, D).

Piscivores in both cichlid (e.g. *Cichla* spp. and *Crenicichla lugubris*) and centrarchid (e.g. *Micropterus* and *Pomoxis* spp.) assemblages had highest $\delta^{15}N$ values (Fig. 3A, C, D). Sunfishes (excluding *L. gulosus*, *L. cyanellus*, and *L. microlophus*), cichlasomatines, heroines, and most geophagines (excluding *C. lugubris*), all of which are known to consume large amounts of aquatic invertebrates, had intermediate to low $\delta^{15}N$ values (approximately between 6–8.5‰ for cichlids in the Cinaruco, 6.9–8.3‰ for cichlids in the

Table 3. Statistics associated with the first three axes of the canonical correspondence analysis (CCA) performed on 11 morphological traits and 20 diet categories used in the analysis of stomach contents of cichlids and centrarchids

	CCA1	CCA2	CCA3
Eigenvalues	0.04	0.01	0.01
% of variance explained	38.40	15.20	5.30
% cumulative explained	38.40	53.60	58.90
Pearson correlation (morphology–diet)	0.86	0.80	0.78
Morphological traits			
Standard length	0.24	−0.46	−0.46
Head length	0.29	−0.05	0.40
Body depth	−0.63	−0.32	−0.07
Inter-orbital distance	−0.47	−0.30	1.28
Mouth (gape) width	1.29	2.94	4.61
Mouth position	0.31	0.12	0.79
Snout length, mouth open	2.64	5.43	−3.40
Eye position	−0.21	1.33	0.08
Eye diameter	−0.14	−0.61	−0.26
Gill raker length	−3.84	1.51	−0.54
Gut length	0.33	−0.48	−0.61
Food items			
Bryozoa	0.31	0.18	0.11
Diatoms	0.15	0.42	−0.20
Algae	0.33	0.02	0.22
Detritus	0.46	−0.04	0.03
Terrestrial material (leaf litter, seeds, flowers, etc.)	0.29	0.34	−0.04
Sand	0.28	−0.13	0.04
Mollusca	0.26	−0.25	0.37
Microfauna	−0.12	0.31	0.26
Microcrustacea	0.19	0.16	0.27
Macrocrustacea	−0.37	−0.29	−0.25
Odonata	0.20	−0.21	−0.02
Coleoptera	0.28	−0.12	0.17
Diptera	0.22	−0.04	0.32
Ephemeroptera	−0.11	0.09	−0.03
Hemiptera	0.04	−0.20	−0.05
Trichoptera	0.21	0.12	0.16
Terrestrial insects	−0.18	−0.03	−0.27
Fishes	−0.39	−0.22	−0.33
Scales	0.45	0.17	−0.37

Tambopata floodplain lake, and between 8‰ and 12‰ for sunfishes in the Neches and Brazos rivers). The cichlasomatine cichlid, *A. vultuosa*, and the sunfishes *L. gulosus* and *L. cyanellus*, which consume both aquatic invertebrates and fishes, had intermediate $\delta^{15}N$ values of approximately 8.0‰ for *A. vultuosa*, between 9.1‰ and 10.0‰ for *L. gulosus* in the Neches and Brazos rivers, and from 10.1‰ to 12.8‰ for *L. cyanellus* in the Neches and Brazos rivers, respectively. Among *Lepomis* species, *L. microlopus* had the lowest $\delta^{15}N$ values of 9.6‰ and 8.3‰ for the Neches and Brazos rivers, respectively.

VERTICAL TROPHIC STRUCTURE

Distributions of species trophic position values for cichlid and centrarchid assemblages were not significantly different when estimates were based on stomach contents data (TP_{SCA}) (K–S test, $P = 0.06$) or isotopic data (TP_{SIA}) (K–S test, $P = 0.55$). Overall, trophic positions estimated from the TP_{SCA} data and the TP_{SIA} data were strongly correlated for both cichlids and centrarchids (r^2 for cichlid data = 0.74, $P < 0.0001$; r^2 for centrarchid data = 0.77, $P < 0.0001$). The two methods yield fairly concordant estimates for piscivorous cichlids and centrarchids, placing these species at high trophic levels (Fig. 4A, B). TP_{SCA} of *Cichla* spp. varied in the range 4.3–4.6, whereas, in *Micropterus* spp., TP_{SCA} was in the range 3.5–4.5 (Fig. 4A, B).

For invertivorous and generalist cichlids, trophic positions calculated from stomach contents data were lower than estimates from stable isotope data (Fig. 4A). For centrarchids, several invertivores also had lower trophic positions calculated from stomach contents data compared to estimates from stable isotope data (Fig. 4B). Most invertivorous and generalist cichlids had TP_{SCA} values in the range 1.1–2.1 (invertivores, e.g. *Apistogramma* spp., *A. diadema*, *Geophagus* spp.) to 3.2 (generalists, e.g. *Hypselecara coryphaenoides*) (Fig. 4A). Invertivorous centrarchids in the Neches and Brazos rivers had TP_{SCA} in the range 1.97–2.5 (e.g. *L. miniatus*, *L. humilis*, *L. megalotis*), whereas generalists such as *L. cyanellus*, *L. gulosus*, and *L. macrochirus* had TP_{SCA} in the range 2.77–3.02. In the Tambopata floodplain lake, the cichlid assemblage consisted primarily of invertivores ($TP_{SCA} < 2.0$) with one generalist species *Crenicichla semicincta* with $TP_{SCA} = 2.2$. Based on TP_{SCA}, *L. microlophus* had the lowest trophic position of any centrarchid in the both Neches (1.93) and Brazos (1.75) rivers. *Lepomis microlophus* also had the lowest TP_{SIA} estimate (approximately 1.8). Other centrarchid species had TP_{SIA} trends similar to those observed for cichlids, with values ranging from 2.8 for invertivores to 4.3 for piscivores (Fig. 4B). The TP_{SIA} distribution of the centrarchid species assemblage from the river channel was not significantly different from those of assemblages from floodplain lakes for both the Neches River (K–S test, $P = 0.14$) and the Brazos River (K–S test, $P = 0.88$).

A relationship between trophic position estimated by stable isotope values (TP_{SIA}) and body size was observed for cichlids in the Cinaruco ($r_s = 0.51$, $P = 0.02$) and centrarchids in the Neches ($r_s = 0.68$, $P = 0.02$) and Brazos rivers ($r_s = 0.70$, $P = 0.02$),
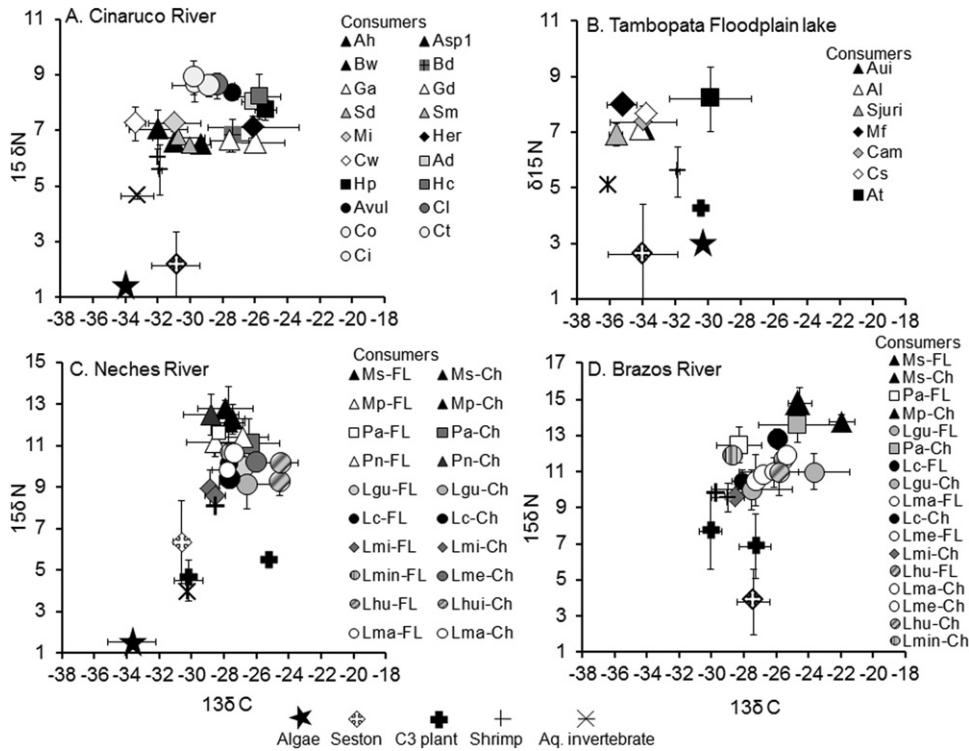
Figure 3. Bi-plots of $\delta^{13}C$ and $\delta^{15}N$ values of cichlid and centrarchid species, invertebrates and basal production sources. Values represent the mean ± SD. A, clear-water Cinaruco River; B, clear-water floodplain Lake Tres Chimbadas in Tambopata River; C, clear-water Neches River; D, turbid-water Brazos River. Species abbreviations correspond to those shown in Table 1. Samples for the Neches and Brazos were taken from floodplain lake (FL) and river channel (Chan).

although no correlation was observed for cichlids of the Tambopata lake ($r_s = 0.03$, $P = 0.90$) where large-bodied cichlids were absent. Large-bodied piscivores, including *Cichla* spp., *C. lugubris*, *Micropterus* spp., and *Pomoxis* spp., had high trophic positions, whereas medium- and small-bodied trophic generalists and invertivores had intermediate and low positions, respectively (for SL ranges of the species examined, see Appendix, Table S1). Overall, perciform species with similar morphology tended to have similar trophic positions (Fig. 5). Exceptions were the centrarchids *Pomoxis* spp. and the geophagine cichlids with laterally-compressed bodies (e.g. *Satanoperca* spp. and *Geophagus* spp.) (Fig. 5) that occupied similar areas within multivariate morphospace but revealed large dietary differences that were reflected by different trophic position estimates; *Pomoxis* spp. had higher trophic position along with other piscivores, whereas invertivorous geophagine cichlids had lower trophic positions. The geophagine *C. lugubris* (Cichlidae) and *Pomoxis* spp. (Centrarchidae) differed in body form (Fig. 5), although they had similar trophic positions consistent with piscivory.

DISCUSSION

Despite the fact that there are more species of Neotropical cichlids and that their lineage is older than that of Nearctic centrarchids, the ecomorphological patterns observed in perciform assemblages from lowland streams represent a convergent evolutionary response to similar ecological conditions and associated fitness challenges. Cichlids and centrarchids are most common in lentic habitats in river channels, backwaters, and floodplain lakes, often in association with structurally-complex, meso- and microhabitats. These two lineages reveal similar distributions of functional morphological traits that allow various species in both groups to exploit similar food resources, as indicated by our dietary and stable isotope analyses.

PATTERNS OF FEEDING ECOLOGY

Cichlid and centrarchid assemblages revealed strong convergence in ecomorphological, dietary, and isotopic space. Several Neotropical cichlid species fed on benthic and epibenthic invertebrates, *Cichla* spp. and
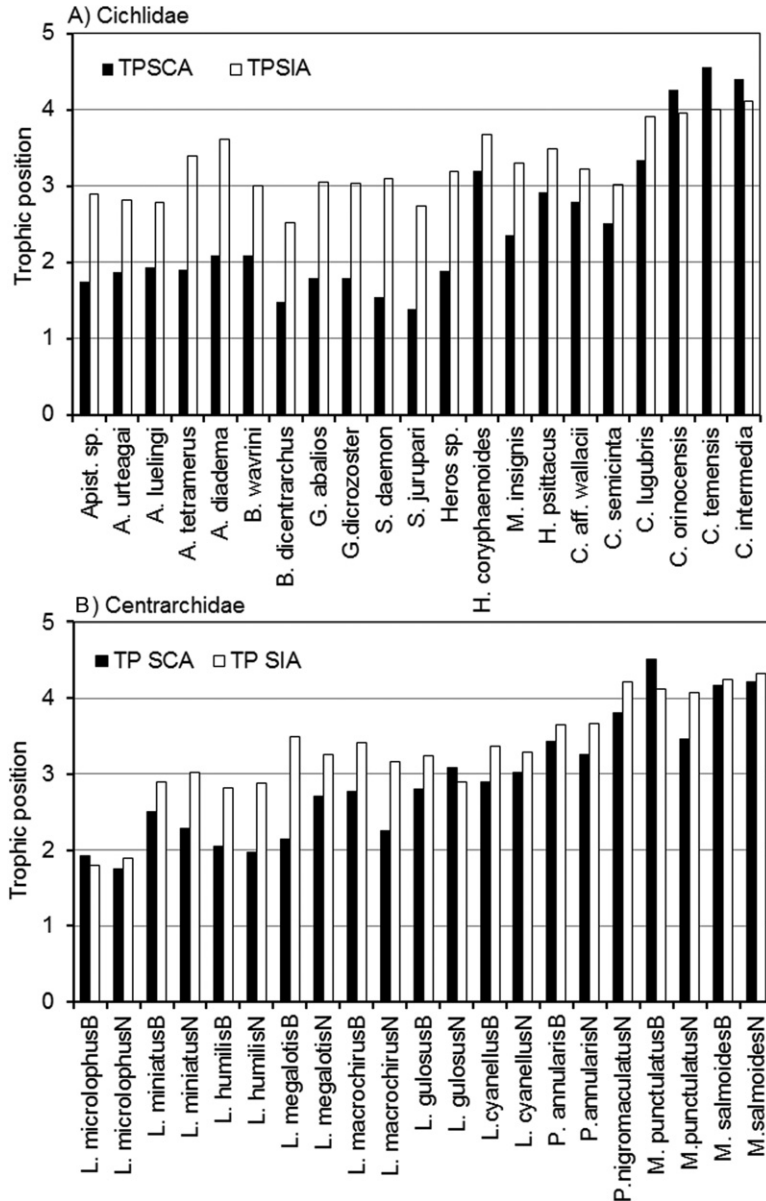
Figure 4. Comparison of trophic position values derived from TP_{SCA} (estimated from volumetric dietary data) versus TP_{SIA} (estimated from $\delta^{15}N$ data) for cichlids (A) and centrarchids (B). Trophic positions for species in the family Centrarchidae are shown for both the Brazos (B) and Neches (N) rivers.

large *Crenicichla* species fed primarily in fish, and *A. vultuosa* had a broad diet containing a mixture of fish, macroinvertebrates, and macrocrustacea. Among centrarchids, four species of sunfish (*L. miniatus*, *L. megalotis*, *L. humilis*, and *L. macrochirus*) had diets convergent with those of invertivorous cichlids, *Micropterus* and *Pomoxis* species were piscivorous, and *L. gulosus* and *L. cyanellus* had broad diets similar to *A. vultuosa*. Despite having high dietary similarity with certain centrarchids, the pike cichlids, *Crenicichla* spp., did not have ecomorphological

equivalents among temperate centrarchids. *Crenicichla lugubris* had a divergent morphology yet occupied a position in diet space near *Cichla*, *Micropterus*, and *Pomoxis*, whereas two smaller congeners with similar morphology, *C. semicinta* and *C.* aff. *wallacii*, had positions in diet space near sunfishes that are trophic generalists (*L. cyanellus* and *L. gulosus*). Several geophagine cichlids, including *Satanoperca* and *Geophagus* spp., were similar to *Pomoxis* spp. in morphology; however, they differed in trophic niche space (Fig. 5), with geophagines being
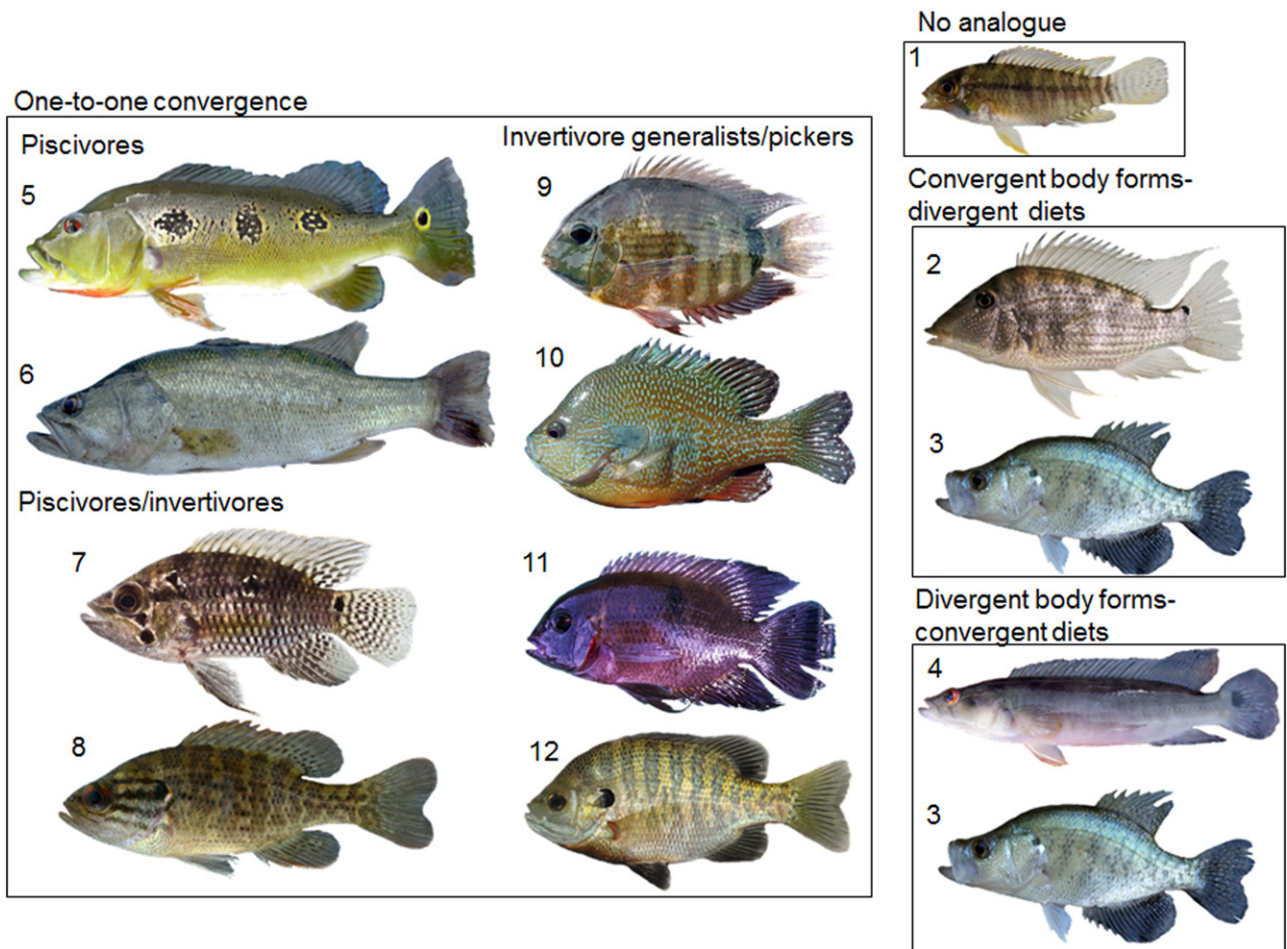
Figure 5. Schematic representation of the cichlid and centrarchid fishes that showed convergence and divergence in functional morphology and diets. The dwarf cichlids including *Apistogramma* (1) did not have an analogue among species in the centrarchid assemblages. *Satanoperca* (2) and *Pomoxis* (3) have convergent morphology but dissimilar diets; *Crenicichla* (4) and *Pomoxis* (3) have similar diets but divergent morphology; *Cichla* (5) and *Micropterus* (6) are strongly convergent pisciores; *Acaronia vultuosa* (7) and *Lepomis gulosus* (8) are strongly convergent invertivore/piscivores; and *Heros* (9), *Lepomis megalotis* (10), *Hypselecara coryphaenoides* (12), and *Lepomis macrochirus* are convergent invertivores with relatively small mouths and discoid body form.

substrate-sifting invertivores and *Pomoxis* being strongly piscivorous. These geophagine cichlids have highly protrusible jaws and relatively narrow mouth gapes that probably enhance their ability to winnow benthic invertebrates from substrate particles within the oropharyngeal chamber (López-Fernández *et al.*, 2012), whereas the highly protrusible jaws and large mouth gapes of *Pomoxis* spp. facilitate suction feeding on small, elusive prey (Caroll *et al.*, 2004).

The four perciform species assemblages revealed similar distributions of trophic position values. Estimates from dietary and isotopic data were similar and placed most sunfishes, heroine cichlids and cichlasomatine cichlids in intermediate to low trophic positions (Fig. 4). Heroine and cichlasomatine cichlid diets contained large fractions of benthic and epibenthic

invertebrates, and this finding contradicts previous studies in which several of the heroine and cichlasomatine species examined in the present study were described as detritivores (Lasso & Machado-Allison, 2000). We found the diets of these species to be dominated by benthic and epibenthic invertebrates. Among sunfishes, *L. gulosus* and *L. cyanellus* had intermediate trophic positions similar to that of the heroine cichlid *A. vultuosa*. These three trophic generalists consumed diverse prey. Strong associations between diet and trophic position also were observed for piscivorous *Cichla* and *Micropterus* (Fig. 5; highest TP values in their respective assemblages).

Although *Pomoxis* spp. and *Crenicichla lugubris* were not strongly convergent in morphology (Fig. 5), these fishes nonetheless had similar trophic positions

and occupied the same regions of diet and isotopic space. This trophic similarity can be understood in terms of the functional morphology of the mouth for prey-capture using the ram-suction mode of foraging (Wainwright *et al*., 2001). *Pomoxis* and *C. lugubris* feed on relatively small and elusive fishes. Their large mouths should increase the area of attack and highly protrusible jaws should enhance the attack velocity during ram feeding (Norton & Brainerd, 1993; Wainwright *et al*., 2001). Substrate-sifting geophagine cichlids had relatively low trophic positions that reflected the consumption of large fractions of aquatic invertebrates, such as chironomid, trichopteran, and ephemeropteran larvae (López-Fernández *et al*., 2012). The most unique diet and the lowest trophic position were observed for *L. microlophus*, a molluscivorous centrarchid. The low $\delta^{15}N$ values observed for this sunfish probably are consistent with the low trophic positions of the herbivorous and detritivorous mollusks common in its diet. Mollusks were not included among the invertebrate samples analyzed for stable isotope ratios; however, previous studies have reported that freshwater mollusks have relatively low $\delta^{15}N$ ratios (Grimaldo, Stewart & Kimmerer, 2009; Winemiller *et al*., 2011) and low trophic positions (Vander Zanden & Rasmussen, 1999) compared to most aquatic insects and crustaceans. The two cichlid assemblages did not have any molluscivores because snails and mussels were absent from the Cinaruco and Tambopata rivers, apparently as a result of the extremely low water hardness. However, a molluscivorous ecomorph has been reported among the Central American heroine cichlids within the genera *Herichthys* (Hulsey *et al*., 2008) and *Astatheros* (Winemiller *et al*., 1995) and within the South American cichlasomatine genus *Aequidens* (Winemiller *et al*., 1995).

Trophic position values were, in some instances, different according to the two methods, and we infer that estimates based on stable isotope data were more accurate. Error in diet-based trophic position estimates could have arisen from a priori and coarse-scale assignment of trophic levels for prey taxa. A potential source of bias for trophic position calculations based on stable isotope analysis could be the low number of samples used, which did not cover the range of size classes used for stomach contents analysis. In addition, there could have been an error in assigning a constant for the trophic fractionation of $\delta^{15}N$ (Post, 2002).

ECOMORPHOLOGICAL PATTERNS

The study of fish jaw functional morphology has revealed diverse mechanisms of prey capture (Motta, 1984; Norton & Brainerd, 1993; Wainwright *et al*., 2004, 2007), including suction feeding (involving expansion of the orobranchial chamber and generation of negative pressure that draws water and prey into the chamber when the mouth is opened), ram feeding (the predator overtakes and engulfs prey within the oropharyngeal chamber), and biting/manipulation (the jaws grasp the prey removing it from substratum, or are used to grasp and tear or scrape material). Strong form–function relationships in fish feeding mechanics and locomotion create great potential for convergent adaptive evolution (Winemiller, 1991). Several studies have demonstrated ecomorphological convergence across freshwater percomorph fishes (Winemiller *et al*., 1995; Ruber & Adams, 2001; Knouft, 2003; Hulsey *et al*., 2008; Carlson & Wainwright, 2010). Similarities in body and jaw shapes between several species of cichlids and centrarchids imply that these characters are adaptive for specific forms of habitat use and/or exploitation of prey of various types (Westneat & Wainwright, 1989; Liem, 1991; Norton & Brainerd, 1993; Wainwright *et al*., 2001).

Although the present study is correlative, ecomorphological axes derived from PCA and CCA have obvious functional interpretations derived from biomechanical studies in cichlids (Wainwright *et al*., 2001) and centrarchids (Caroll *et al*., 2004). Piscivorous *Cichla* and *Micropterus* species have fusiform bodies for rapid acceleration and large mouths and highly protrusible jaws for capture of elusive prey (Norton & Brainerd, 1993). *Micropterus* is phylogenetically more distant from *Pomoxis* than *Lepomis* (Near *et al*., 2005) but, in terms of functional morphology and diets, *Micropterus* is much more similar to the former (Caroll *et al*., 2004). The basal Neotropical cichlid genus *Cichla* and the geophagine genus *Crenicichla* (*C. lugubris*) present a similar case of intrafamilial convergence. In multivariate morphospace, the cichlids *Cichla* and *Crenicichla* and the centrarchids *Micropterus* and *Pomoxis* occupied a region that coincides with the ram-feeding models described by Wainwright *et al*. (2001). Ram feeders have large mouths with a greater jaw protrusion that helps to increase velocity during prey attack (Waltzek & Wainwright, 2003) and that increases the distance from which prey can be drawn into the mouth via suction (Wainwright *et al*., 2001). In combination, these trophic morphological characters are considered to increase the efficiency for feeding on elusive prey (Norton & Brainerd, 1993). The two divergent phenotypes *Pomoxis* spp. and *C. lugubris* represent an interesting case of many-to-one mapping of morphology to function (Wainwright *et al*., 2004). These species have similar diets and occupied same vertical trophic position but diverged in morphological space (Fig. 5).

Heroine and cichlasomatine cichlids and several species of sunfishes (*L. megalotis*, *L. miniatus*, *L. humilis*, *L. macrochirus*) were morphologically convergent, and species in both of these groups ingest small prey using both suction and biting modes of jaw movement (Barel, 1983; Liem, 1993; Norton & Brainerd, 1993). These fishes also possess unicuspid (in the case of cichlids) and conical (in the case of centrarchids) oral teeth that should enhance their ability to grasp prey (Casciotta & Arrata, 1993; Cook & Phillip, 2009). The cichlids *Geophagus* spp. and *Satanoperca* spp. and the centrarchids *Pomoxis* spp. occupied the same region of morphological space. These species possess highly protrusible jaws that may enhance suction (Norton & Brainerd, 1993; Wainwright *et al.*, 2001; Caroll *et al.*, 2004) and facilitate winnowing (sifting of substrate and food particles within the oropharyngeal chamber; López-Fernández *et al.*, 2012), and laterally-compressed, discoid bodies that facilitate lateral maneuverability (Caroll *et al.*, 2004). Greater protrusion of the premaxilla has accompanied the evolution of winnowing behaviour in cichlids (Hulsey & García de León, 2005; López-Fernández *et al.*, 2012), surf perches (Drucker & Jensen, 1991), and carps (Sibbing, Osse & Terlouw, 1986). Jaw protrusion therefore enhances the feeding performance not only for ram feeders (e.g. *Cichla* spp. and *Micropterus* spp.), zooplanktivores, and epibenthic gleaners that use suction (e.g. *L. macrochirus*, *Heros*), but also for benthivorous substrate sifters (e.g. *Geophagus* and *Satanoperca* species) (Wainwright *et al.*, 2001; Hulsey & García de León, 2005). In substrate-sifting geophagine cichlids, the subterminal mouth position probably is an additional feature facilitating benthic feeding (López-Fernández *et al.*, 2012). In specialized molluscivores, such as *L. microlophus*, fusion of the pharyngeal plates and large rounded molariform teeth are associated with an enhanced ability to crush hard-bodied prey (Lauder, 1983). The ability of *L. microlophus* to crush hard-shelled organisms provides it with access to an abundant food resource that is less effectively exploited by other sunfishes.

Interspecific variation in diet within fish assemblages has been attributed to mouth size (Wainwright & Richard, 1995) and body size (Keast & Webb, 1966; Gatz, 1979). Within the perciform families investigated in the present study, piscivory was correlated with fishes having large bodies as well as large mouth gapes. Similar patterns have been observed in other studies dealing with tropical cichlids (Winemiller *et al.*, 1995; Jepsen, Winemiller & Taphorn, 1997; Montaña, Layman & Winemiller, 2011) and temperate centrarchids (Keast & Webb, 1966; Hambright, 1991; Winemiller, 1991), as well as in other teleost fishes (Hugueny & Pouilly, 1999). These two genera have convergent morphology for the effective use of the ram-suction mode to capture large, elusive prey (Norton & Brainerd, 1993).

CONVERGENT EVOLUTION

Kerr & James (1975) proposed that, if environmental conditions impose constraints on adaptation, and these constraints are simultaneously expressed in morphology and ecology, then predictions can be made as to which morphological attributes are associated with a specific ecological niche and vice versa. In the case of cichlids and centrarchids, strong ecomorphological convergence indicates that the two lineages have evolved to fill similar arrays of ecological niches in their respective freshwater communities. Concordant patterns of interspecific similarity in morphology and trophic ecology in these distantly-related groups (Near *et al.*, 2012) support the hypothesis of convergent adaptive evolution (Schluter, 2000). A similar striking case of evolutionary convergence has been proposed for weakly electric South American gymnotiform and African mormyriform fishes. Despite being distantly related (Fink & Fink, 1981) and occurring in different zoogeographic regions, these fishes are phenotypically and ecologically similar in many important respects, including body form, swimming behaviour, feeding behaviour, reproductive behaviour, nocturnal activity, and the generation and reception of electric impulses (Marrero & Winemiller, 1993; Winemiller & Adite, 1997; Sullivan, Lavoué & Hopkins, 2000; Lovejoy *et al.*, 2010; Lavoué *et al.*, 2012).

Our findings are consistent with those reported in other studies revealing a strong relationship between morphology and diet in fish assemblages (Wikramanayake, 1990; Norton, 1995; Winemiller *et al.*, 1995; Motta *et al.*, 1995b; Hugueny & Pouilly, 1999; López-Fernández *et al.*, 2012) and refute the proposition proposed by Douglas & Matthews (1992) that valid ecomorphological studies should be restricted to fishes within the same family. Norton & Brainerd (1993) demonstrated convergence between tropical cichlids and temperate centrarchids in the biomechanics of feeding, and Winemiller (1991) showed that several cichlids and centrarchids occupy similar positions within the ecomorphological spaces defined by local fish assemblages in lowland streams. The present study provides additional specific evidence of convergent evolution in cichlids and centrarchids based on the analysis of morphology and trophic ecology of coexisting species from natural habitats of lowland rivers.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Main diet categories of the different cichlid and centrarchid species.