

Altitudinal gradients in stream fish diversity and the prevalence of diadromy in the Sixaola River basin, Costa Rica

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Abstract Landscape-scale patterns of freshwater fish diversity and assemblage structure remain poorly documented in many areas of Central America, while aquatic ecosystems throughout the region have been impacted by habitat degradation and hydrologic alterations. Diadromous fishes may be especially vulnerable to these changes, but there is currently very little information available regarding their distribution and abundance in Central American river systems. We sampled small streams at 20 sites in the Sixaola River basin in southeastern Costa Rica to examine altitudinal variation in the diversity and species composition of stream fish assemblages, with a particular focus on diadromous species. A set of environmental variables was also measured in the

study sites to evaluate how changes in fish assemblage structure were related to gradients in stream habitat. Overall, fish diversity and abundance declined steeply with increasing elevation, with very limited species turnover. The contribution of diadromous fishes to local species richness and abundance increased significantly with elevation, and diadromous species dominated assemblages at the highest elevation sites. Ordination of the sampling sites based on fish species composition generally arranged sites by elevation, but also showed some clustering based on geographic proximity. The dominant gradient in fish community structure was strongly correlated with an altitudinal habitat gradient identified through ordination of the environmental variables. The variation we observed in stream fish assemblages over relatively small spatial scales has significant conservation implications and highlights the ecological importance of longitudinal connectivity in Central American river systems.

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Introduction

Central America has a distinctive freshwater fish fauna that reflects a complex history of colonization from South America and subsequent diversification (Miller 1966; Myers 1966; Bussing 1985; Bermingham and Martin 1998). Barriers to dispersal have resulted in

limited geographic ranges for many fish species, and high levels of endemism in the region (Smith and Bermingham 2005). Although biogeographical patterns in Central America are becoming increasingly well documented, landscape-scale variation in stream fish diversity and assemblage structure remains poorly understood in many areas of the region. Understanding how fish communities vary across the landscape is crucial for developing effective conservation strategies (Angermeier and Winston 1999), which is an increasingly urgent concern as freshwater ecosystems throughout Central America face ongoing and projected alteration from deforestation, pollution and hydroelectric development (Pringle and Scatena 1999; Anderson et al. 2006; Lorion and Kennedy 2009).

Studies of freshwater fishes in Central America have generally emphasized variation in fish assemblages along gradients in stream size, distance from the ocean or both (e.g. Angermeier and Karr 1983; Lyons and Schneider 1990; Winemiller and Leslie 1992; Rodiles-Hernández et al. 1999; Esselman et al. 2006). These studies have documented relationships between fish diversity and stream size, as well as longitudinal zonation from headwater to coastal areas. However, small tributary streams throughout the region exhibit diverse physicochemical conditions over relatively small spatial scales, owing to differences in catchment geology (Esselman et al. 2006) and gradients in geomorphology from coastal lowlands to montane areas further inland. A better understanding of the variation in fish assemblage structure among streams of similar size located in different parts of the river network could provide new insight into how fishes respond to environmental gradients and directly inform freshwater conservation efforts.

In this study, we sampled fish populations in small streams along an altitudinal gradient spanning nearly 500 m in the Sixaola River basin of southeastern Costa Rica. We chose to work in the Sixaola basin because it is one of the least-impacted watersheds of its size in Costa Rica (Sanchez-Azofeifa et al. 2002), and has no hydroelectric facilities or other major engineered barriers to fish passage. Furthermore, there are few published studies describing fish assemblages in the Sixaola basin or other river basins within the Bocas biogeographical province of Smith and Bermingham (2005). Altitudinal gradients in fish diversity and species composition are particu-

larly relevant to conservation in the study area because anthropogenic impacts have been concentrated in lowland areas, while many montane streams are relatively pristine.

Our objectives were to examine how stream fish diversity varies along an altitudinal gradient in the Sixaola River basin, describe underlying patterns in fish species composition, and investigate relationships between fish assemblage structure and altitudinal gradients in stream habitat. We were particularly interested in diadromous fishes, which make obligatory migrations between freshwater and marine habitats during their life cycle (McDowall 1987) and can be a significant component of stream communities in Central America (Cruz 1987; Esselman et al. 2006). There is currently very little information available regarding the distribution and abundance of diadromous fishes in Central American river systems, and these species are expected to be disproportionately affected by increasing hydroelectric development in the region (Anderson et al. 2006; McLarney and Mafla 2007). Based on altitudinal range information that is available for species in our study area (Bussing 1998), diadromous fishes were expected to be present throughout our sampling gradient and to be more diverse in lower elevation streams.

Methods

Study area

The study was conducted in the Costa Rican portion of the Sixaola River basin (9°35' N, 83°00' W), an international river basin encompassing approximately 2780 km² on the Caribbean slope of Costa Rica and Panama (Fig. 1). Study streams were located in several major sub-basins and ranged in elevation from near sea level to 500 m in elevation. Annual precipitation varies along this gradient from approximately 2500 mm in the lowlands to over 3500 mm at the highest elevation sites (Hijmans et al. 2005). Rainfall is not strongly seasonal in the study region (Coen 1983), but precipitation tends to be lowest between February and May. Natural vegetation varies along the altitudinal gradient from tropical moist forest at lowland sites to premontane wet forest at the highest elevation sites (Holdridge 1967).

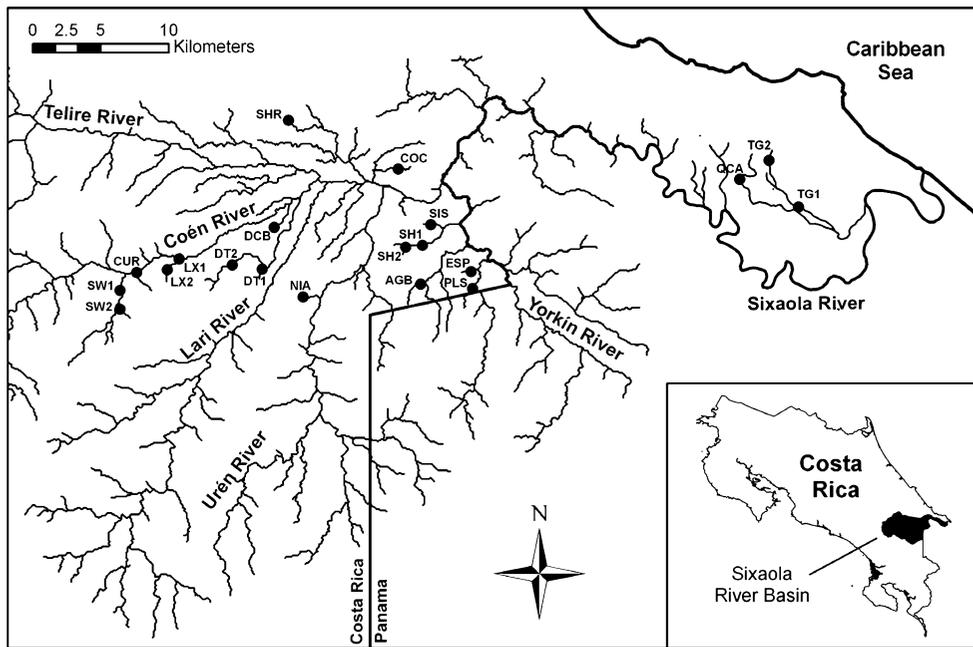


Fig. 1 Map of the study area in southeastern Costa Rica, with locations of the 20 sampling sites in the Sixaola River basin

Twenty sites on second- and third-order streams were selected for the study and sampled once between February–June 2006. Only minimally-disturbed sites with forested riparian zones were considered for the study, and streams were always near base flow when sampling took place. Accessibility was a major constraint, as there was no road access to much of the study area. Potential study sites were identified from 1:50 000 scale topographic maps (Instituto Geográfico Nacional, Costa Rica) and then scouted in advance of sampling to investigate current land use patterns in riparian and upland areas. We purposely avoided sites above waterfalls that would restrict fish passage. At each site, we selected a study reach 20 times the mean wetted channel width (range 65–130 m) that was representative of stream habitat conditions for several hundred meters upstream and downstream of the chosen site.

Fish sampling

Fishes were sampled at all sites using a backpack electrofishing unit (Model B-12, Smith-Root Inc., Vancouver, Washington, USA). The goal was to capture a representative sample of the fish assemblage at each site, in terms of species presence and relative

abundance, and our methods reflect time constraints associated with accessing the most remote sites. Sampling reaches were divided into 3–4 sub-reaches and one very thorough pass was made through all habitats in each sub-reach. Our preliminary work in high and low elevation streams showed that fish were concentrated in deeper pool and cascade habitats, and so a second pass was made through all pools, as well as cascade habitats >30 cm in depth. Fish from all passes at a site were combined for the analyses. Block nets were used to isolate sub-reaches when deemed necessary. All fishes >20 mm in length were identified to the lowest possible taxonomic level using keys in Bussing (1998), and then released back into the stream. Two goby species, *Sicydium adelum* and *Sicydium altum*, often co-occurred at our sampling sites, but most individuals were too small to be identified in the field and so these fish were grouped at the genus level in all analyses.

Fishes were classified as diadromous based on references from Costa Rica or other parts of their range (Gilbert and Kelso 1971; Loftus et al. 1984; Cruz 1987; Cruz 1989; Bussing 1998). For *Awaous banana*, *Eleotris*, and *Pomadasys crocro*, diadromy is assumed based on several lines of evidence, especially their presence in *tismiches*, or mass upstream

migrations of juvenile fishes and shrimps that occur in coastal rivers of the study region (Gilbert and Kelso 1971; Nordlie 1981; Winemiller and Ponwith 1998). Evidence of diadromy in *Gobiomorus dormitor* is equivocal (Gilmore 1992), but this species was rare in our collections and assuming diadromy has little effect on our results. Catadromous and amphidromous life histories (see McDowall 1987) are likely represented in the diadromous fish fauna of the Sixaola basin (Bussing 1998), but given the general lack of life history information for the species in this study, we did not attempt to make these designations.

Environmental variables

A set of habitat variables was measured at each site to investigate relationships between stream habitat and fish assemblage structure along the altitudinal sampling gradient (Table 1). All channel geomorphic units in each sampling reach were categorized as pools, riffles, runs, or cascades based on criteria in

Hawkins et al. (1993), and the proportion of the sampling reach occupied by each channel unit type was estimated visually. Mean water depth and stream substrate composition in the study reaches were quantified following methods adapted from Iwata et al. (2003) at ten transects spaced two channel widths apart. At each transect, stream depth was measured at five equally-spaced points across the stream channel and the dominant substrate in a 25 × 25 cm area surrounding each point was classified as sand or silt (particle size <2 mm), gravel (2–16 mm), pebble (17–64 mm), cobble (65–256 mm), boulder (>256 mm), or bedrock.

Stream canopy cover was estimated visually to the nearest 10% at 5 equally spaced points in the center of the wetted channel and then averaged for the reach. Channel slope was determined using a clinometer and measuring staff. Water temperature was measured with a thermometer in a well-mixed area of the stream channel between 09:30–10:00 h. Stream discharge data were not available for any of the sampling sites,

Table 1 Habitat characteristics of the 20 study sites in the Sixaola River basin, Costa Rica

Site Code	Elevation (m)	Catchment Area (km ²)	Stream Width (m)	Channel Slope (%)	Mean Depth (cm)	Pool Area (%)	Water Temp (°C)	Canopy Cover (%)	Distance from Ocean (km)	C-Link	Dominant Substrates
TG1	9	5.9	4.6	0.2	37.2	95	26	76	20	3	Sand/Silt
QCA	22	5.5	4.5	0.5	29.1	90	25	84	27	3	Sand/Silt
TG2	39	1.0	3.0	0.2	22.2	85	25	90	24	4	Gravel/Cobble
DCB	97	2.1	4.7	1.5	20.5	50	23	78	83	27	Pebble/Cobble
SH1	100	6.0	5.1	1.7	19.3	65	25	54	75	22	Cobble/Bedrock
SIS	112	1.1	3.7	1.7	12.6	55	24	54	74	21	Pebble/Cobble
SH2	125	1.7	4.0	2.5	20.3	50	25	76	77	22	Gravel/Cobble
ESP	132	2.2	4.5	0.8	12.9	55	22	80	78	24	Pebble/Cobble
PLS	149	4.2	4.6	2.2	16.9	35	22	54	79	25	Pebble/Cobble
AGB	159	6.0	6.4	2.8	19.1	50	24	58	79	22	Pebble/Boulder
COC	163	3.0	4.4	5.0	14.9	40	23	68	76	21	Pebble/Cobble
DT1	168	4.2	7.2	4.0	25.2	20	23	70	87	28	Cobble/Boulder
NIA	225	2.1	4.9	9.0	24.4	25	23	78	85	24	Cobble/Boulder
LX1	261	5.5	4.7	5.2	17.9	20	23	60	91	31	Cobble/Boulder
DT2	264	2.0	4.0	4.6	15.1	45	23	72	90	28	Cobble/Boulder
SHR	266	1.7	3.8	4.0	12.5	30	21	68	83	24	Pebble/Cobble
CUR	298	6.2	5.4	6.5	28.6	10	22	52	94	35	Cobble/Boulder
LX2	350	2.7	4.0	9.0	16.3	25	23	50	92	32	Cobble/Boulder
SW1	375	1.8	3.7	6.0	19.0	40	23	60	96	37	Gravel/Cobble
SW2	500	5.3	5.4	11.0	33.7	20	21	28	98	39	Cobble/Boulder

and so we used catchment area as a proxy for stream size. Catchment boundaries were delineated using a digital elevation model of the study area with approximately 90-m resolution from the Shuttle Radar Topography Mission (SRTM; United States Geological Survey 2002). Elevation at the mid-point of each sampling reach was also determined using the SRTM elevation data. The position of each sampling site in the stream network was defined using the C-link metric (Fairchild et al. 1998), which is the number of confluences downstream from a given site to the river mouth. This metric has been found to perform well compared with other variables when evaluating relationships between landscape position and fish assemblage structure (Smith and Kraft 2005).

Data analysis

Relationships between elevation, fish diversity, and the relative abundance of diadromous species were examined using linear regression analysis in SAS Version 9.1 (SAS Institute Inc. 2002). Fish diversity in the study reaches was expressed as species richness, and using Fisher's alpha diversity index, which is less sensitive to sample size (Magurran 1988). To investigate how fish species composition varied among sites and how this variation related to changes in stream habitat along the altitudinal sampling gradient, we used ordination to reduce the dimensionality of the fish and environmental data sets to a smaller set of uncorrelated variables. Linear relationships between these variables were then examined to determine whether the major gradients in fish assemblage structure were significantly related to gradients in the environmental variables that we measured.

For the environmental data, ordination of the sampling sites was done using Principal Components Analysis (PCA) in the program PC-ORD (McCune and Mefford 1999). Prior to analysis, variables expressed as a proportion were arcsine square root-transformed to improve normality. Likewise, the variables mean depth, catchment area, water temperature, and distance to ocean were \log_{10} -transformed, and channel slope was square root-transformed. The PCA was performed on the correlation matrix, and the number of non-trivial principal components was determined using the Rnd-Lambda criteria of Peres-Neto et al. (2005), which is based on comparisons of

observed eigenvalues with eigenvalues from randomizations of the data matrix.

A different ordination technique, Nonmetric Multidimensional Scaling (NMDS), was used for the fish species composition data because this method is more appropriate for community data with non-linear relationships among variables (McCune and Grace 2002). The distance matrix for the NMDS ordination was constructed using Bray-Curtis distances (Bray and Curtis 1957) among sites based on the composition of fish assemblages, and all species were retained in the analysis. Prior to analysis, catch data were converted to relative abundance for each site because sampling area varied among sites. The final ordination was based on the best configuration from 250 runs with random starting points. Appropriate dimensionality for the ordination was determined from a scree plot and significance tests of stress values based on 250 Monte Carlo randomizations.

Results

Fish diversity and species composition

A total of 6689 fishes representing 26 species and 11 families were captured in the study streams (Table 2). Thirteen of the 26 species belonged to the families Characidae, Poeciliidae, or Cichlidae. Characids and poeciliids were numerically dominant at all but the highest elevation sites and accounted for 38% and 30%, respectively, of all fish captured. Diadromous fishes, including two *Sicydium* species, accounted for eight of the 26 species and approximately 25% of all individuals collected in the study streams (Table 2).

Significant changes in fish diversity were observed along the altitudinal sampling gradient (Fig. 2a), with fish species richness declining rapidly with increasing elevation ($r^2=0.74$, $P<0.001$). Our sampling methods did not allow us to make precise estimates of fish density, but fish abundance also showed a declining trend with increasing elevation. Sample size appeared to have little influence on the altitudinal diversity gradient we observed, however, as Fisher's alpha diversity index showed a negative relationship with elevation ($r^2=0.69$, $P<0.001$) that was very similar to the pattern observed for species richness. Changes in fish diversity with elevation were mostly driven by

Table 2 List of fish species captured in the 20 study sites in the Sixaola River basin, with the total number of individuals of each species captured across all sites. Diadromous species are in bold

Family	Species	Number of Individuals
Characidae	<i>Astyanax aeneus</i>	266
	<i>Astyanax orthodus</i>	294
	<i>Bryconamericus scleroparius</i>	1980
	<i>Hyphessobrycon panamensis</i>	14
Rhamphichthyidae	<i>Hypopomus occidentalis</i>	67
Pimelodidae	<i>Rhamdia guatemalensis</i>	56
	<i>Rhamdia rogersi</i>	79
Rivulidae	<i>Rivulus isthmensis</i>	16
Poeciliidae	<i>Alfaro cultratus</i>	368
	<i>Brachyrhaphis parismina</i>	13
	<i>Phallichthys amates</i>	220
	<i>Poecilia gillii</i>	638
	<i>Priapichthys annectens</i>	790
	<i>Synbranchus marmoratus</i>	5
Haemulidae	<i>Pomadasys crocro</i>	1
Cichlidae	<i>Astatheros bussingi</i>	140
	<i>Archocentrus myrnae</i>	58
	<i>Archocentrus nigrofasciatus</i>	32
	<i>Parachromis loisellei</i>	4
Mugilidae	<i>Agonostomus monticola</i>	506
	<i>Joturus pichardi</i>	28
Gobiidae	<i>Awaous banana</i>	13
	<i>Sicydium adelum</i>	
	<i>Sicydium altum</i>	992 ^a
Eleotridae	<i>Eleotris</i> sp.	106
	<i>Gobiomorus dormitor</i>	3

^a total number of individuals of both *Sicydium* species captured

species addition from the highest to lowest elevation sites, with limited species turnover (Table 3).

Diadromous fishes exhibited very different patterns of diversity and abundance along the altitudinal sampling gradient compared to the overall fish assemblage. In fact, there was no significant relationship between elevation and the number of diadromous fish species collected at a site ($r^2=0.07$, $P=0.26$). As a result, diadromous fishes accounted for an increasing proportion of the total number of species present at our sampling sites as elevation increased ($r^2=0.62$, $P<0.001$; Fig. 2b). There was also a significant positive relationship between elevation and the proportion of individuals at the sampling sites with diadromous life histories ($r^2=0.65$, $P<0.001$; Fig. 2c). Although diadromous species richness showed no significant relationship with elevation, the species composition of the diadromous group did vary among

sites (Table 3). In the three lowest elevation sites, *Eleotris* was the dominant diadromous taxon, while *Sicydium* and *Joturus pichardi* were completely absent. In the remaining sites, *Sicydium* was abundant and ubiquitous, while *J. pichardi* occurred at many sites, always in low abundance. *Agonostomus monticola* was present in all but one of the sampling sites and showed the widest altitudinal range of any species in the study.

Environmental gradients and fish assemblage structure

The PCA extracted two significant principal components that together explained 70% of the variance in the environmental data (Table 4) and described two distinct environmental gradients encompassed by the study sites. The first principal component (PC1)

Fig. 2 Linear relationships between elevation and (a) fish species richness, (b) percent diadromous species, and (c) percent diadromous individuals in the 20 study sites ($P < 0.001$ for all regressions)

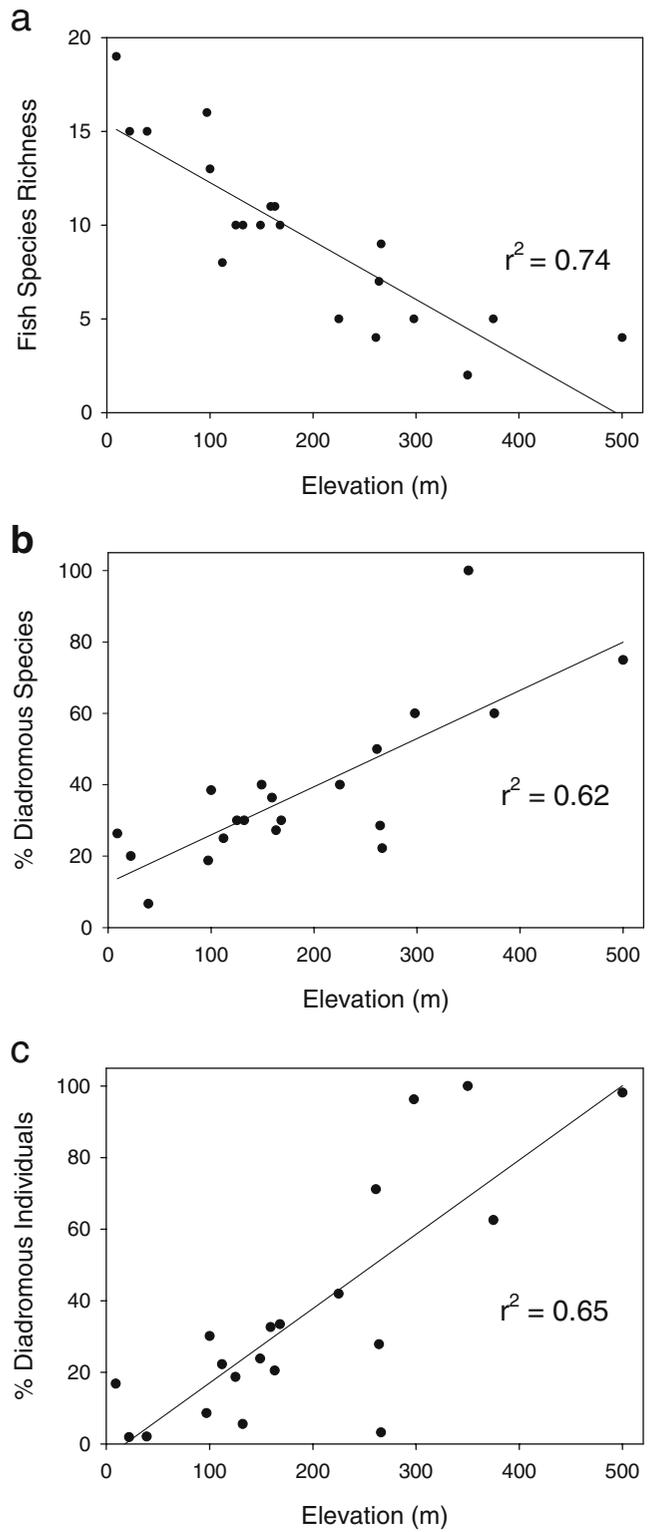


Table 3 Distribution of stream fishes along an altitudinal gradient in the Sixaola River basin. Diadromous species are in bold

Species	TG1	QCA	TG2	DCB	SHI	SIS	SH2	ESP	PLS	AGB	COC	DT1	NIA	LX1	DT2	SHR	CUR	LX2	SW1	SW2
Site code and elevation (m)	9	22	39	97	100	112	125	132	149	159	163	168	225	261	264	266	298	350	375	500
<i>Brachyraphis parismina</i>	x																			
<i>Pomadoury crocro</i>	x																			
<i>Hyphessobrycon panamensis</i>	x		x																	
<i>Parachromis loisellei</i>	x		x																	
<i>Eleotris</i> sp.	x	x	x																	
<i>Astyanax aeneus</i>	x	x	x	x																
<i>Alfaro cultratus</i>	x	x	x	x																
<i>Phallitichthys amates</i>	x	x	x	x																
<i>Archocentrus nigrofasciatus</i>	x	x	x	x																
<i>Synbranchus marmoratus</i>	x	x	x	x																
<i>Astyanax orthodus</i>	x	x	x	x	x															
<i>Gobiomorus dormitor</i>	x	x	x	x	x															
<i>Awaous banana</i>	x	x	x	x	x															
<i>Rivulus isthmensis</i>	x																			
<i>Rhamdia guatemalensis</i>	x	x	x	x	x															
<i>Hypopomus occidentalis</i>	x	x	x	x	x															
<i>Poecilia gillii</i>	x	x	x	x	x															
<i>Astatheros bussingi</i>	x	x	x	x	x															
<i>Bryconamericus scleropardius</i>	x	x	x	x	x															
<i>Agonostomus monticola</i>	x	x	x	x	x															
<i>Priapichthys annectens</i>		x	x	x	x															
<i>Archocentrus myrmae</i>			x	x	x															
<i>Sicydium</i> sp.																				
<i>Joturus pichardi</i>																				
<i>Rhamdia rogersi</i>																				

Table 4 Results of Principal Components Analysis (PCA), showing the loadings of environmental variables on the first two principal components and the percent of total variance explained by these components. Correlation coefficients >0.60 are in bold

Variables	Principal Component	
	1	2
Mean Width	0.32	0.63
Mean Depth	-0.26	0.85
Catchment Area	0.08	0.77
Channel Slope	0.88	0.23
% Pool Habitat	-0.96	-0.02
% Riffle Habitat	0.04	-0.78
% Cascade Habitat	0.83	0.38
% Sand/Silt	-0.83	0.37
% Gravel	-0.27	-0.26
% Pebble	0.49	-0.74
% Cobble	0.72	-0.39
% Boulder	0.83	0.41
Water Temperature	-0.78	0.01
Canopy Cover	-0.67	-0.25
Distance from Ocean	0.93	-0.18
C-link	0.94	0.00
Percent Variance Explained	47.2	23.0
Cumulative Percent Explained	47.2	70.3

accounted for 47% of the variance, was strongly correlated with elevation ($r^2=0.92$, $P<0.001$ for relationship between PC1 site scores and \log_{10} -transformed elevation), and captured the major physical habitat gradient from low to high elevation sites. In particular, PC1 showed strong positive correlations with channel slope, % cascade habitat, and the percentages of cobble and boulder substrates. PC1 was negatively correlated with % pool habitat, % sand/silt substrate, water temperature and canopy cover. Two variables describing the spatial position of study sites, distance to ocean and C-link, were also strongly correlated with PC1. The second principal component (PC2) accounted for an additional 23% of the variance and appeared to primarily represent a gradient in stream size. PC2 was positively correlated with mean width, mean depth, and catchment area, and negatively correlated with % riffle habitat and % pebble substrate (Table 4). The PCA ordination did not reveal strong groupings among the study sites, except that PC1 clearly distinguished the

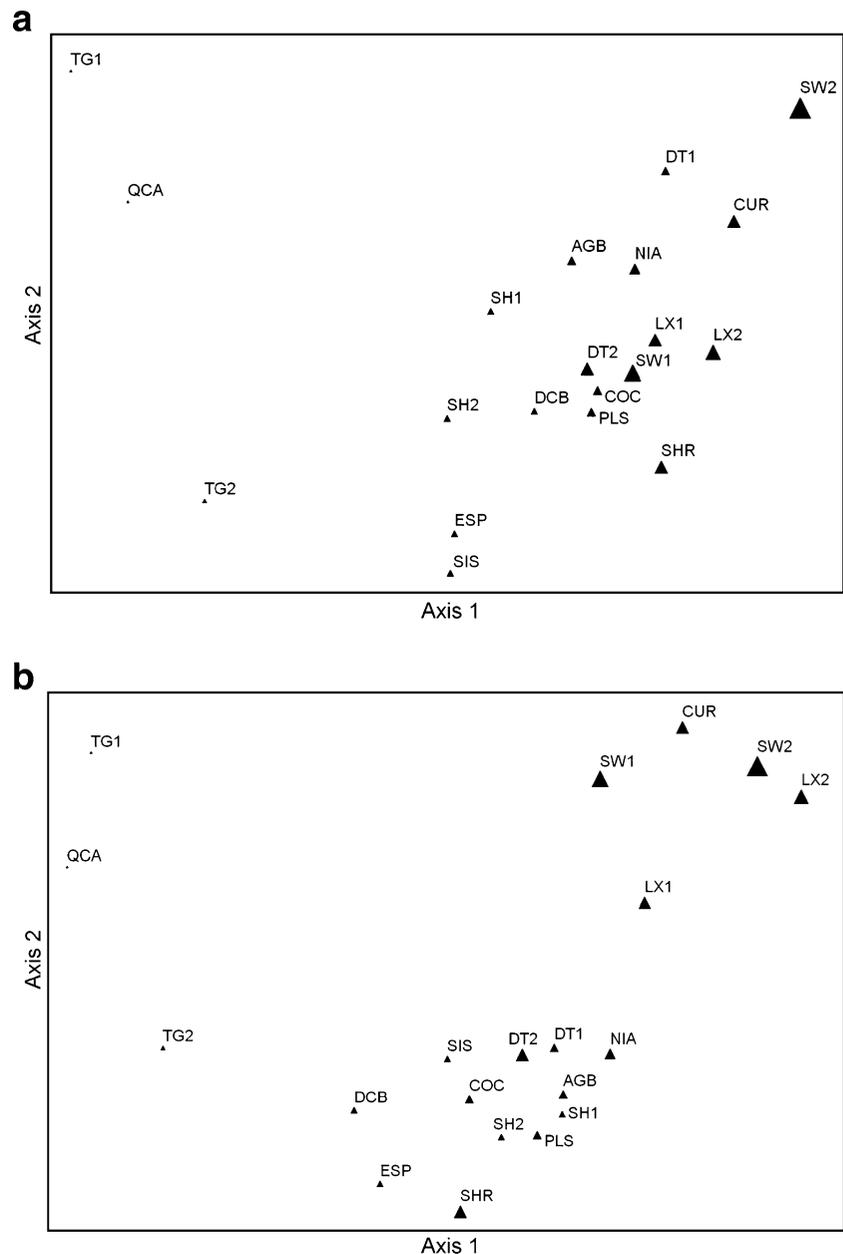
three lowest elevation sites from all other sites (Fig. 3a).

Ordination of sampling sites based on fish species relative abundances using NMDS also resulted in two significant axes, with a final stress value for the ordination of 8.7. The two NMDS ordination axes together explained 94% of the variation in fish species composition among sampling sites, with the first axis alone accounting for 72.6% of the total variation. As observed in the PCA ordination based on environmental variables, the NMDS ordination generally arranged sites according to elevation and identified the three lowest elevation sites as being quite distinct (Fig. 3b). The NMDS ordination also showed that five high elevation sites located in the Coén River sub-basin (Fig. 1) formed a distinct group which was not apparent in the PCA ordination. Despite this difference, there was a highly significant correlation between site scores for PC1 and the first NMDS axis ($r^2=0.86$, $P<0.001$), indicating a strong congruence between the altitudinal habitat gradient identified by the PCA ordination and the major gradient in fish community structure extracted using NMDS. There was also a significant correlation between site scores for PC2 and the second NMDS axis ($r^2=0.39$, $P=0.003$), suggesting that the secondary gradient in fish community structure was related to stream size.

Discussion

Stream fish assemblages in the Sixaola River basin exhibited striking changes in diversity and species composition along our altitudinal sampling gradient, and these changes were strongly associated with a gradient in the physical structure of the stream environment. Although our study streams were all similar in size, the diversity gradient we observed was similar in magnitude to changes that could be expected along a considerable longitudinal stream gradient (Lowe-McConnell 1987; Matthews 1998). Many different factors have been proposed to explain longitudinal diversity gradients, including increasing habitat diversity (Gorman and Karr 1978), decreasing temporal variability (Horwitz 1978), and greater habitat volume, especially the development of larger pools (Sheldon 1968), in downstream areas. These factors affect a variety of biotic and abiotic processes in streams, and interact in important ways to influence

Fig. 3 Ordinations of the 20 sampling sites based on (a) PCA using correlation matrix of environmental variables and (b) NMDS using relative abundance of all fish species. Symbol sizes are proportional to the elevation of sampling sites



the structure and diversity of stream fish assemblages (Schlosser 1982). Our results, like those of Pouilly et al. (2006), illustrate that altitudinal gradients in the stream environment can have similar effects, irrespective of stream size.

The high covariance we observed among environmental variables complicates interpretation of their influence on fish diversity and community composition. However, geomorphic changes associated with variation in channel slope along the altitudinal

gradient appeared to be especially important. In particular, we found large differences among sites in the distribution of channel unit types, with the prevalence of pools decreasing considerably from the lowest to highest elevation sites (Table 1). Pool development is thought to be an important factor in determining the structure of fish assemblages in small temperate streams through its influence on habitat heterogeneity, biotic interactions and temporal variability (Schlosser 1987). Though the impacts of

seasonal dynamics are generally very different in tropical ecosystems, the availability of deeper pool habitats are likely to have similarly important effects on biotic interactions and population dynamics across temperate and tropical streams (e.g. Power 1984). Many fish species in the region appear to have affinities for specific water velocities (Bussing and Lopez 1977), and so flow conditions in pools and other channel unit types may be as important as water depth in determining local fish species composition.

Although the composition of fish assemblages appeared to be strongly linked to abiotic conditions in our study streams, spatial factors may also be important (Jackson et al. 2001). Variables describing the spatial position of sampling sites in the stream network showed strong correlations with the first principal component in the PCA, and ultimately with the major gradient in fish assemblage structure. These relationships may reflect differences in colonization (Gorman 1986; Osborne and Wiley 1992) or other spatially influenced ecological processes within the stream network, but it is very difficult to disentangle spatial and abiotic factors in our study streams. Sites at higher elevations were increasingly distant from potential source pools of immigrants in the largest, most temporally stable mainstem habitats, but also had very different habitat conditions than lowland streams. Little is known about the home range size or dispersal abilities of any of the fish species in our study area, which would also influence interpretations of the importance of spatial relationships within the stream network. By necessity, we captured a snapshot of fish assemblages in our study basin. Concurrent work based upon repeated sampling of lowland streams of this study area showed that fish assemblage structure was consistent among seasons and between years (Lorion and Kennedy 2009). Nevertheless, long-term studies across comparative watersheds will be needed to determine how local disturbance and larger-scale colonization dynamics influence diversity and species composition in this region.

Diadromous species constitute a significant portion of the fish fauna in the Sixaola basin, and understanding the spatial representation of diadromy and the consequences that migratory movements have on assemblage structure is critical for interpreting fish diversity patterns. In Caribbean island streams, where diadromous species have received more research

attention (e.g. Holmquist et al. 1998; March et al. 2003), diadromous fish distributions tend to be strongly influenced by physical barriers to dispersal, as well as interactions among migratory taxa. Insular streams in the Caribbean, however, generally have depauperate fish assemblages dominated by diadromous species at all elevations (Fièvet et al. 2001; Greathouse et al. 2006). Mainland Central American streams are quite different in that they also support a relatively diverse non-diadromous freshwater fish fauna, particularly at lower elevations. The extent to which biological interactions with resident freshwater fishes influence the distribution of diadromous fishes is not yet clear, but the overall pattern we observed is likely common on the Caribbean slope of Central America, where diadromous fishes are able to penetrate far inland and are among the few species adapted to high gradient montane streams (Cruz 1987; Bussing and López 1977; Esselman et al. 2006).

Our findings have important implications for conservation in the Sixaola River basin, and more broadly in the region. Small streams in the study area exhibit diverse habitat conditions and support very different fish assemblages depending on their location in the stream network. Recent studies from other neotropical regions have also found high spatial heterogeneity in fish assemblages among small streams (Gerhard et al. 2004), and discussed the implications for reserve design (Mendonça et al. 2005). The current distribution of protected areas in the Sixaola River basin illustrates the difficulty of building representative reserve networks to conserve stream fishes and their habitats. Over half of the Costa Rican portion of the Sixaola watershed is currently protected by national parks or reserves, but there is virtually no formal protection of lowland streams and their associated watersheds, which support the most diverse fish assemblages. Furthermore, although montane streams in the Sixaola basin are generally protected by national park status and a lack of human infrastructure, obligate migrations by diadromous fishes connect these streams with more heavily impacted areas downstream. As a result, downstream alterations in hydrologic connectivity, stream habitat, and water quality are likely to have a significant influence on sites upstream (Pringle 1997; Greathouse et al. 2006), including streams within protected areas (Pringle 2001).

Declines in diadromous herbivore-detritivores like *Sicydium* and *J. pichardi*, whose feeding activities directly affect benthic communities, could have especially important ecological consequences. *Sicydium* gobies were abundant at many of our sampling sites, and have been shown to significantly influence algal standing crops and benthic macroinvertebrate abundance in Costa Rican streams (Barbee 2002). The mullet *J. pichardi* was not as common in the small streams we sampled, but is much larger in size and has traditionally been the most important species for subsistence fishing by indigenous communities in the study area (Borge and Castillo 1997; McLarney and Mafla 2007). There is a clear need for more detailed ecological information on these and other diadromous fishes in the region, and life history studies that build on previous work (e.g. Cruz 1987) would be an important first step. The life history requirements and ecological role of diadromous fishes in Central American streams deserve important consideration as hydropower development continues to increase in the region (Anderson et al. 2006; McLarney and Mafla 2007).

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