Functional diversity and trait–environment relationships of stream fish assemblages in a large tropical catchment

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SUMMARY

1. The species composition of stream fish assemblages changes across the longitudinal fluvial gradient of large river basins. These changes may reflect both zonation in species distributions and environmental filtering of fish traits as stream environments change from the uplands to the lowlands of large catchments. Previous research has shown that taxonomic diversity generally increases in larger, lowland streams, and the River Continuum Concept, the River Habitat Template and other frameworks have provided expectations for what functional groups of fishes should predominate in certain stream types. However, studies addressing the functional trait composition of fish assemblages across large regions are lacking, particularly in tropical river basins.

2. We examined functional trait–environment relationships and functional diversity of stream fish assemblages in the Río Grijalva Basin in southern Mexico. Traits linked to feeding, locomotion and life history strategy were measured in fishes from streams throughout the catchment, from highland headwaters to broad, lowland streams. Relationships between functional traits and environmental variables at local and landscape scales were examined using multivariate ordination, and the convex hull volume of trait space occupied by fish assemblages was calculated as a measure of functional diversity.

3. Although there were a few exceptions, functional diversity of assemblages increased with species richness along the gradient from uplands to lowlands within the Grijalva Basin. Traits related to swimming, habitat preference and food resource use were associated with both local (e.g. substratum type, pool availability) and landscape-scale (e.g. forest cover) environmental variables.

4. Along with taxonomic structure and diversity, the functional composition of fish assemblages changed across the longitudinal fluvial gradient of the basin. Trait–environment relationships documented in this study partially confirmed theoretical expectations and revealed patterns that may help in developing a better understanding of general functional responses of fish assemblages to environmental change.

Keywords: ecomorphology, fluvial gradient, functional diversity, habitat template, southern Mexico

Introduction

The distribution and abundance of stream fishes are influenced by many factors operating at multiple scales (Schlosser, 1987; Poff, 1997). Local-scale habitat variables, such as substratum composition, presence of pools and the amount of available cover, have been shown to correlate strongly with fish assemblage structure (Ibarra & Stewart, 1989; Fischer & Paukert, 2008; Rowe, Pierce & Wilton, 2009). Many local environmental characteristics in

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a drainage basin are shaped by larger-scale features such as underlying geology, riparian vegetation and fluvial geomorphology (Frissell *et al.*, 1986; Richards, Johnson & Host, 1996), and the role of landscape-level factors in shaping stream communities is increasingly recognised (Allan, 2004). Across catchments of large rivers, stream environments generally change in predictable ways. Stream size, hydrological variability, diversity of habitat types and availability of in-stream production sources are some key environmental variables that shift along the fluvial gradient from upland headwaters to downstream reaches (Hynes, 1970; Horwitz, 1978; Vannote *et al.*, 1980). Corresponding with these environmental shifts, the taxonomic structure of stream fish assemblages has been shown to change, and species richness typically increases along with stream size in higher order, lowland streams (e.g. Horwitz, 1978; Rahel & Hubert, 1991). Patterns of functional diversity in stream fish assemblages are expected to be similar (Schlosser, 1987), but have not been well studied across large fluvial gradients.

Previous studies have provided some theoretical expectations regarding functional diversity in streams across environmental gradients. The River Continuum Concept (RCC; Vannote *et al.*, 1980) provides a framework for predicting how aquatic communities change with longitudinal abiotic changes in large river basins. According to the RCC, changes in food sources along the fluvial continuum constrain the trophic groups of aquatic organisms within communities. Based on this concept, fish species that are generalised invertebrate feeders are expected in upstream reaches, while omnivores, detritivores, herbivores and piscivores become more abundant in larger streams further downstream in a river basin (Vannote *et al.*, 1980; Schlosser, 1987). Recently, Thorp, Thoms & Delong (2008) outlined the Riverine Ecosystem Synthesis, which incorporates previous work on hierarchical patch dynamics and describes river networks as arrays of hydrogeomorphic patches functional process zones (FPZ) instead of longitudinal continua as described in the RCC. Temporal variability and habitat complexity of these patches influence functional community structure, and patches within longitudinal zones of a basin may be no more similar than those upstream or downstream (Poole, 2002).

Townsend & Hildrew's (1994) River Habitat Template (RHT) theory also makes predictions about how stream communities change across large-scale gradients. The RHT predicts that two main features, temporal variability and spatial heterogeneity, influence the traits of species in stream communities. In streams with high temporal variability and low spatial heterogeneity (e.g. flashy headwater streams), the RHT predicts that species are more likely to have traits that confer resistance and resilience, such as small body size, streamlined shape, high fecundity and short reproductive cycles. Streams with diverse habitats and refuges during disturbances should be associated with species assemblages with a greater range of traits. Poff (1997) proposed the idea of 'landscape filters', which describes how environmental variables select for traits of species from the catchment to the microhabitat scale. For example, at the catchment scale, seasonality of flow may constrain the life history strategies of species. Progressively finer filters at the stream reach and microhabitat scales, such as riparian conditions and substratum composition, may influence the trophic and reproductive guilds present in a local species assemblage.

An emerging view in community ecology is that a focus on functional traits as they relate to environmental gradients can reveal general patterns and improve our ability to predict responses of natural communities to environmental change (McGill *et al.*, 2006; Poff *et al.*, 2006; Olden *et al.*, 2010). The aforementioned theoretical frameworks allow for explicit predictions of how functional traits of fishes respond to environmental factors at multiple scales. Testing these concepts for stream fish assemblages across large fluvial gradients has been difficult, however, as a result of limited knowledge of functional traits, and most previous studies have examined the relationships across gradients in relatively small catchments. A large-scale study by Lamouroux, Poff & Angermeier (2002) examined the relationships between reach-scale stream hydraulics, geomorphology and six functional traits related to swimming, habitat use and life history for fish assemblages in France and Virginia. They found that in both continents, these environmental variables were related to traits such as body shape, fecundity and habitat preference within stream communities. In rivers of western Africa, Tedesco *et al.* (2008) found that traits such as egg size and degree of parental care varied along a gradient of hydrological seasonality as predicted by life history theory (Winemiller, 1989; Winemiller & Rose, 1992). Other broad-scale studies have generally assigned fish species to functional groups or guilds rather than examining specific functional traits. For example, Poff & Allan (1995) found that hydrologically variable streams were more likely to contain generalists in terms of trophic guild and substratum preference. Similarly, Ibañez *et al.* (2009) found that the proportion of invertebrate feeders decreased, while the proportion of omnivores increased from upstream to downstream reaches in streams in four continents.

In this study, we examined the influence of environmental variables on the functional traits of stream fish assemblages from the highlands to the lowlands along the fluvial gradient of the Río Grijalva Basin of southern Mexico, one of the largest rivers in Mesoamerica. The broad spatial extent of the study region allowed us to examine environmental influences at local and landscape scales across a range of habitat types. First, we documented the species composition and habitat variables at multiple scales across the catchment. We then examined the relationships between functional traits of fish species and environmental gradients within the region. Finally, we measured the volume of functional trait space occupied by assemblages to gauge changes in functional diversity across the basin. Based on expectations from the RCC and previous studies of fish diversity across large river networks, we predicted that functional trait diversity would be greater in larger stream reaches in the lowlands of the Grijalva Basin and that traits associated with feeding would reflect the relative importance of food resources along the longitudinal gradient. Because our study was limited to wadeable streams, we could not explicitly test RCC predictions (i.e. comparisons across a broad range of stream orders). However, based on other studies of stream assemblages across river networks (e.g. Angermeier & Karr, 1983; Oberdorff, Guilbert & Lucchetta, 1993; Ibañez *et al.*, 2007), we expected longitudinal position would influence functional structure through RCC-related processes. Based on the FPZ concept, we anticipated that exceptions to this trend might occur where stream habitat conditions differ from general expectations based on longitudinal position (e.g. fine substrata and warm temperatures in a headwater stream in the upper basin). In accordance with the RHT, we expected smaller, flashy headwater streams to be characterised by fishes with traits related to disturbance resistance and demographic resilience, whereas larger, lowland streams would be characterised by fish assemblages containing a more diverse array of traits among species revealing greater degrees of ecological specialisation. Finally, we expected that relationships between environmental variables and fish functional traits would reflect the importance of environmental filters at multiple spatial scales.

To our knowledge, this represents the first examination of functional trait diversity and trait–environment relationships for stream fishes along the longitudinal fluvial gradient of a large tropical river basin. Patterns of stream fish assemblage structure in tropical basins may not conform to expectations based on studies in temperate regions owing to differences in climate and zoogeography. For example, higher autochthonous productivity in tropical food webs (Davies, Bunn & Hamilton, 2008) may lead to different patterns in trophic structure. Additionally, unique features of the Mesoamerican fish fauna (e.g. high endemism, paucity of primary freshwater lineages and putative adaptive radiations within the families Cichlidae and Poeciliidae) may result in assemblages ecologically distinct from those found in similar stream environments in temperate regions.

Methods

Study region and field data collection

The Río Grijalva begins in Guatemala and flows through the states of Chiapas and Tabasco in southern Mexico. As the Grijalva nears the Gulf of Mexico in Tabasco, it joins the Río Usumacinta, and together they form the largest river in Mesoamerica. Approximately 115 fish species from 31 families have been documented in the region, and an estimated 36% of species are endemic (Miller, 2005). This study focusses on wadeable streams within the Grijalva Basin above its confluence with the Río Usumacinta, an approximately 60 000-km^{-2} region (Fig. 1). The environmental characteristics of stream habitats within the Grijalva Basin change markedly along a longitudinal gradient from the mountainous Sierra Madre de Chiapas to the coastal plains in Tabasco. Upland, high-gradient streams in the headwaters give way to broad and sinuous channels in the middle sections, and ultimately, the channels are transformed into a mosaic of wetlands before draining into the Gulf of Mexico (Hudson *et al.*, 2005). Upland stream habitats are more environmentally harsh, with high temporal variation in flow, low spatial heterogeneity and relatively few low-velocity microhabitats. Further downstream on the fluvial gradient, stream habitats become progressively more stable, with more low-velocity pools, more structurally complex microhabitats and a broader prey resource base. We designated the area above the Angostura reservoir as the 'upper Grijalva', the portion of the catchment below Angostura and above the Malpaso reservoir as the 'middle Grijalva', and the section below Malpaso to the confluence with the Río Usumacinta as the 'lower Grijalva'.

We conducted this study in 20 streams across a range of landscapes within the Grijalva Basin. Study sites were selected to ensure roughly equal representation in upper, middle and lower portions of the basin with data from a range of stream orders (from small headwaters to broad, high-order, major tributaries). We sampled the streams during March and April of 2008 and 2009. These months
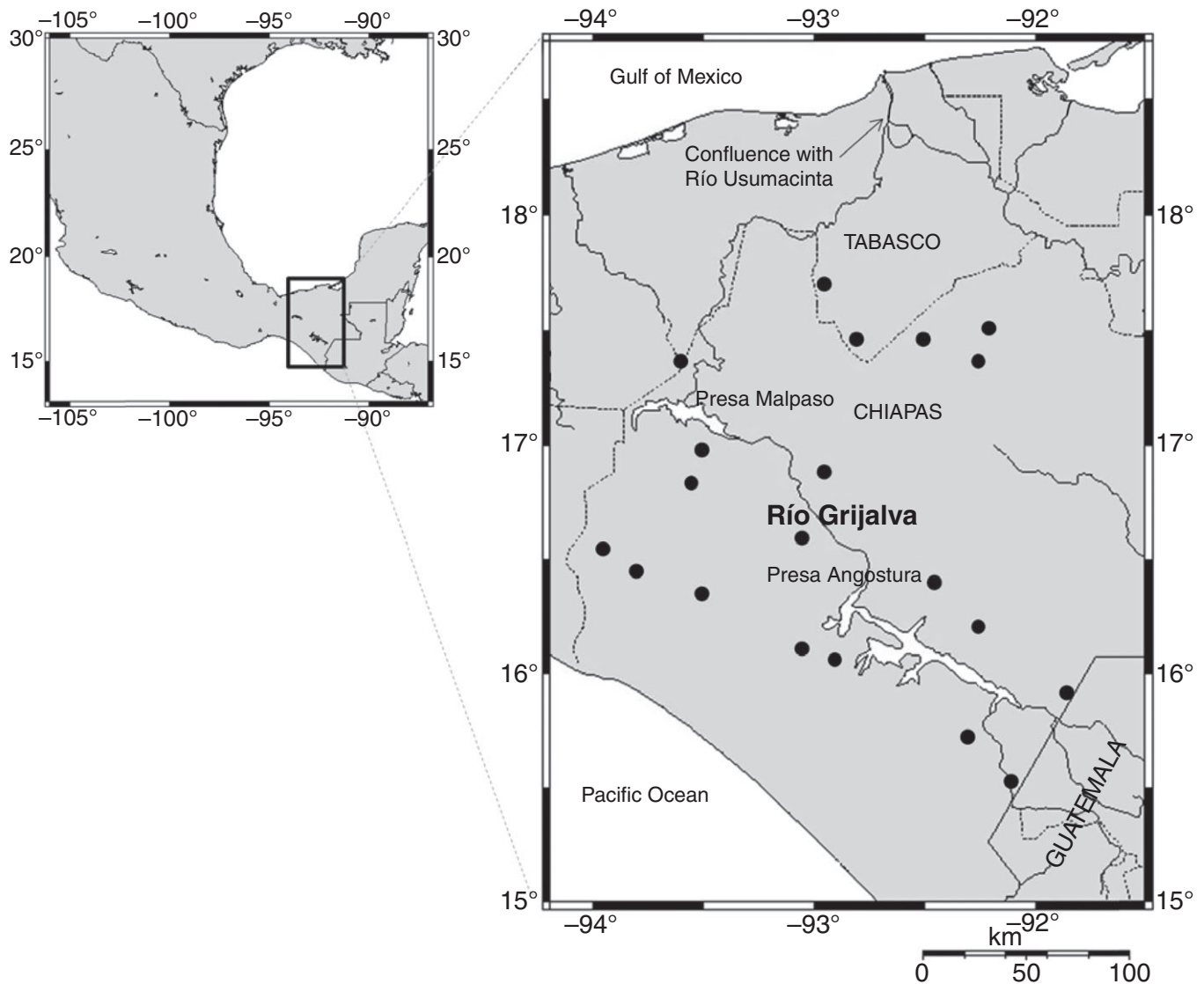
Fig. 1 Map of the study region, the Río Grijalva Basin, in Chiapas and Tabasco, Mexico. Solid dots indicate locations of surveyed stream reaches.

are within the dry season for this region, a time when flows are lower and fish can be captured more efficiently. At each survey site, a 200-m stream reach encompassing all available macrohabitat types (e.g. pools, runs and riffles) was designated for fish collection and local habitat measurements. Within each study reach, fishes were collected by performing a minimum of six seine hauls of 10 m (seine dimensions = 5 × 2 m, 5-mm mesh). Where appropriate, sampling was supplemented using a cast net (2-m diameter, 1-cm mesh). In sites with rocky substratum where seining was inefficient, fishes were sampled using a backpack electrofisher (Smith-Root Model LR-24). Electrofishing was performed with a single pass moving upstream across the entire study reach. As a result of the diversity of habitat types across this large region, multiple fish capture techniques were necessary (e.g. seining would have been likely to miss key components of local assemblages in reaches strewn with cobble and boulders), but care was taken to ensure that nearly the same effort was expended within each 200-m study reach. We assume that capture efficiency and estimates of abundance per reach were directly comparable among sites. Captured fishes were identified, counted and either released into the habitat or preserved in 10% buffered formalin to serve as taxonomic vouchers and to provide specimens for morphological and life history analyses. Preserved specimens were deposited in the museum collection of El Colegio de la Frontera Sur in San Cristobal de Las Casas, Chiapas.

At each study site, 34 local habitat variables were measured (Table 1). Prior to fish sampling, water temper-

Table 1 Local-scale and landscape-scale environmental variables recorded for Río Grijalva study sites

Category	Abbreviation	Variable
Substratum	BEDROCK	Per cent of substratum – bedrock
	LG_BLDR	Per cent of substratum – large boulders (>45 cm)
	SM_BLDR	Per cent of substratum – small boulders (25–45 cm)
	COBBLE	Per cent of substratum – cobble (6–25 cm)
	GRAVEL	Per cent of substratum – gravel (2–60 mm)
	SAND	Per cent of substratum – sand (0.06–2 mm)
	MUDSILT	Per cent of substratum – mud or silt (<0.06 mm)
	GRV_LRG	Per cent of substratum – gravel or larger
Algae/macrophytes	ALGAE_AB	Abundance of algae in study reach (scored as abundant, common, rare or absent)
	MCRPH_AB	Abundance of aquatic macrophytes in study reach (scored as abundant, common, rare or absent)
In-stream cover	STRM_COV	Visually estimated per cent cover
	FILA_ALG	Per cent of cover – filamentous algae
	MACRPHYT	Per cent of cover – aquatic macrophytes
	LWD	Per cent of cover – large woody debris
	SWD	Per cent of cover – small woody debris
	ROOTS	Per cent of cover – submerged roots
	OVR_VEG	Per cent of cover – overhanging terrestrial vegetation
	UNDERCUT	Per cent of cover – undercut banks
	LEAFPACK	Per cent of cover – submerged leaf packs
	BOULDER	Per cent of cover – boulders and other large substrata
Stream morphology	WETWIDTH	Wetted width of stream (averaged across transects)
	THAL_DEP	Thalweg depth (averaged across transects)
	NO_RIFF	Number of riffles in study reach
	POOL_WID	Maximum pool width
	POOL_DEP	Maximum pool depth
	VELDEPTH	Velocity/depth regime score (optimal, suboptimal, marginal or poor)
Local riparian buffer	BUFFER	Width of riparian buffer (averaged across transects)
	CANOPY	Per cent of stream shaded by tree canopy (measured with densitometer)
Water parameters	DO	Instantaneous dissolved oxygen (mg L^{-1})
	PH	pH
	SPCOND	Specific conductivity (μs)
	SALINITY	Salinity (ppt)
	TEMP	Water temperature (°C)
Landscape-scale variables	ELEV	Elevation (m)
	LAT	Latitude (decimal degrees)
	LON	Longitude (decimal degrees)
	PRECIP	Annual precipitation in catchment (mm)
	STRM_ORD	Stream order
	MAIN_DIS	Distance to main stem of Río Grijalva (km)
	FOREST	Per cent forested land in catchment
	POP_DEN	Mean population density in catchment (people/km^{-2})

ature (°C), dissolved oxygen (mg L^{-1}), specific conductivity (μs) and salinity (ppt) were measured using a hand-held meter (YSI model 85). Average wetted width, average depth and thalweg depth were calculated based on the measurements taken across three transects within the study reach. Water velocity (m s^{-1}) was measured at 60% depth at ten evenly spaced points across each transect using a portable electromagnetic flow meter (Marsh-McBirney Flo-Mate Model, 2000). Depth and water velocity measurements were used to calculate a velocity–depth regime score reflecting the diversity of flow and depth habitats available within the study reach. The score is based on the number of different velocity–depth regimes present (scored 1–20) following U.S. Environmental Protection Agency stream bioassessment protocols (Barbour *et al.*, 1999). Canopy cover was measured using a spherical densiometer at four locations across each transect to calculate the average per cent cover. To characterise substratum composition, the percentage of bedrock, large boulders (>45 cm diameter),

small boulders (26–45 cm), cobble (6–25 cm), gravel (2–60 mm), sand (0.06–2 mm) and mud/silt (<0.06 mm) were estimated visually. We also estimated the proportion of in-stream structural cover provided by rocks, large and small woody debris, roots, leaf packs, aquatic vegetation, overhanging terrestrial vegetation, algae, undercut banks and artificial structures. The overall average per cent of stream habitat containing structural cover was estimated visually for each reach. The number of riffles within the study reach, maximum pool depth and maximum pool width also was recorded. We scored the abundance of algae and aquatic macrophytes within the reaches as abundant (3), common (2), rare (1) or absent (0). The width of the riparian buffer on each bank was estimated in metres.

Topographic maps, publicly available databases and field observations were used to compile eight additional environmental variables at the landscape or regional scale (Table 1). We measured geographical position (latitude and longitude in decimal degrees) using a handheld global positioning system unit at the time of in-stream and riparian habitat data collection. Elevation, stream order and distance to the main stem of the Rio Grijalva were measured using 1 : 250 000 scale topographic maps available from the Mexican federal agency for geography and statistics (Instituto Nacional de Estadística y Geografía, INEGI). Annual precipitation data were obtained from Mexican federal databases (Comisión Nacional de Agua, http://smn.cna.gob.mx). Percent forest cover within the catchment was estimated from digital maps of land cover also obtained from INEGI (http://www.inegi.org.mx). Population density in the surrounding catchment was estimated from maps produced by the United Nations Food and Agriculture Organization.

Functional traits

We measured 28 functional traits (Table 2) of at least three adult individuals of each fish species from each of the 20 stream survey sites. These traits were chosen because they have well-known relationships with feeding, habitat use, swimming behaviour or life history strategies of stream fishes. For example, traits such as gape size, mouth position, head length and gut length relate to food resource use in fishes (Gatz, 1979). Morphological features related to habitat preference and locomotion include relative body depth, fin dimensions and dimensions of the caudal peduncle (Gatz, 1979; Webb, 1984). We measured egg diameter and mean clutch size to reflect interspecific differences in life history strategies (Winemiller & Rose, 1992). Traits were defined and measured

following the methods of Winemiller (1991) for morphological traits and Winemiller & Rose (1992) for life history traits. For species with sexual dimorphism in these traits (e.g. the anal fin of poeciliids), only females were measured. All length measurements were made to the nearest 0.1 mm using vernier callipers. Because functional traits sometimes are not informative for community-level analyses if there is substantial within-species variation in trait values (McGill *et al.*, 2006; Poff *et al.*, 2006), we confirmed that interspecific variation was significantly greater than intraspecific variation by performing an *F*-test on the variance ($P < 0.05$) of all traits before carrying out multivariate analyses. By directly measuring species traits from each assemblage rather than assigning a single value or relying on published values, we aimed to avoid a common shortcoming in functional trait studies whereby unrepresented intraspecific variation may contribute to weak trait–environment relationships (Brind'Amour *et al.*, 2011). While many studies of functional traits in stream fishes and other groups rely on categorical traits or functional groups or guilds (e.g. Goldstein & Meador, 2004; Ibañez *et al.*, 2007), we chose to use a broad suite of measurable, quantitative traits to characterise multiple niche dimensions and to allow for the use of recently developed multidimensional methods of estimating functional diversity (Villeger, Mason & Mouillot, 2008; Laliberte & Legendre, 2010).

Statistical analyses

We quantified among-site differences in taxonomic assemblage structure by performing non-metric multidimensional scaling (NMS) on log-transformed species abundances. Because it avoids assumptions of linearity, NMS is considered well suited for analysing patterns in assemblage structure without some of the problems associated with other commonly used methods (McCune & Grace, 2002). We used Bray–Curtis dissimilarity (BCD) as the distance measure and retained a three-dimensional solution because stress values were substantially greater when only two axes were included in the ordination. A principal components analysis (PCA) was performed on log-transformed environmental variables (local and landscape scales) to identify the primary environmental gradients among stream sites.

To examine among-species differences in functional traits, a PCA was performed on the matrix of species traits. Because body size has a substantial influence on trait values, all traits were regressed against standard length and residuals were used as the trait values for the PCA. Mouth position, egg diameter and clutch size were

Table 2 The 27 functional traits used for Río Grijalva fish assemblages with measurement methodology. Trait definitions and functional categories follow Gatz, 1979; Webb, 1984; Winemiller, 1991; Winemiller & Rose, 1992; and Sibbing & Nagelkerke, 2001;

Trait	Trait code	Trait definition	Functional category
Maximum standard length	MAX_SL	Maximum standard length from the populations in this study and published records	Habitat use, feeding, life history strategy
Head length	HEAD_L	Distance from the tip of the jaw to the posterior edge of the operculum	Feeding
Head depth	HEAD_D	Vertical distance from dorsum to ventrum passing through the pupil	Feeding
Oral gape	GAPE	Vertical distance measured inside of fully open mouth at tallest point	Feeding
Mouth position	MOUTH_P	The angle between an imaginary line connecting the tips of the open jaws and an imaginary line running between the centre of the pupil and the posterior-most vertebra (e.g. 90° representing a terminal mouth)	Feeding, habitat use
Eye position	EYE_POS	Vertical distance from the centre of the pupil to the ventrum	Habitat use
Eye diameter	EYE_D	Horizontal distance from eye margin to eye margin	Feeding
Snout length	SNT_L	Distance from the pupil to the tip of the upper jaw with mouth shut	Feeding
Snout protrusion	SNT_PR	Additional distance from the pupil to the tip of the upper jaw with mouth fully open and extended	Feeding
Body depth	BOD_D	Maximum vertical distance from dorsum to ventrum	Locomotion, habitat use
Body width	BOD_W	Maximum horizontal distance from side to side	Locomotion
Caudal peduncle length	PED_L	Distance from the posterior proximal margin of the anal fin to the caudal margin of the ultimate vertebra	Locomotion
Caudal peduncle depth	PED_D	Minimum vertical distance from dorsum to ventrum of caudal peduncle	Locomotion
Caudal peduncle width	PED_W	Horizontal width of the caudal peduncle at midlength	Locomotion
Body depth below midline	DEP_MID	Vertical distance from midline to ventrum	Locomotion, habitat use
Dorsal fin length	DORS_L	Distance from the anterior proximal margin to the posterior proximal margin of the dorsal fin	Locomotion
Dorsal fin height	DORS_HT	Maximum distance from the proximal to distal margin of the dorsal fin (excluding filaments)	Locomotion
Anal fin length	ANAL_L	Distance from the anterior proximal margin to the posterior proximal margin of the anal fin	Locomotion
Anal fin height	ANAL_HT	Maximum distance from proximal to distal margin of the anal fin	Locomotion
Caudal fin depth	CAUD_D	Maximum vertical distance across the fully spread caudal fin	Locomotion
Caudal fin length	CAUD_L	Maximum distance from proximal to distal margin of the caudal fin (excluding filaments)	Locomotion
Pectoral fin length	PEC_L	Maximum distance from proximal to distal margin of pectoral fin	Locomotion, habitat use
Pelvic fin length	PELV_L	Maximum distance from the proximal to distal margin of the pelvic fin	Locomotion, habitat use
Gut length	GUT_L	Length of gut from the beginning of the oesophagus to the anus (extended without stretching)	Feeding
Gill raker length	RAKER_L	Length of the longest gill raker	Feeding
Egg diameter	EGG_D	Mean diameter of mature (fully yolked) oocytes	Life history strategy
Clutch size	CLUTCH	Average clutch size (from published accounts for some species)	Life history strategy

not correlated with body size, so log-transformed values for these variables were used instead of residuals. The PCA was performed using the mean-transformed values for each functional trait for each species (averaged across sites). The NMS and PCA analyses were carried out using PC-ORD software version 5.2 (MjM Software, Gleneden Beach, OR, U.S.A.).

An RLQ analysis was used to relate patterns of environmental differences and functional traits of fish assemblages among sites. RLQ is a multivariate technique based on ordinations of three separate matrices (species abundance, environmental variables and species traits) that has been shown to be a powerful tool for studying trait–environment relationships (e.g. Mellado Díaz, Suarez Alonso & Vidal-Abarca Gutiérrez, 2008; Brind'Amour *et al.*, 2011). RLQ was proposed by Doledec *et al.* (1996) as an extension of co-inertia analysis to relate species traits directly to environmental characteristics through ordination of the matrix of species abundance for sites. The first step in RLQ analysis was the separate ordination of the species abundance, environmental variables and species traits matrices. The 'R' matrix containing the log-transformed environmental variables for the study sites was analysed with PCA. The 'L' matrix contains the log-transformed species abundances for sites, and correspondence analysis (CA) was used to identify gradients in

taxonomic assemblage structure following the RLQ specifications. Next, the functional traits of species in the 'Q' matrix were analysed using PCA on trait residuals. The significance of the relationship between the environmental variables (R) and functional traits of species (Q) was tested with a Monte Carlo permutation test with 1000 random permutations of the rows of both the functional traits and environmental variables matrices (Doledec *et al.*, 1996). The ADE-4 package (Dray & Dufour, 2007) for R version 2.10.1 (The R Foundation for Statistical Computing) was used for all analyses associated with the RLQ.

Trait diversity was calculated for each fish assemblage using three multidimensional functional diversity indices that reflect functional trait-space occupation, functional evenness and functional divergence as described by Villeger *et al.* (2008). The multivariate volume of trait space occupied by each local fish assemblage was measured using the convex hull volume method of Cornwell, Schwilk & Ackerly (2006). Because trait dimensions cannot be greater than the number of species when calculating the convex hull volume for local assemblages, we used the scores for the first six PC axes from the functional traits PCA for species' traits. These calculations were performed with the Quickhull algorithm (Barber, Dobkin & Huhdanpaa, 1996) in MATLAB software (Mathworks Inc., 2009). Functional evenness, which describes the evenness of the distribution of species in functional trait space, was calculated following the study by Villeger *et al.* (2008). Functional divergence, which describes how abundance is distributed in relation to the centre of gravity of the functional trait space of a community, was calculated using the FDiv equation of Villeger *et al.* (2008). The FD package (Laliberte & Legendre, 2010) for R version 2.11.1 (R Foundation for Statistical Computing, 2010) was used to calculate functional evenness and divergence.

Results

Taxonomic assemblage structure

A total of 33 species was collected from the streams sampled in our study region (Table S1). Local stream fish assemblages were dominated by the Cichlidae and Poeciliidae, the two families that dominate the freshwater ichthyofauna of Mesoamerica. Non-native tilapia (*Oreochromis* species, family Cichlidae) were present at five sites in the middle Grijalva region. Species richness ranged from 1 in the high-elevation Río Lajas to 14 in one middle Grijalva stream and one lower Grijalva

stream. Species richness was generally greater in assemblages further downstream along the south-north fluvial gradient of the Grijalva Basin. A few species were collected throughout the basin (e.g. *Astyanax aeneus* Günther, *Rhamdia quelen* Quoy & Gaimard); however, patterns of species turnover were apparent from uplands to lowlands owing to longitudinal zonation in species distributions. Four cichlid species, *Paraneetroplus hartwegi* (Taylor & Miller), '*Cichlasoma*' *grammodes* (Taylor & Miller), *Amphilophus macracanthus* (Günther) and '*Cichlasoma*' *trimaculatum* (Günther), were found only in streams within the upper and middle Grijalva regions. Further downstream in the basin, these species were replaced by lowland cichlids such as '*Cichlasoma*' *salvini* (Günther), *Theraps intermedius* (Günther), *Paraneetroplus bifasciatus* (Steindachner) and *Thorichthys* species. Among poeciliids, *Poecilia sphenops* (Valenciennes) and *Poeciliopsis* species were abundant in communities in the upper and middle reaches, whereas a more diverse suite of species including *Poecilia mexicana* (Steindachner), *Heterandria bimaculata* (Heckel), *Belonesox belizanus* (Kner), *Xiphophorus hellerii* (Heckel) and *Priapella* species were collected in lowland streams. Two killifish species, *Profundulus labialis* (Günther) and *Profundulus punctatus* (Günther), were collected only in higher elevation streams in the upper and middle Grijalva.

The NMS analysis identified three axes that explained 89.5% of the variance in abundance of species among sites (Fig. 2). Sites appear to separate on the first axis (37.5% of variance) according to elevation and position along the fluvial gradient. Sites plotting on the left side of axis 1 had the lowest species richness and contained highland species such as *P. hartwegi*, *C. grammodes* and *Profundulus* species. Local fish assemblages plotting on the right side of the first axis were more species rich and contained lowland species such as *Atherinella alvarezi* (Díaz-Pardo), *P. mexicana* and *Thorichthys* species. The second axis (33.4% of variance) appeared to separate middle Grijalva sites dominated by sand substratum (high scores on axis 2) from sites in the upper and lower regions with rocky substratum (low scores on axis 2). Species assemblages that plotted high on axis 2 contained *C. salvini* and *Poecilipsis fasciata* (Meek). Species preferring habitats with coarse substratum, such as *Theraps lentiginosus* (Steindachner), were more abundant in stream reaches with low scores on axis 2. The third axis (18.6% of variance) revealed a gradient that contrasted dryer regions that had higher abundances of *P. labialis*, *A. macracanthus* and *P. fasciata* to wetter zones characterised by species such as *T. intermedius* and *X. hellerii*.
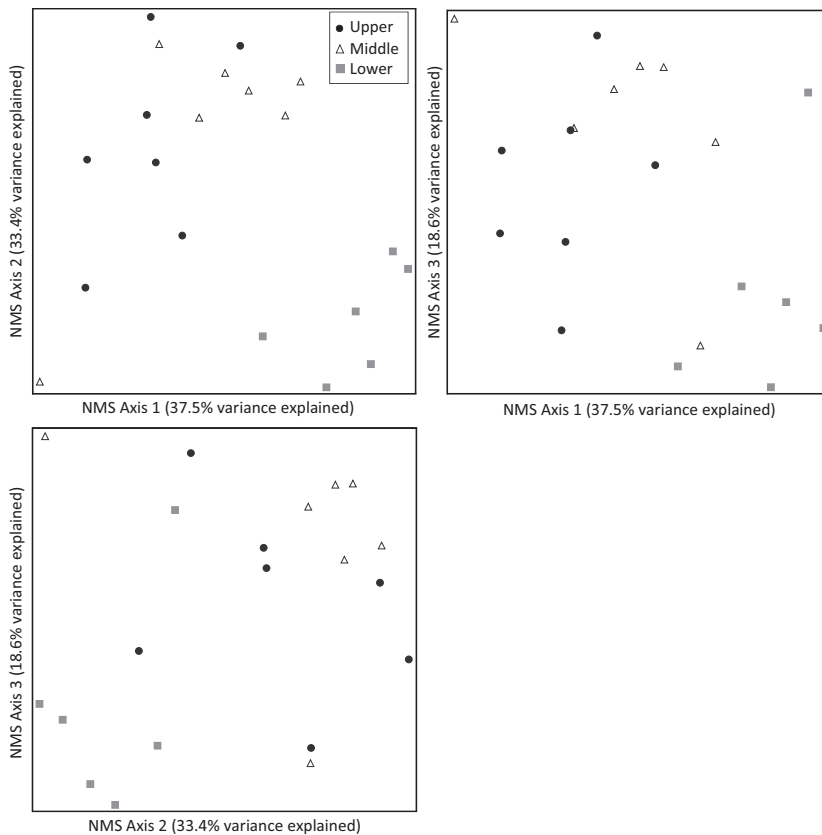
Fig. 2 NMS ordination of Río Grijalva stream reaches based on species composition of fish assemblages.

Trait–environment relationships

Environmental characteristics of stream habitats within the Grijalva Basin varied widely along the longitudinal gradient from the highlands to the lowlands. Streams in the lower Grijalva were largest, with mean wetted channel width of 20 m, larger pool habitats, a mixture of rocky and sandy substrata and more in-stream structures. Highland streams in the upper Grijalva were smaller (mean wetted width = 9 m), had rocky substrata and small pools or else lacked pools entirely. Middle Grijalva streams were also generally narrow (mean wetted width = 11 m) with more riffle habitats, few small pools and substrata dominated by sand and gravel. The first three axes of the PCA of environmental variables explained 48.1% of variation among sites (Fig. 3). The dominant gradient (PC1, 23.6% of variance) was most strongly associated with substratum type, depth and the diversity of flow–depth regimes. Sites with high scores on axis 1 had sandy substrata and relatively shallow channels with small pools or lacking pool habitat. These sites were mostly within the middle Grijalva region, but included some streams in the upper and lower sections. Sites with low scores on axis 1 had rocky substrata, more diverse mesohabitats and deeper channels. Most streams in the lower Grijalva had negative

scores on axis 1. The second gradient (PC2, 12.8% of variance) revealed a gradient that contrasted sites with more forest cover in the landscape, wider riparian buffers, more riffle habitats and more in-stream cover in the form of wood and leaves with sites that had less forest cover, wider channels and more aquatic macrophytes. The third axis (11.7% of variance) contrasted sites on the basis of elevation, latitude, precipitation, distance to the Grijalva main stem, human population density and presence of filamentous algae turfs.

PCA performed on functional traits resulted in two axes that explained 66.3% of variance among species (Fig. 4). The primary axis (PC1, 49.2% of variance) largely reflected differences in head length and depth, body depth, fin lengths and eye diameter. Cichlid species with relatively large heads and snouts, long fins and deep bodies had low scores on axis 1. Catfishes (*Rhamdia* spp.) and killifishes (*Profundulus* spp.) have relatively streamlined bodies, short fins and small eyes, and had high scores on axis 1. Axis 2 (17.1% of variance) contrasted species with different life history strategies (e.g. egg diameter, clutch size) as well as differences in gill raker length, mouth position and maximum body size. The two characid species have large clutch sizes, small eggs and relatively longer gill rakers, and these species had high
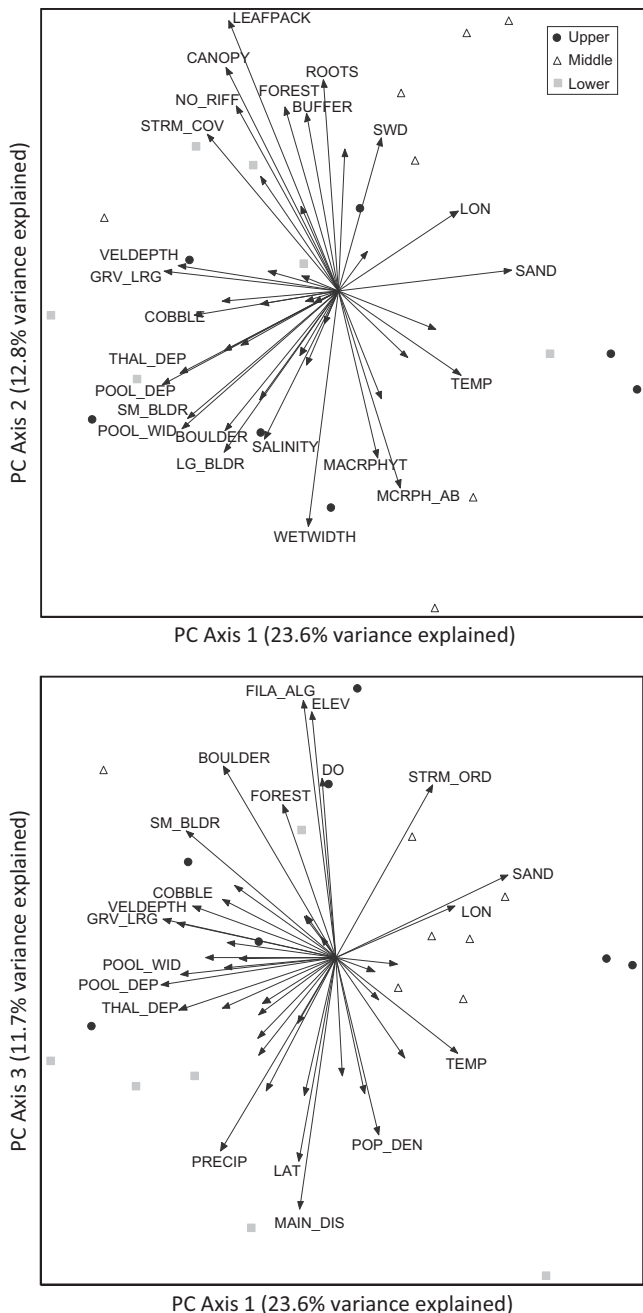
Fig. 3 PCA ordination of Río Grijalva stream reaches based on local-scale and landscape-scale environmental variables. Environmental variables labelled on the joint plots have correlation coefficients ≥ 0.4.

scores on axis 2. Poeciliid species, which have relatively small clutches of large eggs, small body sizes and upturned mouths, had low scores on axis 2. Axis 3 (8.8% of variance) reflected a gradient of trophic traits (e.g. differences in gape size, snout protrusion and gut length). Species with relatively long snouts, larger gapes and relatively short gut lengths had high scores on axis 3. These species, including *B. belizanus*, *C. grammodes* and

T. lentiginosus, tend to feed on macroinvertebrates or other fishes. Herbivorous fishes, such as *Oreochromis* species and *Poecilia* species, have very long intestines and had the lowest scores on axis 3.

The first two axes of the RLQ accounted for 33.8% and 19.3%, respectively, of the total variance in the matrix that related the environmental characteristics of sites to the functional traits of species. The permutation test showed that the relationship between functional traits and environmental variables was greater than expected at random given the regional species pool, but the relationship was not considered statistically significant ($P = 0.09$, 1000 permutations). The first RLQ axis corresponded with changes in latitude, elevation and climate corresponding with the longitudinal fluvial gradient of the Grijalva (Fig. 5). Environmental variables with high positive correlations with the first axis included elevation, per cent sand in substratum and longitude. Annual precipitation, latitude, pool and channel depth, and proportion of rocky substratum had high negative correlations with RLQ axis 1. Gape and body width of species were positively associated with the high elevation, sandy streams on axis 1. Traits plotted on the opposite end of axis 1 (lower on the fluvial gradient with wetter climates, deeper habitats and rocky substratum) included larger eye diameter, deeper body and longer head, snout and fins. Sites with more riffle habitat, abundant in-stream cover and a higher percentage of forest cover in the landscape were positively associated with RLQ axis 2. Traits correlated with RLQ axis 2 include gill raker length, egg diameter and mouth position (higher scores on RLQ axis 2 were associated with more inferior mouth positions). Environmental variables associated negatively with RLQ axis 2 included stream width, aquatic macrophyte abundance, pH and temperature. Functional traits that correlated with these variables on axis 2 included gut length, caudal peduncle width, body depth below the midline, body width and clutch size.

Functional diversity along the fluvial gradient

The volume of functional trait space occupied by fish assemblages generally increased along with species richness ($R^2 = 0.75$, $P < 0.01$) from the highlands in the south to the lowlands in the north on the fluvial gradient of the Grijalva Basin (Fig. 6). Sites with the largest convex hull volumes of functional trait space as well as highest species richness were in the lower Grijalva region. Streams with similarly high species richness in the middle Grijalva had lower functional richness, indicating that faunal shifts in the region affected the functional space occupied by fish
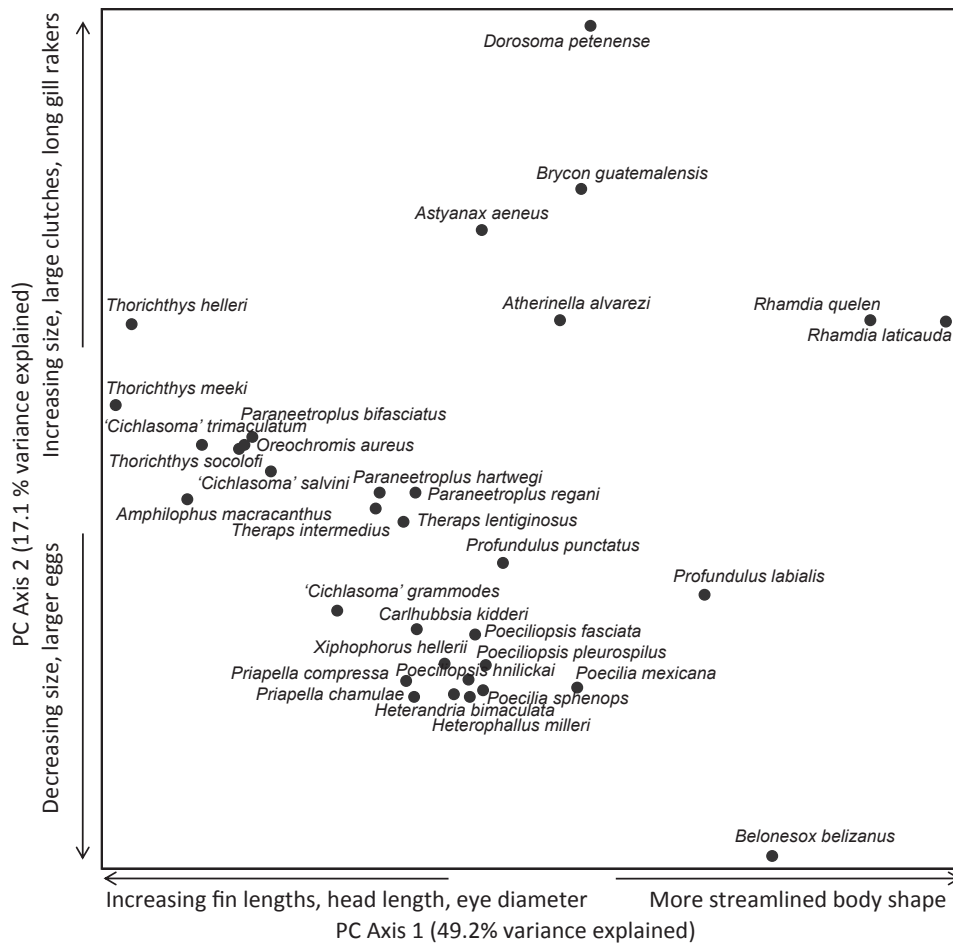
Fig. 4 PCA ordination of functional traits defining the position of Río Grijalva fish species in two dimensions of functional trait space. Traits used to characterise the two axes had correlation coefficients ≥0.25.
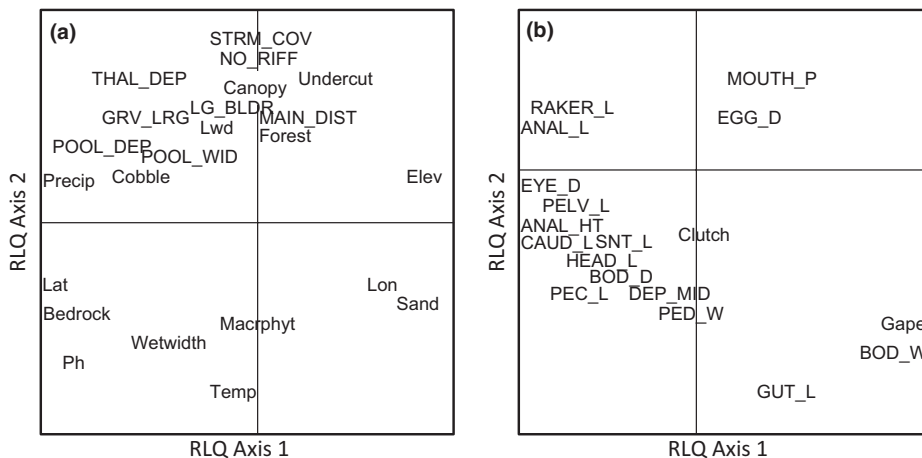

Fig. 5 Ordination of RLQ scores of environmental variables and functional traits of Río Grijalva fish species. See Tables 1 and 2 for environmental variables and functional traits that correspond to abbreviations.

assemblages. The lower Grijalva streams that had the fewest species also had disproportionately lower functional diversity. These sites lacked certain lowland species, such as *B. belizanus* and *Thorichthys helleri* (Steindachner), which are ecologically and morphologically distinctive. Functional evenness, a measure of regularity and spacing
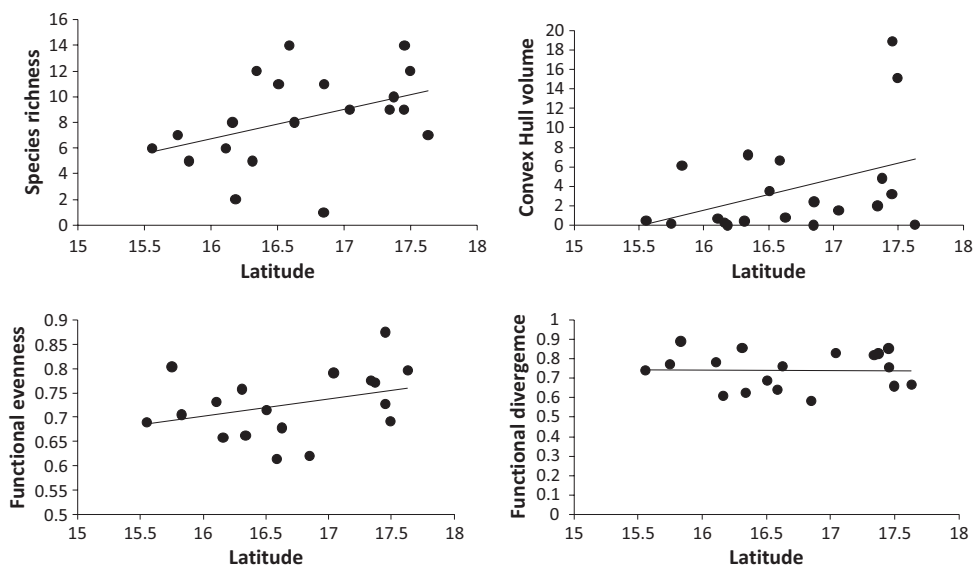
Fig. 6 Regression of species richness and three indices of functional diversity on latitude for the Río Grijalva Basin. Latitude corresponds to a great extent with the fluvial gradient of the Río Grijalva, which flows from south to north.

between species in functional trait space, was generally higher in more species-rich streams positioned lower in the fluvial gradient. Several streams with low species richness in the highlands also had high functional evenness despite having a lower range of trait values (smaller volume in trait space). There was no relationship between functional divergence and elevation. Hence, the degree of average species divergence from the centre of trait space did not increase in species-rich lowland assemblages, even though total functional trait diversity was greater.

Discussion

As shown for other large catchments, stream fish assemblages within the Río Grijalva Basin displayed patterns of longitudinal zonation in structure. Faunal turnover was apparent as we examined fish assemblages from the highlands in southern Chiapas to the more mesic lowlands of the Grijalva Basin. Ordination of stream sites based on species composition revealed that differences in species assemblage structure corresponded with the position of streams along the fluvial gradient. In general, species richness increased with increasing latitude and decreasing elevation along the fluvial gradient, a finding consistent with patterns observed for fish assemblages in rivers and streams globally. Zonation in distribution of fishes along the fluvial gradient of large river basins in other regions has been related to differences in climate, geology, disturbance frequency, stream hydraulics and habitat size that correspond with fluvial position in the

catchment (e.g. Horwitz, 1978; Ibarra & Stewart, 1989; Hoeinghaus, Winemiller & Taphorn, 2004; Esselman, Freeman & Pringle, 2006). In the Grijalva Basin, faunal zonation seems to follow regional gradients in climate, elevation, stream size and substratum composition. Species richness has been shown to increase from upstream to downstream along river gradients in both temperate and tropical regions (e.g. Horwitz, 1978; Rahel & Hubert, 1991; Edds, 1993; Gerson Araujo, Carvalho Teixeira Pinto & Pires Teixeira, 2009). Streams located further downstream are expected to support more diverse fish assemblages as they become larger, warmer, more hydrologically stable and more spatially heterogeneous (Schlosser, 1987). Migration from main-stem channel habitats also can contribute to higher species richness in streams located further downstream along a fluvial gradient (Osborne & Wiley, 1992; Hitt & Angermeier, 2006).

In this study, we found that a variety of environmental variables at multiple scales were correlated with aspects of fish assemblage structure. The dominant environmental gradient influencing functional and taxonomic structure of fish communities (highest correlations with RLQ axis 1) separated sites according to latitude, elevation and climate, factors that are spatially intercorrelated within the Grijalva Basin. Important local-scale environmental differences among sites also occurred along this gradient and appeared to influence assemblage structure. These local factors were substratum type and presence of pool habitats, with streams further downstream in the fluvial gradient characterised by rockier substrata and wider,

deeper pools. Other important local-scale environmental influences revealed by the RLQ analysis included the amount of in-stream structure, number of riffles, stream depth and canopy cover. The amount of forest in the catchment was correlated with these variables and most probably influenced channel canopy cover and the amount of in-stream cover provided by woody debris. Stream width and abundance of aquatic macrophytes were negatively correlated with these variables and also were strongly associated with fish assemblage structure.

The PCA based on species traits revealed that principal functional differences among species were associated with locomotion and habitat use (fin lengths, body depth, caudal peduncle dimensions), trophic ecology (gill raker length, snout length and protrusion, head length, eye diameter, gut length) and life history strategy (egg diameter, clutch size). Results of the RLQ analysis showed that differences in the trait composition of local assemblages were related to environmental differences among stream sites. Small, high-elevation streams lacking pool habitats contained fish species with more streamlined bodies. This was consistent with expectations based on the RHT (Townsend & Hildrew, 1994), which predicts that fishes with more streamlined body shapes will be abundant in high-elevation streams because these forms are more resistant to the fluctuating hydrology typical of headwater streams. Streams at lower elevations in the fluvial gradient tended to have more pool habitat and deeper channels, experienced more rainfall and tended to contain fishes with longer fins, longer gill rakers, deeper bodies and larger eyes. Longer gill rakers are associated with filter feeding (Gatz, 1979), which is expected to be more common in downstream reaches based on the RCC and findings of Poff & Allan (1995). Species with deeper bodies and longer fins are expected to be common in lowland streams with more pool habitats because such traits are associated with fine-scale manoeuvring in low-velocity habitats (Gatz, 1979; Webb, 1984). Lamouroux et al. (2002) also found that in Europe and North America, stream reaches with more pool habitats supported proportionally more species with deep, non-streamlined bodies. This suggests an important role for reach-scale filtering of traits by hydrological and geomorphological characteristics as described by Poff (1997).

Species occurring in streams with greater in-stream structure, deeper channels, greater canopy cover and more forested catchments had larger eggs and smaller clutch sizes. This pattern in reproductive traits corresponded with RLQ axis 2, and there was no clear relationship between these traits and the overall fluvial gradient (RLQ axis 1). Thus, RHT predictions of larger clutch size and smaller egg size (traits often associated with demographic resilience; but see discussion of the periodic life history strategy in Winemiller & Rose, 1992; Winemiller, 2005) in upstream reaches were not confirmed. The lack of a clear relationship between reproductive traits and position in the catchment was probably due to the widespread distribution of poeciliid species, live-bearing fishes with relatively large eggs and small clutch sizes, throughout the entire basin. Most poeciliids would be characterised as opportunistic strategists according to the Winemiller & Rose's (1992) gradient of primary life history strategies; opportunistic strategists should have high demographic resilience that enhances success in frequently disturbed habitats, such as headwater streams subject to scouring flash floods or shallow, marginal habitats of lowland rivers having broad floodplains. Fishes with long intestines were more abundant in wider streams with open canopies and more abundant aquatic macrophytes. Long intestines in fishes are associated with herbivory and detritivory (Gatz, 1979), which are expected to be more common in lowland streams according to the RCC (Vannote et al., 1980) and have been shown to increase with stream size (Goldstein & Meador, 2004). Although this trait was not highly correlated with the latitude/elevation gradient, it was associated with habitat characteristics (i.e. wide channels, low canopy cover, high in-stream productivity) typical of streams lower on the river continuum (Vannote et al., 1980). Thus, this pattern partially confirms expectations of the RCC and suggests the action of reach-scale filters via riparian characteristics and in-stream production.

In general, the functional trait space occupied by fish assemblages increased in stream reaches located further downstream along the Grijalva fluvial gradient. The RHT suggests that assemblage-wide diversity of functional traits should increase from upstream to downstream as streams become more stable and a greater diversity of habitats is available for refugia from disturbance (Townsend & Hildrew, 1994). This also confirms RCC expectations that functional diversity should increase in lower reaches within a drainage basin as increasing diversity of resources promotes trophic diversity of fishes (Thorp et al., 2008). The lower reaches of large rivers, such as the Grijalva, typically have lower gradients with broad and meandering channels that interconnect and exchange materials and organisms with aquatic floodplain habitats that are spatially heterogeneous and temporally dynamic. As a result, these lower reaches tend to provide more diverse habitats and food resources and more aquatic production because of the greater size of the ecosystem and reduced effects of hydraulic disturbance (Thorp et al.,

2008). Total trait-space occupation also generally increased with species richness along the Grijalva fluvial gradient, a pattern shown in studies that have compared fish assemblages within river basins (e.g. Hoagstrom & Berry, 2008) and among basins across biogeographical regions (e.g. Winemiller, 1991). Exceptions to this trend occurred, however, with certain streams of the middle Grijalva having species richness equal to lower Grijalva streams yet revealing lower functional diversity (in terms of trait space occupied). Such exceptions are consistent with the idea that habitat filters at the local scale may limit the range of trait space that species can occupy (Keddy, 1992; Cornwell *et al.*, 2006). This pattern is also consistent with RHT expectations that more specialisation in the use of food and habitat resources should occur in larger, more stable lowland streams (Townsend & Hildrew, 1994).

In summary, we found that environmental variables at local and landscape scales were related to the functional structure of stream fish assemblages in the Grijalva Basin. We observed an increase in functional diversity along with increasing species richness from the highlands to the lowlands along the fluvial gradient of the catchment. These results provide support for some aspects of the RCC, RHT and landscape filtering conceptual frameworks for trait–environment relationships in stream fish assemblages. Despite major differences in climate and zoogeography, this tropical Mesoamerican basin generally conforms to expectations derived from research on temperate streams. Adoption of a functional trait approach in this study allows inferences to be compared to patterns from research in other rivers, including those in biogeographical regions with highly divergent taxa and different environmental conditions. Compared to studies that focus on taxonomic identity, research that analyses functional trait diversity should translate better across regions and thus provide opportunities to discover general ecological patterns (Poff, 1997; Poff *et al.*, 2006; Olden *et al.*, 2010). Moreover, improved knowledge of how functional traits of fishes respond to natural environmental gradients will greatly enhance our ability to predict the manner in which local species assemblages are likely to respond to human-induced environmental changes.

Acknowledgments

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Supporting Information

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

Appendix S1. Distribution of fish species captured in this study among the upper, middle and lower regions of the Río Grijalva Basin.

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(Manuscript accepted 16 February 2012)