

Aquatic community structure across an Andes-to-Amazon fluvial gradient

Nathan K. Lujan^{1*†}, Katherine A. Roach¹, Dean Jacobsen², Kirk O. Winemiller¹, Vanessa Meza Vargas³, Vania Rimarachín Ching³ and Jerry Arana Maestre³

¹Department of Wildlife and Fisheries, Texas A&M University, College Station, TX, USA, ²Freshwater Biological Section, Department of Biology, University of Copenhagen, Copenhagen, Denmark, ³Natural History Museum, University of San Marcos, Lima, Peru

ABSTRACT

Aim Little is known about factors affecting the elevational and longitudinal zonation of tropical Andean stream communities. We investigated epilithon, macroinvertebrate and fish assemblages along a 4100-m elevational–longitudinal gradient in an Andean headwater of the Amazon Basin. We interpret our results within the context of environmental factors, emphasizing temperature, as well as ecological theory relating shifts in metazoan functional feeding groups to shifts in basal resources along the fluvial continuum.

Location Arazá-Inambari-Madre de Dios watershed, south-eastern Peru.

Methods We sampled water physicochemistry, epilithon and macroinvertebrate diversity and abundance, and fish diversity at 18 main-stem and 14 tributary sites from high puna grasslands (4300 m a.s.l.) to Amazon Basin lowlands (200 m a.s.l.).

Results Water physicochemical parameters and the taxonomic and ecological structure of invertebrate and fish assemblages displayed mostly nonlinear responses to elevation: water temperature and percentage of macroinvertebrate taxa identified as leaf shredders had U-shaped responses; dissolved oxygen and percentage of macroinvertebrate taxa identified as grazers had hump-shaped responses. Epilithon richness increased slightly with elevation whereas macroinvertebrate and fish richness decreased.

Main conclusions Elevational gradients in physicochemical parameters are insufficient to explain abrupt and nonlinear shifts in community taxonomic and functional structure. Rather, trophic interactions, including predation and longitudinal turnover in basal food resources, seem to exert a stronger influence on the distributions of Andean aquatic organisms. A steep elevational decline in relative taxonomic diversity of leaf-shredding (versus algae-grazing) insects supports the hypothesis that temperature affects the functional composition of insect assemblages via its influence on microbial decomposition rates. This relationship, and the distributions of several insect and fish species across narrow elevational bands, suggests that Andean stream communities may be sensitive to global warming. Placer mining and road building impacts have already altered stream community structure, including the absence of many benthic species from low-elevation habitats.

Keywords

Anthropogenic impacts, fluvial gradient, global warming, longitudinal connectivity, mining, Neotropics, river continuum concept, sediment, shredders.

*Correspondence: Nathan K. Lujan, Department of Natural History, Royal Ontario Museum, 100 Queen's Park, Toronto, ON, Canada.
E-mail: nklujan@gmail.com
†Present address: University of Toronto, 25 Willcocks St., Toronto, ON, Canada

INTRODUCTION

Andean watersheds comprise a minor portion of the Amazon Basin's total area, yet contribute a disproportionate amount of the Amazon's total discharge (*c.* 40%; Goulding *et al.*, 2003) and deliver major loads of inorganic sediment and organic carbon to lowlands (Aufdenkampe *et al.*, 2001; Townsend-Small *et al.*, 2008; Laraque *et al.*, 2009). Despite over a century of research (see Appendix S1 in Supporting Information for a summary of previous studies), we still have a poor understanding of the taxonomic and geographical limits of many Andean stream species, and of the longitudinal ecological processes that may affect species distributions across the Andes-to-Amazon fluvial continuum. To address this, and to assess anthropogenic threats to Andean streams, we investigated physicochemical conditions and aquatic community structure in the Arazá-Inambari-Madre de Dios watershed: a drainage basin that spans over 4000 vertical metres and a major headwater of the Madeira River, itself the largest tributary of the Amazon Basin. Andean rivers face a number of threats, including climate change (Maldonado *et al.*, 2011), dam construction (Finer & Jenkins, 2012; Castello *et al.*, 2013), and sedimentation from agriculture, mining and road construction (Hardin, 2006; Swenson *et al.*, 2011). Moreover, aggregate anthropogenic impacts appear to be expanding more rapidly in Andean watersheds than in any other area of the Amazon Basin (Anderson & Maldonado-Ocampo, 2011).

One of our goals was to evaluate the extent to which existing theory regarding longitudinal shifts in organic matter processing and community trophic structure in streams may be applicable to the Andes, and to use our data to refine models applicable to tropical mountain rivers globally. As a starting point, we examined the river continuum concept (RCC; Vannote *et al.*, 1980; Thorp *et al.*, 2006; Freeman *et al.*, 2007; Tomanova *et al.*, 2007), which postulates that longitudinal shifts in the relative contributions of autochthonous primary production (algae) versus allochthonous detritus (leaf litter) drives turnover in macroinvertebrate functional feeding group (FFG) dominance, from shredders (consumers of coarse particulate organic matter, CPOM) in forested headwater reaches, to epilithon scrapers further downstream where streams are wide enough to allow sunlight to penetrate and support algal growth (Vannote *et al.*, 1980).

The RCC has proven useful for understanding longitudinal turnover in stream taxa and functional groups, particularly at temperate latitudes where the concept was originally developed (Vannote *et al.*, 1980; Gomi *et al.*, 2002). Limited research on tropical montane streams suggests that certain RCC predictions require revision in order to explain patterns at low latitudes. The abundance and taxonomic composition of shredders, in particular, can be very different in tropical versus temperate streams, with tropical streams having lower overall abundance and diversity of specialized shredding insects (Irons *et al.*, 1994; Dobson *et al.*, 2002; Wantzen &

Wagner, 2006) and greater abundance and diversity of decapods and fishes capable of consuming CPOM (Greathouse & Pringle, 2006; Lujan *et al.*, 2011). In addition to the potential influence of competition and predation by decapods and fishes (Rosemond *et al.*, 2001; Hall *et al.*, 2011), food limitation could explain the scarcity of shredding insects in tropical streams (Irons *et al.*, 1994; Dobson *et al.*, 2002; Wantzen & Wagner, 2006). Warmer year-round temperatures in the tropics may stimulate faster rates of microbial decomposition of CPOM, which in turn reduces food availability for detritivorous insects (Boyero *et al.*, 2011a). Tests of this hypothesis could refine predictions of how global climate change will influence fluvial ecosystems, and Dobson *et al.* (2002) proposed a test in which diversities of shredding insect taxa are examined along broad elevational–thermal gradients in tropical rivers.

Many Andean rivers originate in montane (puna or páramo) grasslands above the tree line where sunlight is abundant and terrestrial CPOM inputs are scarce and of low quality (Jacobsen, 2008a). In the absence of a closed tree canopy and abundant headwater influxes of CPOM, one would expect to see at least a partial reversal of RCC predictions regarding the longitudinal distribution of macroinvertebrate FFGs. Specifically, the relative abundance of scraping macroinvertebrate taxa should show a U-shaped response to elevation, with elevated richness in both the sunlit, high-elevation grasslands and in lowland rivers large enough to prevent riparian vegetation from covering the channel. In contrast, shredder taxa should show a hump-shaped response to elevation, peaking at middle elevations where forest cover and CPOM inputs are greatest, but declining again at lower elevations due to the positive effect of temperature on microbial degradation of CPOM and the addition of many macro-consumer competitors and predators (e.g. decapods and fishes). We also predicted a longitudinal turnover in fish functional feeding groups from insectivore dominance at the highest elevations supporting fishes, typically around 2500 m a.s.l. in the Andes (Appendix S1), to the inclusion at lower elevations of algivores and detritivores capable of filling the same ecological niche as macroinvertebrates, with this latter group having reduced overall abundance due to the combined effects of predation and resource competition.

To investigate the effects of human impacts on aquatic communities along the main channel of the Arazá-Inambari River, including road construction and mining, we compared main-channel sites with nearby tributary habitats that showed little indication of human impact. We predicted that mid- and low-elevation main-stem sites, where impacts were most severe, would have greater turbidity and inorganic nutrient concentrations compared with upstream main-stem sites and tributary streams at the same elevation. Because increased sedimentation frequently reduces algal production by limiting light availability (Lloyd *et al.*, 1987; Henley *et al.*, 2000), we also predicted that, in contrast to RCC predictions, benthic and water-column chlorophyll *a* would be lowest at the furthest downstream main-stem sites.

Finally, we expected to see distinct elevational clines in the taxonomic richness of epilithon, macroinvertebrate and fish assemblages, but disruptions in the consistency of these patterns at low elevations due to anthropogenic impacts. Taxonomic richness displays a strong response to elevation in rivers globally (Fu *et al.*, 2004; Albert *et al.*, 2011; Wang *et al.*, 2011). For most organisms, including diatoms (Ormerod *et al.*, 1994; Wang *et al.*, 2011), macroinvertebrates (Jacobsen, 2004) and fishes (Albert *et al.*, 2011; Appendix S1), this relationship is a monotonic decrease in response to increased elevation. Given the wide range of factors potentially affecting elevational trends in aquatic species richness, including temperature, oxygen availability, habitat diversity, abiotic disturbance regime, species–area relationships, ultraviolet radiation and dissolved organic carbon (Jacobsen, 2008b; Jaramillo-Villa *et al.*, 2010; Albert *et al.*, 2011; Verberk *et al.*, 2011; Wang *et al.*, 2011), we predicted that patterns in the Arazá–Inambari would be similar to those observed in previous studies, but that relationships would be more significant in tributary sites less subject to the aggregate influence of human activity.

MATERIALS AND METHODS

Field methods

From 18 July to 8 August (dry season) 2010, we sampled 41 sites in the Arazá–Inambari watershed, a major headwater of the Madre de Dios River in the south-western Amazon Basin (Cusco and Madre de Dios departments, Peru; Fig. 1, Table 1). Most sites were accessed via the Interoceanic Highway, although several lowland Inambari River sites were surveyed during a five-day boat trip between an

uppermost site (S28) near Puerto Carlos and a lowermost site (S32) near the mouth of the Inambari. At each site, fishes were surveyed and photographs were used to document the condition of riparian habitats, including evidence of human impacts (Fig. 2). Subsets of sites (Table 1) were sampled for physicochemical and biological parameters [turbidity (FTU), temperature (°C), specific conductivity (microsiemens cm^{-1}), pH, salinity (parts per thousand)], nutrient concentrations [ammonia, nitrate, nitrite, soluble reactive phosphorus (mg L^{-1})], chlorophyll *a* [benthic (mg m^{-2}), water column (mg m^{-3})], and epilithic algae, macroinvertebrate and fish diversity and assemblage structure. Most survey sites ($n = 32$) were in the Arazá–Inambari watershed, and these included both main-stem ($n = 18$) and tributary ($n = 14$) habitats distributed across 4100 m of elevation (4304–200 m a.s.l.; Table 1). Main-stem sites ranged in stream order from first (highest elevation) to sixth (lowest elevation; Fig. 1); tributary sites ranged from first to fourth order, and tributary stream order had no systematic relationship with elevation. Survey sites spanned five Andean elevational vegetation zones: puna (4500–3500 m), upper cloud forest (3500–2500 m), lower cloud forest (2500–1000 m), piedmont (1000–400 m) and lowlands (400–50 m; Young & Leon, 1999; Brack & Mendiola, 2000; Table 1).

Water physicochemical parameters (temperature, pH, specific conductivity, salinity and dissolved oxygen) were measured using a Hydrolab internally monitoring MiniSonde (Hach Hydromet, Loveland, CO, USA), and turbidity was measured using a Hanna microprocessor turbidity meter (Hanna Instruments, Woonsocket, RI, USA). Triplicate turbidity measurements were taken, and other measurements were taken repeatedly at 5-min intervals over *c.* 1 h, with

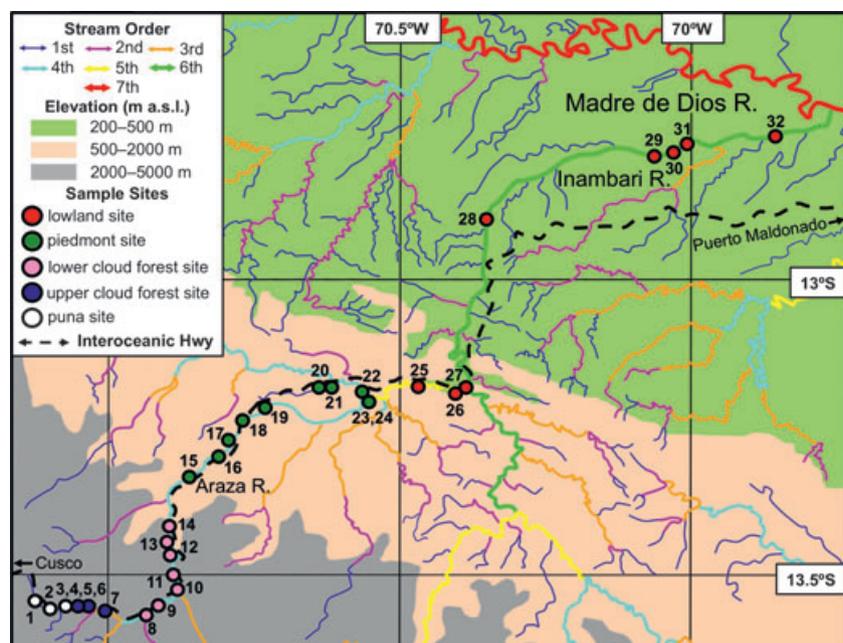


Figure 1 Map of the Arazá–Inambari watershed in south-eastern Peru showing the location, stream order, and elevational zone of survey sites S1–S32. Sites S33–S41 were located in tributaries of the Madre de Dios north of Puerto Maldonado (not illustrated).

Table 1 Geographical, biotic and physicochemical data gathered at each of 18 main-stem and 14 tributary sites in the Arazá-Inambari-Madre de Dios watershed, south-eastern Peru.

	Site	Elevation (m a.s.l.)	Latitude (DD)	Longitude (DD)	M/T/O	Taxon Richness				Turb. (FTU)	Temp. (°C)	pH	SpCond ($\mu\text{S cm}^{-1}$)	Sal. (ppt)	DO (% sat.)	DO (mg mL ⁻¹)	DIN (mg L ⁻¹)	SRP (mg L ⁻¹)	Chlor. <i>a</i> : water (mg m ⁻³)	Chlor. <i>a</i> : benthic (mg m ⁻²)
						E	MI	F	MI#											
Puna	S1	4304	-13.6293	-71.0705	M	48	6	0	540	2.7	11.9	6.6	87.4	0.03	46.0	5.0	0.34	0.18	0.89	1.59
	S2	3958	-13.6047	-71.0517	M	52	11	0	886	0.0	11.8	7.5	104.5	0.04	61.9	6.7	0.66	0.17	1.16	3.77
	S3	3516	-13.5748	-71.0264	M	36	9	0	3030	0.2	9.9	7.5	98.7	0.04	64.3	7.3	0.39	0.07	1.34	4.15
Upper cloud forest	S4	3051	-13.5830	-70.9871	M	44	11	0	525	2.2	8.1	7.5	0.0	0.03	66.9	7.9	0.24	0.10	0.62	8.67
	S5	2630	-13.5914	-70.9565	M	40	8	0	495	25.8	12.2	7.8	178.4	0.08	73.6	7.9	0.44	3.04	1.07	14.30
	S6	2630	-13.5911	-70.9570	T	43	9	2	375	7.9	14.6	7.7	135.5	0.06	80.2	8.2	1.05	0.37	0.62	10.40
	S7	2630	-13.5914	-70.9559	T	37	13	0	1395	-	9.8	8.1	126.0	0.05	77.3	8.8	-	-	-	-
Lower cloud forest	S8	2218	-13.5572	-70.8996	M	31	8	2	960	33.6	13.7	7.7	220.4	0.10	82.6	8.6	0.65	3.12	0.71	23.39
	S9	1966	-13.5281	-70.8967	T	-	-	1	593	-	13.0	8.1	109.8	0.04	83.2	8.8	-	-	-	-
	S10	1721	-13.5051	-70.8998	T	42	16	2	593	0.0	14.9	7.6	84.9	0.03	87.7	8.9	0.37	0.98	0.53	38.51
	S11	1587	-13.4813	-70.8887	M	-	12	1	178	84.0	16.4	8.1	164.3	0.07	91.4	9.0	0.61	0.19	1.78	1.73
Piedmont	S12	1334	-13.4411	-70.9024	T	26	12	4	315	0.3	15.0	7.6	83.6	0.03	90.1	9.1	0.09	0.66	0.53	0.09
	S13	1253	-13.4271	-70.9043	M	46	12	3	1232	33.8	15.1	8.0	149.7	0.06	86.3	8.7	1.06	0.22	2.14	7.04
	S14	1118	-13.3964	-70.9000	T	-	-	4	-	-	16.9	7.8	57.5	0.02	87.6	8.5	-	-	-	-
	S15	842	-13.3247	-70.8428	M	48	14	7	712	28.1	19.5	7.8	93.3	0.03	88.2	8.1	0.06	1.82	2.37	11.49
	S16	767	-13.2957	-70.7933	T	50	16	9	194	0.7	18.8	7.6	29.1	0.00	85.4	8.0	0.51	0.17	1.07	13.49
	S17	700	-13.2634	-70.7801	M	44	17	13	741	98.0	22.5	7.6	85.4	0.03	84.4	7.3	0.66	0.33	0.59	7.49
	S18	666	-13.2244	-70.7601	T	-	21	17	225	-	-	-	-	-	-	-	-	-	-	-
	S19	604	-13.2182	-70.7212	M	32	14	17	488	118.0	22.1	7.9	91.2	0.03	88.8	7.8	0.83	1.20	2.97	88.00
	S20	482	-13.1857	-70.6266	T	39	12	10	164	13.0	24.9	7.6	65.3	0.02	71.9	6.0	0.25	0.15	0.09	3.13
	S21	478	-13.1860	-70.6187	T	37	18	10	90	7.9	22.7	8.3	67.6	0.02	91.4	7.9	0.80	0.90	1.36	6.13
	S22	472	-13.1915	-70.5543	T	-	19	4	297	-	-	-	-	-	-	-	-	-	-	-
	S23	429	-13.2090	-70.5449	T	41	21	16	208	2.4	-	-	-	-	-	-	0.07	0.20	35.39	37.83
Lowland (Inambari)	S24	419	-13.2090	-70.5445	M	36	19	11	387	64.6	24.4	7.8	95.6	0.04	80.8	6.8	1.05	1.76	-	122.74
	S25	397	-13.1755	-70.4945	T	9	20	8	433	0.2	-	-	-	-	-	-	0.57	5.56	0.00	7.40
	S26	358	-13.1736	-70.3829	T	18	14	12	193	168.7	21.2	5.0	7.7	0.00	18.9	1.7	-	-	0.00	0.82
	S27	348	-13.1934	-70.3900	M	-	-	11	-	-	25.6	8.0	340.0	0.17	78.7	6.4	-	-	-	-
	S28	279	-12.8904	-70.3395	M	-	7	28	30	178.0	-	-	-	-	-	-	0.13	5.46	4.45	0.45
	S29	231	-12.7867	-70.0536	M	-	-	2	-	313.0	23.1	7.1	49.4	0.01	62.0	5.3	0.16	6.94	0.00	3.59
	S30	221	-12.7689	-70.0000	M	-	-	18	-	-	-	-	-	-	-	-	-	-	-	-
	S31	220	-12.7851	-70.0099	M	-	-	13	-	-	-	-	-	-	-	-	-	-	-	-
	S32	200	-12.7608	-69.8476	M	-	8	19	15	479.3	22.6	6.7	47.9	0.01	70.0	6.0	0.66	2.06	34.27	0.00

Table 1 Continued

Site	Elevation (m a.s.l.)	Latitude (DD)	Longitude (DD)	Taxon Richness			Turb. (FTU)	Temp. (°C)	pH	SpCond ($\mu\text{S cm}^{-1}$)	Sal. (ppt)	DO (% sat.)	DO (mg mL ⁻¹)	DIN (mg L ⁻¹)	SRP (mg L ⁻¹)	Chlor. <i>a</i> : water (mg m ⁻³)	Chlor. <i>a</i> : benthic (mg m ⁻²)
				M/T/O	E	MI											
Lowland (MDD)																	
S33	272	-11.7833	-69.1852	O	-	15	-	21.6	7.3	94.8	0.04	78.4	6.9	-	-	-	-
S34	248	-12.2771	-69.1524	O	-	29	-	22.7	4.9	6.0	0.00	61.6	5.3	-	-	-	-
S35	268	-11.4090	-69.4738	O	-	17	23	193	-	-	-	-	-	-	-	-	-
S36	264	-11.4321	-69.3415	O	-	3	-	-	-	-	-	-	-	-	-	-	-
S37	262	-11.5050	-69.3008	O	-	8	-	-	-	-	-	-	-	-	-	-	-
S38	256	-11.4631	-69.3064	O	-	10	-	-	-	-	-	-	-	-	-	-	-
S39	242	-11.0106	-69.5557	O	39	29	17	282	6.8	-	-	-	-	0.05	2.59	0.00	0.05
S40	225	-10.9454	-69.5723	O	-	21	-	22.2	7.0	381.2	0.19	25.9	2.3	-	-	-	-
S41	206	-12.7851	-70.0099	O	-	18	31	45	6.9	22.8	0.00	61.0	5.3	0.91	1.40	30.97	0.00

DD, decimal degrees; DIN, dissolved inorganic nitrogen; DO, dissolved oxygen; E, epilithon; F, fish; M, main stem of the Arazá-Inambari; MDD, Madre de Dios; MI, macroinvertebrate; MI#, number of macroinvertebrate individuals per 1000 cm²; m a.s.l., metres above sea level; O, outside of Arazá-Inambari watershed; Sal., salinity; SpCond, specific conductivity; SRP, soluble reactive phosphorus; T, tributary of the Arazá-Inambari river; Temp., temperature; Turb., turbidity.

a-
v-
er-
a-
ge-
v-
al-
u-
es-
b-
ei-
ng
r-
e-
p-
o-
rt-
e-
d.
To

minimize diel variation in solar insolation, most measurements were taken between 12:00 and 16:00 h. Dissolved nutrient concentrations were measured by collecting water samples in polyethylene bottles that had been repeatedly rinsed with stream water, filtering the water through Whatman GF/F filters (Whatman Inc., Piscataway, NJ, USA), and then using Hach colorimetric test kits and a Hach DR 2800 mass spectrophotometer (Hach Co., Loveland, CO, USA) to obtain estimates. Water-column and benthic chlorophyll *a* were measured following the methods of Wetzel & Likens (1991). Briefly, triplicate water samples were collected in polyethylene bottles that had been rinsed with stream water and filtered through Whatman GF/C filters. Triplicate sediment samples were taken using a small plastic Petri dish (5 cm diameter \times 1.3 cm height) and a spatula. For extraction, filters were immediately placed into individual dark vials with 90% ethanol for 24 h. Chlorophyll *a* concentration was measured spectrophotometrically and corrected for pheophytin by subtracting absorbances after addition of 0.1 N HCl.

Epilithon assemblages were sampled qualitatively by using a toothbrush to dislodge detritus and attached algae from the surface of a rock arbitrarily selected from flowing water, then rinsing the loosened epilithon into a jar with 10% formalin. Macroinvertebrates were sampled quantitatively using a Surber sampler (200 cm², 0.200 mm mesh, five replicates per site for a total of 1000 cm²), and qualitatively using a dipnet and targeted searches of all obvious habitat types: the samples were then preserved in 70% ethanol. Fishes were sampled using combinations of electrofishing, seines, dipnets, gillnets and hook-and-line. Fish sampling effort was similar across sites (i.e. 1–2 h of electrofishing at all sites with fish, combined with similar periods of gill-netting at lowland sites) but was not standardized, with the exception of sites S28–S32 where these methods were supplemented by 58 person-hours of fishing with hook and line. Specimens were euthanized by immersion in a 1% solution of tricaine methanesulfonate (MS-222), preserved in 10% formalin, and later transferred to 70% ethanol and catalogued at museums affiliated with universities in Peru (Museo de Historia Natural, Universidad Nacional Mayor de San Marcos) and the USA (Auburn University Museum). Specimens were counted and identified using microscopes and a variety of keys and checklists.

Data analysis

We used regression analysis to examine how physicochemical parameters changed with elevation for main-channel (partially affected) and tributary (relatively unaffected) sites. Effects of both elevation and stream type (tributary versus main channel) on species richness of epilithic algae, macroinvertebrates and fishes were examined using analysis of covariance (ANCOVA). We also compared assemblage structure between tributary and main-channel sites using non-metric multidimensional scaling (NMDS) analysis of either



Figure 2 Examples of representative habitats (a–c) and anthropogenic impacts (d, e) in the Arazá–Inambari watershed, south-eastern Peru: (a) source of the Arazá River (site S1, 4304 m a.s.l.); (b) the upper Arazá main stem (site S4, 3051 m a.s.l.); (c) the lower Inambari River (site S34, 200 m a.s.l.); (d) construction of the Interoceanic Highway along the Arazá main stem (site S11, 1587 m a.s.l.); (e) placer mine targeting gold along the banks of the Inambari River (near site S33, 220 m a.s.l.).

absolute (macroinvertebrates and fish) or relative (algae) abundance data with Sørensen (Bray–Curtis) distance measures. All data were $\log_{10}(n + 1)$ -transformed in order to approximate a normal distribution. Analysis of similarity (ANOSIM) was used to test for significant differences in epilithon assemblage structure between sites without (S1–S7) and with (S8–S26) fish; macroinvertebrate assemblage structure between sites without (S1–S7) and with (S8–S32) fish; and macroinvertebrate and fish assemblage structure (separately) between sites upstream (S1–S26) and downstream (S27–S32) of the onset of intense placer mining. For sites where both assemblage and environmental data were collected, canonical correspondence analysis (CCA) was used to explore relationships between epilithon, macroinvertebrate and fish assemblage structure and physicochemical data. Multivariate analyses were conducted using the programs PC-ORD 5.21 and PRIMER-E 6.

Predictions made by the RCC regarding distributional responses of macroinvertebrate functional feeding groups (FFGs) to availability of alternate food sources (i.e. coarse allochthonous detritus versus autochthonous benthic algae) were tested by comparing the taxonomic richness of shredders versus scrapers as a percentage of total macroinvertebrate richness.

RESULTS

Physicochemical gradients

Water temperature had a left-skewed U-shaped response to elevation ($R^2 = 0.93$ for main-channel sites), decreasing slightly from 12 °C at 4300 m a.s.l., and then increasing to around 25 °C at 200 m (Fig. 3a). Dissolved oxygen (DO) showed a strongly centre-weighted hump-shaped response to elevation ($R^2 = 0.89$ for main-channel sites), increasing from 5.0 mg L⁻¹ at 4300 m a.s.l. to c. 9.0 mg L⁻¹ between 2700 and 1200 m, then decreasing again to 200 m (Fig. 3b). Across all sites, pH ranged from 4.9 to 8.3 (Table 1), and dissolved inorganic nitrogen (DIN, the sum of ammonium, nitrate and nitrite) concentrations ranged from 0.05 to 1.06 mg L⁻¹ (Fig. 3g). Neither pH nor DIN appeared to be related to either elevation or stream type. Water-column chlorophyll *a* (range: 0.0–35.4 mg m⁻³) also showed no strong relationship, although higher values generally were recorded at lower-elevation sites (Fig. 3j). Maximum benthic chlorophyll *a* concentrations (range: 0.0–122.7 mg m⁻²) were also measured at lower elevations (Fig. 3k).

Regression analyses indicated that turbidity increased with declining elevation among Inambari main-stem sites

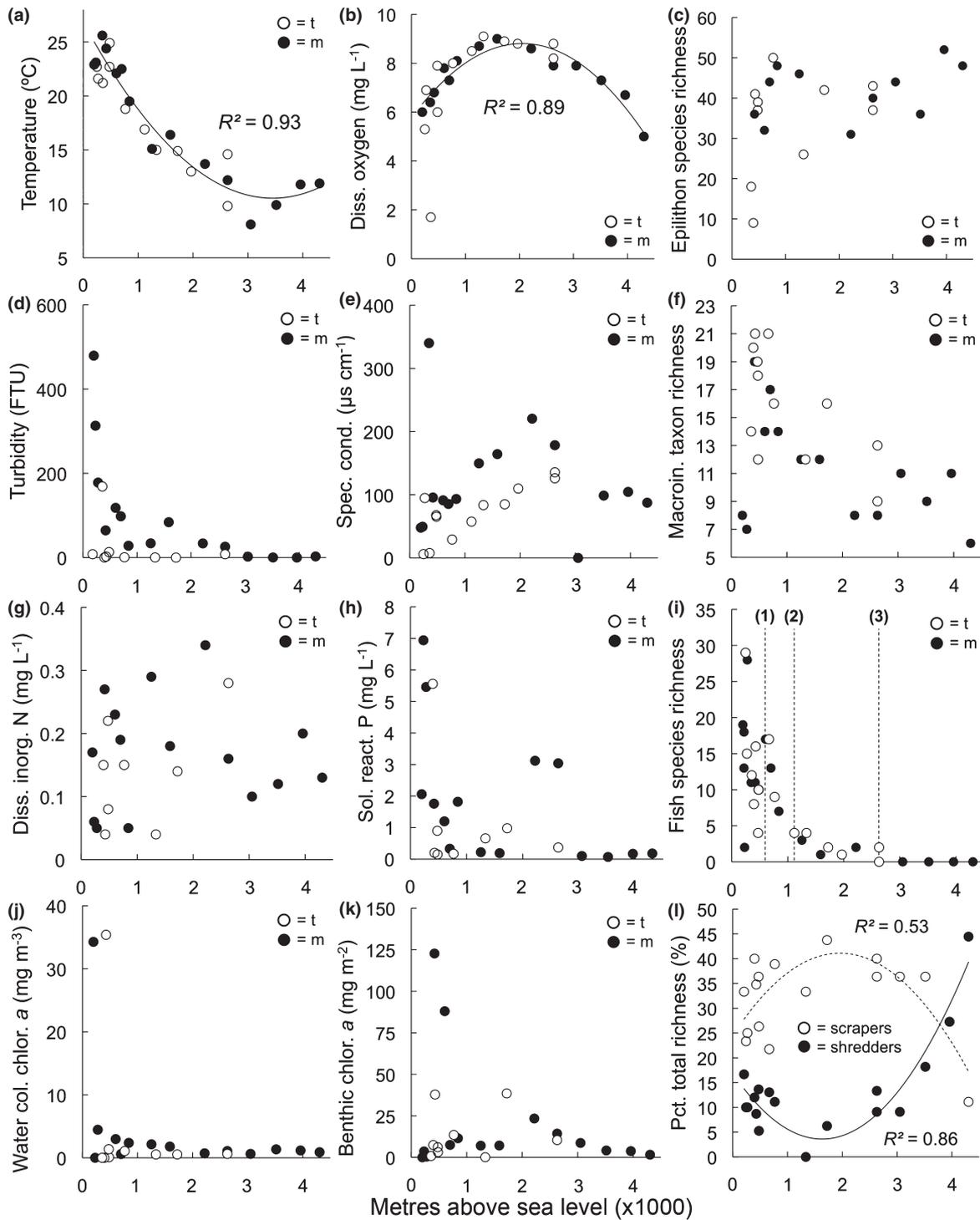


Figure 3 Physicochemical and biological trends along a 4100-m elevational range in the Arazá-Inambari watershed, south-eastern Peru. In plots (a–k), open symbols represent tributaries (t) and closed symbols represent main-channel sites (m). Subsets of sites were sampled for physicochemical and biological parameters: (a) temperature (°C); (b) dissolved oxygen (DO) (mg L⁻¹), (c) epilithon species richness; (d) turbidity (FTU); (e) specific conductivity (µS cm⁻¹), (f) macroinvertebrate taxon richness; (g) dissolved inorganic nitrogen (mg L⁻¹); (h) soluble reactive phosphorous (mg L⁻¹); (i) fish species richness, vertical dashed lines represent (1) the upper elevational limit of piscivorous fishes, (2) the upper elevational limit of herbivorous-detritivorous fishes, and (3) the upper elevational limit of fishes (Fig. 5); (j) water column chlorophyll a (mg m⁻³); (k) benthic chlorophyll a (mg m⁻²); and (l) percentage total richness of macroinvertebrates identified as scrapers (open symbols) and shredders (closed symbols). In (l) model for scrapers: $y = -0.000004x^2 + 0.017x + 24.47$; shredders: $y = 0.000005x^2 - 0.016x + 16.91$. Regression equations and R^2 values for temperature and dissolved oxygen calculated for main-stem data only (model for temperature: $y = 0.000001x^2 - 0.0095x + 26.85$; DO: $y = -0.0000007x^2 + 0.003x + 5.77$).

($R^2 = 41.6$, $P < 0.05$) but not among tributaries ($R^2 = 8.1$, $P = 0.26$), indicating that anthropogenic impacts within the main channel were likely to be the primary source of suspended sediment. Anthropogenic activities associated with sediment fluxes shifted from road construction (Fig. 2d) at intermediate elevations (c. 2600–400 m) to placer mining (Fig. 2e) at lower elevations (c. 400–200 m) where turbidity reached 479 FTU (Fig. 3d). Erosion also appeared to have altered specific conductivity, which was markedly higher in main-channel sites than in tributary sites (Fig. 3e), and soluble reactive phosphorus concentrations, which were highest at lower-elevation sites where river sediments were being mined (Fig. 3h).

Taxonomic diversity gradients

The species richness of epilithic algae (228 total species; Dryad data repository: <http://datadryad.org>, doi:10.5061/dryad.28mb1) showed a slightly positive overall relationship with elevation ($R^2 = 0.15$, $P = 0.08$), but this pattern was not observed in main-stem or tributary sites when viewed separately (Fig. 3c). Macroinvertebrate taxon richness (79 total taxa; Dryad data repository, doi:10.5061/dryad.28mb1) decreased ($R^2 = 0.38$, $P < 0.0001$) and abundance increased with elevation ($R^2 = 0.37$, $P < 0.0001$) across both habitat types (Fig. 3f; Dryad data repository, doi:10.5061/dryad.28mb1). Mean macroinvertebrate abundance at the highest six sites (1145 individuals 1000 cm⁻²), all of which lacked fish, was more than twice that of the next highest six sites having fish (502 individuals 1000 cm⁻²). Although elevational patterns in macroinvertebrate richness and abundance spanned both habitat types, relationships were not as significant or as consistent in the main channel (richness: $R^2 = 0.22$, $P = 0.09$; abundance: $R^2 = 0.29$, $P = 0.05$) when compared with tributaries (richness: $R^2 = 0.41$, $P = 0.03$; abundance: $R^2 = 0.57$, $P < 0.05$). Macroinvertebrate abundances at main-stem sites where anthropogenic impacts were most obvious (e.g. S28, S32) were extremely low (15–30 individuals 1000 cm⁻², Table 1), and macroinvertebrate assemblages at main-stem sites generally had significantly fewer taxa (mean = 11) than tributaries (mean = 16 taxa; Student's *t*-test: $t = 3.12$, $P = 0.005$). Moreover, after accounting for variance in species richness caused by elevation (ANCOVA, $F = 8.06$, $P < 0.01$), stream type (tributary versus main-stem) significantly affected macroinvertebrate species richness ($F = 5.92$, $P < 0.05$).

No fishes were collected between 4304 and 2630 m a.s.l. (Table 1), but below this elevation we collected 140 species (5589 individuals; Dryad data repository, doi:10.5061/dryad.28mb1), approximately half of the 287 species known for the Madre de Dios Basin (Ortega *et al.*, 2011), including one non-native species (rainbow trout, *Oncorhynchus mykiss*) collected only at 2630 and 2218 m. Fish species richness increased with decreasing elevation in both main-stem ($R^2 = 0.52$, $P < 0.05$) and tributary ($R^2 = 0.72$, $P < 0.0001$) habitats. Although this relationship was stronger in tributaries than in the main channel, ANCOVA indicated that fish species richness was not

significantly affected by site type ($F = 0.01$, $P = 0.93$) after removing the variance caused by elevation ($F = 19.22$, $P < 0.001$). Few fishes were collected from main-stem sites of the lower Inambari River where placer mining was most intense (sites S28 and S31–S34). Fifty-eight person-hours of hook-and-line effort by experienced fishermen yielded only three specimens at these sites: two catfish (*Ageneiosus inermis* and *Cetopsis coecutiens*) and a freshwater stingray (*Potamotrygon motoro*). Moreover, intensive electrofishing of these sites over a period of 5 days yielded a total of only six specimens of the suckermouth armoured catfish *Chaetostoma lineopunctatum*, a species that was otherwise common in the region. For example, 73 specimens of *C. lineopunctatum* were collected in < 1 h of electrofishing at a relatively unaffected tributary site (S26) with a similar elevation and physical habitat to those main-stem sites yielding only six specimens in 5 days of sampling (Dryad data repository, doi:10.5061/dryad.28mb1).

Assemblage composition

All non-metric multidimensional scaling (NMDS) analyses yielded three-dimensional solutions (Fig. 4). NMDS axes using data collected at all sites explained 89.2% of variation in epilithon assemblages (axis 1 = 36.1%, axis 2 = 27.9%, axis 3 = 25.2%), 81.3% of variation in macroinvertebrate assemblages (axis 1 = 30.6%, axis 2 = 29.5%, axis 3 = 21.2%), and 72.9% of variation in fish assemblages (axis 1 = 25.8%, axis 2 = 25.6%, axis 3 = 21.5%). The final stress level of the best solution was 9.7 for epilithon assemblages indicating a 'good' ordination (stress range 5–10; McCune & Mefford, 1999), 13.7 for macroinvertebrate assemblages, and 15.0 for fish assemblages, with the latter two indicating a 'fair' ordination (stress range 10–20). Multivariate analyses of epilithic algae and macroinvertebrate assemblages displayed a close clustering of high elevation sites where fishes were mostly absent (S1–S7; only two fish species were found at S6 and they were present in low numbers), and a strong divergence from this cluster in association with the presence of fish at lower elevations (Fig. 4). ANOSIM indicated significant differences in epilithon and macroinvertebrate assemblage structure between sites where fish were absent and sites where fish were present (epilithon: $R = 0.43$, $P < 0.05$; macroinvertebrate: $R = 0.23$, $P < 0.05$). Although placer mining (S27–S32) did not appear to be associated with distinctive clustering of assemblages in multivariate space, ANOSIM detected significant differences in macroinvertebrate and fish assemblage structure between sites upstream and downstream of placer mining (macroinvertebrate: $R = 0.85$, $P = 0.01$; fish: $R = 0.18$, $P < 0.05$).

Physicochemical influences on assemblage composition

Canonical correspondence analysis resulted in three canonical axes that explained a total of 26.5% of variation in epilithon assemblage structure (axis 1 = 11.2%, axis 2 = 8.6%, axis 3 = 6.7%), 31.1% of variation in macroinvertebrate

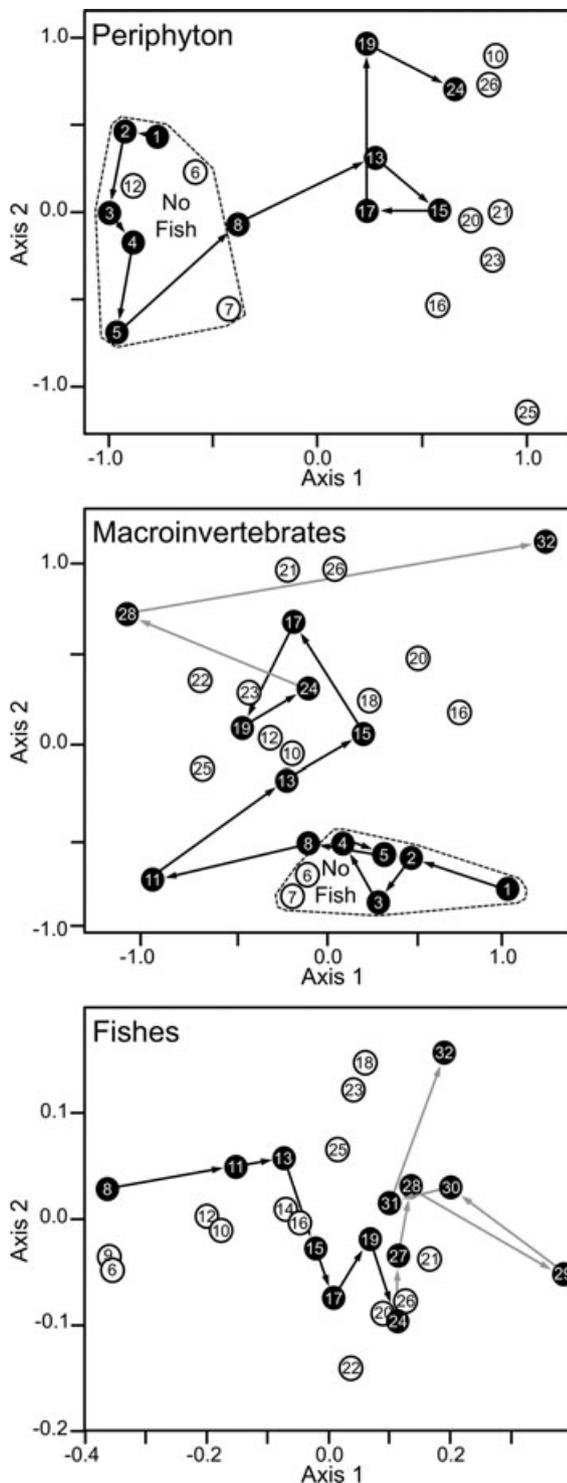


Figure 4 Non-metric multidimensional scaling (NMDS) analysis of assemblages of epilithic algae, macroinvertebrates and fishes from relatively unaffected tributary sites (open circles) and main-channel sites (closed circles with transitions indicated by arrows) within the Arazá-Inambari-Madre de Dios watershed, south-eastern Peru. Numbers within circles indicate sample sites, with the lowest numbers indicating the highest elevation sites (i.e. site 1 = 4304 m a.s.l. and 34 = 200 m a.s.l.). Intensive placer mining began between sites 24 and 25 and continued through site 34 (indicated by grey arrows).

assemblage structure (axis 1 = 15.3%, axis 2 = 8.5%, axis 3 = 7.3%), and 45.8% of variation in fish assemblage structure (axis 1 = 19.0%, axis 2 = 17.3%, axis 3 = 9.5%). Elevation, turbidity, temperature and specific conductivity were associated with distributions of all three assemblages. For epilithon assemblages, axis 1 contrasted high-elevation, main-channel sites having low turbidity and temperature with low-elevation sites having high turbidity and temperature. Axis 2 contrasted sites having high turbidity with sites having high DO concentrations (S6, S10, S12, S16). For macroinvertebrate assemblages, canonical axis 1 contrasted high-elevation sites having high conductivity with low-elevation sites having higher temperatures and turbidity. Axis 2 contrasted sites with high pH versus sites with high DO. For fish assemblages, axis 1 contrasted high-elevation sites with high conductivity and DO versus sites with high temperature and high turbidity. Axis 2 contrasted sites with high turbidity versus sites with high pH.

Functional feeding groups

In contrast to our hypothesis that assumed poor quality and quantity of allochthonous detritus in puna grasslands near the source of the Arazá-Inambari, macroinvertebrate functional feeding groups in headwater reaches matched RCC predictions. Shredders dominated at higher elevations (c. 4300–3500 m a.s.l.) but rapidly declined at middle elevations where scrapers dominated (c. 3500–2000 m; Fig. 3l). These trends began to reverse at lower elevations (i.e. below 2000 m; Fig. 3l). The highest reaches occupied by fishes were dominated by the invertivorous catfish genera *Astroblepus* (2630–358 m) and *Trichomycterus* (1721–348 m; Fig. 5). A nektonic invertivore (*Hemibrycon*, 1253–200 m) was the third fish taxon to occur, followed by benthic (*Ancistrus*, 1118–206 m) and nektonic (*Parodon*, 842–348 m) herbivore–detritivores (Fig. 5). Below 842 m, fish diversity increased rapidly, with two piscivorous species (*Crenicichla* sp. and *Hoplias malabaricus*) appearing at 666 m (Fig. 5), and the wood-eating catfish (*Hypostomus pyrineusi*) and several electrogenic invertivores (Gymnotiformes) appearing at 279 m (Dryad data repository, doi:10.5061/dryad.28mb1).

DISCUSSION

We observed strong elevational trends in physicochemical parameters, taxonomic richness and trophic diversity of macroinvertebrates and fishes, although some relationships were weaker at low-elevation sites where human impacts were more prevalent. Water temperature and dissolved oxygen displayed nonlinear, U-shaped and hump-shaped relationships with elevation. High water temperatures in the puna grasslands (> 4000 m a.s.l.) were probably caused by intense solar radiation given the high elevation and the lack of shrubs or trees to provide shade, whereas shade from montane forest below the tree line probably contributed to decreased temperatures at middle elevations, and increased

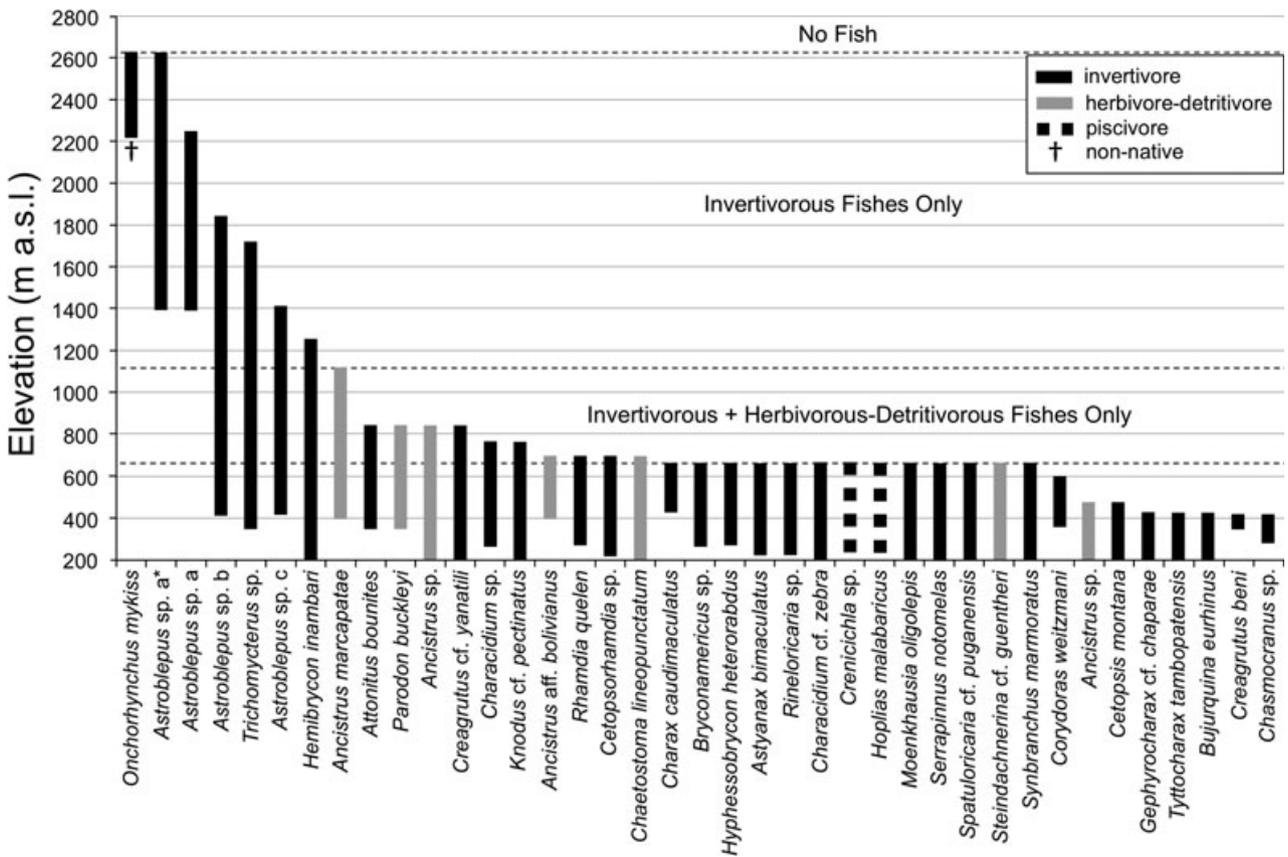


Figure 5 Elevational ranges and trophic specializations of fish species occurring at elevations > 400 m a.s.l. in tributary and main-channel sites within the Arazá-Inambari-Madre de Dios watershed, south-eastern Peru.

ambient temperatures probably drove a steady increase in water temperature at lower elevations. Oxygen concentrations should be negatively correlated with water temperature, but we recorded highest dissolved oxygen values at sites *c.* 1000 m below the elevation where the lowest water temperatures were recorded (Fig. 3a,b): a pattern most likely caused by low partial pressures of atmospheric O₂ at high elevations (Jacobsen, 2000).

Macroinvertebrate and fish assemblages followed a general pattern of lower taxonomic richness at higher elevations, consistent with previous research in Andean streams (Jacobsen, 2004; Albert *et al.*, 2011; Appendix S1). Both assemblages contained taxa with ranges restricted to relatively narrow elevational zones, and these taxa are candidates for range shifts in response to global warming. Within macroinvertebrate assemblages, these restricted-range taxa were distributed across several orders (Dryad data repository, doi:10.5061/dryad.28mb1), but among native fishes, only the loricioid catfish genera *Ancistrus*, *Astroblepus* and *Trichomycterus* held species with distributions entirely limited to elevations greater than 400 m, including some limited to elevational bands varying as little as 3.4 °C (Table 1, Fig. 5). Moreover, phylogeographical studies of these same genera describe high levels of drainage-specific genetic structure (Vélez-Espino, 2006; Unmack *et al.*, 2009; Schaefer *et al.*,

2011) consistent with recent experimental and theoretical research showing that headwaters are crucial to the maintenance of regional biodiversity (Carrara *et al.*, 2012). Therefore, despite low α -diversity in high-elevation aquatic communities, regional biodiversity across Andean streams is likely to be quite high, highlighting the overall threat that regional impacts like climate change pose to aquatic biodiversity.

NMDS ordinations of epilithon and macroinvertebrate assemblage structure resulted in clustering of high-elevation sites where fishes were absent (Fig. 4). Predation is the most likely cause of this compositional shift, given that high-elevation fish assemblages consisted exclusively of benthic invertivores and the first six main-channel sites with fishes had less than half as many benthic macroinvertebrates as the six sites immediately upstream that lacked fish (mean = 502 individuals 1000 cm⁻² versus 1145). Macroinvertebrates were the sole primary consumers in streams from the source of the Arazá-Inambari to *c.* 1100 m a.s.l., where the first herbivorous-detritivorous fishes appeared. Between *c.* 1100 and 700 m, taxonomic diversity of fish primary consumers increased and the relative dominance of macroinvertebrate grazers decreased (Figs 3i,l & 5), but no other fish trophic levels were added. Piscivores became a regular component of local fish assemblages at *c.* 700 m, but most other distinctive elements of the diverse Amazonian fish fauna (e.g. electro-

genic knife-fishes, wood-eating and parasitic catfishes) were restricted to elevations below 400 m.

Across these elevational zones (i.e. 4304–2500, 2500–1100, 1100–700, 700–400, and 400–200 m a.s.l.) no differences were observed in abundances of either planktonic or attached algae (*F*-test for water-column chlorophyll *a*: $P = 0.23$, and benthic chlorophyll *a*: $P = 0.49$). However, epilithic algae taxonomic richness displayed a weak positive trend with elevation (Fig. 3c), and several orders of diatoms and green and blue-green algae included taxa with ranges restricted to high elevations (Dryad data repository, doi:10.5061/dryad.28mb1). Our observation of greater taxonomic richness at higher elevations contrasts with two previous studies of algal diversity in the subtropical Himalayas that revealed the opposite pattern (Ormerod *et al.*, 1994; Wang *et al.*, 2011). More research is needed to determine (1) if elevational trends in epilithon diversity are widespread, (2) the underlying factors that drive these trends, and (3) whether or not such factors differ across continents or latitudes.

In contrast to the patterns of low variance in algae diversity and invariance in algal abundance with increasing elevation, patterns of variation in the quality of particulate organic matter (Townsend-Small *et al.*, 2007) and variation in the relative diversity of detritivores suggest that longitudinal processing of detritus might play a more important role in driving elevational–longitudinal shifts in Andean aquatic community structure. We had predicted that the importance of allochthonous material would be relatively low for food webs of streams draining grasslands at high elevations in the Andes, but this prediction was not supported. Rather, macroinvertebrate assemblages of high-elevation grassland streams were dominated by leaf-shredders, as predicted by the river continuum concept, indicating that allochthonous CPOM remained an important food resource in headwaters. Taxonomic dominance shifted to biofilm scrapers at c. 3800 m and, for reasons that are not immediately apparent, this trend began to reverse below 2000 m (Fig. 3l). The inferred importance of CPOM as a food resource for aquatic macroinvertebrates at high elevations in the Andes, as well as the linkage between biodiversity and organic matter processing, was supported by Dangles *et al.* (2011), who found that at least eight species of macroinvertebrate shredders contributed to decomposition of the dominant terrestrial grass *Calamagrostis intermedia* in high-elevation (3200–3900 m) Ecuadorian grassland streams, and that both shredder diversity and abundance significantly affected decomposition rates.

Relatively little is known about allochthonous detrital sources, sinks and cycling in Andean rivers, although the available data suggest that detrital quality declines along the longitudinal continuum. In a study of isotopic variation in particulate and dissolved organic carbon across a 1700-m (2040–360 m) vertical–longitudinal gradient within a tributary of the Pachitea River in central Peru, Townsend-Small *et al.* (2007) found that POM in high-elevation Andean headwater streams is qualitatively distinct and more hetero-

geneous than POM in lower-elevation main-channel sites, and POM along the fluvial continuum probably has various components subject to different decomposition rates. Relatively low nutritional quality of POM in lower-elevation Andean rivers is suggested by Lujan *et al.* (2011), who used isotopes to examine trophic partitioning among detritivorous loricarioid fishes at a 200-m site in the Marañón River of northern Peru. They found that POM (seston) was underutilized as a food resource, whereas cellulosic carbon from coarse woody debris was preferentially assimilated.

Tropical streams generally have lower diversity and abundance of shredding macroinvertebrates than streams at higher latitudes (Boyero *et al.*, 2011a). Irons *et al.* (1994) and Dobson *et al.* (2002) proposed that this could be due to higher temperatures in tropical streams that increase microbial metabolism and leaf-litter decomposition rates (Webster & Benfield, 1986; Boyero *et al.*, 2011b), which in turn would limit the availability of particulate organic matter for metazoan consumers. According to this microbial metabolism hypothesis, Dobson *et al.* (2002) predicted that macroinvertebrate shredders should be more common at higher elevations in tropical streams. Results from our study are consistent with the idea that elevational and latitudinal differences in temperature regimes influence both the quality and quantity of detrital resources in streams and the diversity and distribution patterns of metazoan shredders.

A second hypothesis is that the shredder niche in tropical streams is occupied by shrimps, crabs and fishes, and that these larger, more mobile consumers, which are not typically collected by macroinvertebrate Surber samplers, compete with and prey upon macroinvertebrate shredders (Dobson *et al.*, 2002; Hall *et al.*, 2011). Our observations of a sharp decline in macroinvertebrate abundance at the first occurrence of fishes, and a longitudinal increase in the diversity of detritivorous fishes, support this second hypothesis. However, these hypotheses are not mutually exclusive, and it should be noted that the longitudinal decline in shredder dominance began well upstream of the first occurrence of either fishes (Fig. 3i,l) or decapods. The strong patterns that we observed highlight the likely importance of trophic interactions in shaping longitudinal distributions of organisms along fluvial continua throughout the Andes. To achieve a synthetic model of aquatic community structure in the region, however, research on more Andean drainage basins that takes into account additional factors influencing the longitudinal distributions of species and functional groups is needed.

Anthropogenic impacts

Strong patterns of longitudinal zonation and restricted elevational distributions among both invertebrate and vertebrate taxa imply that Andean stream communities may respond to global warming via changes in species' elevational distributions in a manner similar to that already documented for

certain terrestrial organisms (Forero-Medina *et al.*, 2011; Larson *et al.*, 2011). Warmer temperatures in the Andes could also result in a faster microbial processing of particulate organic matter in streams (Boyero *et al.*, 2011b) that may lead to decreased diversity of leaf-shredding insects. In temperate North American and subtropical Asian streams, aquatic insect emergence times (Harper & Peckarsky, 2006), diversity and abundance (Li *et al.*, 2012) have already shifted in response to recent warming trends. Impacts of climate change on aquatic communities of tropical montane streams should be even greater than in temperate and polar regions where organisms are evolutionarily adapted to inherently highly variable thermal regimes (Sheldon *et al.*, 2011).

Of immediate concern, however, are the acute impacts of mining and road construction. Soluble reactive phosphorus concentrations near affected areas were more than ten times higher than at similar elevations in the neighbouring Tambopata River, where mining is uncommon (K.A. Roach, unpublished data). Turbidity and specific conductivity, both of which increase in streams with high suspended sediment loads (Bjerklie & LaPerriere, 1985; Gray, 1996), were highest at main-channel sites immediately downstream of affected areas. At the most affected low-elevation sites, benthic macroinvertebrates and fishes were largely absent and species assemblage structure was significantly different from that recorded at less affected sites upstream. Economically important fishes present in the Madre de Dios main channel were apparently absent from the Inambari River (e.g. large species of the catfish family Pimelodidae and characiform family Serrasalminidae; Chang, 1998). Similar impacts of mining on fish stocks have been observed in other regions of the Andes and elsewhere in the Neotropics (Fossati *et al.*, 2001; Mol & Ouboter, 2004; Van Damme *et al.*, 2008; Couceiro *et al.*, 2011).

Trends that we observed in the Arazá-Inambari River imply that longitudinal fluvial connectivity is important not only for regional biodiversity (Carrara *et al.*, 2012), but also to ecosystem function. Unfortunately, challenges to the maintenance of aquatic biodiversity and fluvial connectivity within the Amazon Basin are increasing due to the rapid expansion of roads, dams and other human impacts throughout the region (Finer & Jenkins, 2012; Castello *et al.*, 2013). During this period of rapid and expansive development, scientists should prioritize baseline research documenting the biodiversity and ecological structure and function of fluvial ecosystems that unite the Andes and Amazon Basin.

ACKNOWLEDGEMENTS

We thank Hernan Ortega (Natural History Museum of San Marcos University, Lima, Peru) for assistance with permits, logistics and fieldwork; Don Taphorn, José Birindelli, David Brooks, Max Hidalgo, Rosemary Argomedo, Juan Valadez, Brian Booth, Mark Dion, Clay Risen and Scott Schaefer for assistance with collecting and identifying specimens; David Werneke and Jonathan Armbruster (Auburn University

Museum) for cataloguing and curating fish specimens; and Paulo Petry (The Nature Conservancy) for stream order maps. Funding came from a Coypu Foundation grant to N.K.L., NSF grant OISE-1064578 to N.K.L., the Aquatic Critter, Inc., and the estate of George and Carolyn Kelso via the International Sportfish Fund.

REFERENCES

- Albert, J.S., Petry, P. & Reis, R.E. (2011) Major biogeographic and phylogenetic patterns. *Historical biogeography of neotropical freshwater fishes* (ed. by J.S. Albert and R.E. Reis), pp. 21–57. University of California Press, Berkeley, CA.
- Anderson, E.P. & Maldonado-Ocampo, J.A. (2011) A regional perspective on the diversity and conservation of tropical Andean fishes. *Conservation Biology*, **25**, 30–39.
- Aufdenkampe, A.K., Hedges, J.I., Richey, J.E., Krusche, A.V. & Llerena, C.A. (2001) Sorptive fractionation of dissolved organic nitrogen and amino acids onto fine sediments within the Amazon Basin. *Limnology and Oceanography*, **46**, 1921–1935.
- Bjerklie, D.M. & LaPerriere, J.D. (1985) Gold-mining effects on stream hydrology and water quality, Circle Quadrangle, Alaska. *Water Resources Bulletin*, **21**, 235–243.
- Boyero, L., Pearson, R.G., Dudgeon, D. *et al.* (2011a) Global distribution of a key trophic guild contrasts with common latitudinal diversity patterns. *Ecology*, **92**, 1839–1848.
- Boyero, L., Pearson, R.G., Gessner, M.O. *et al.* (2011b) A global experiment suggests climate warming will not accelerate litter decomposition in streams but might reduce carbon sequestration. *Ecology Letters*, **14**, 289–294.
- Brack, E.A. & Mendiola, V.C. (2000) *Ecología del Peru*. Bruño, Lima, Peru.
- Carrara, F., Altermatt, F., Rodriguez-Iturbe, I. & Rinaldo, A. (2012) Dendritic connectivity controls biodiversity patterns in experimental metacommunities. *Proceedings of the National Academy of Sciences USA*, **109**, 5761–5766.
- Castello, L., McGrath, D.G., Hess, L.L., Coe, M.T., Lefebvre, P.A., Petry, P., Macedo, M.N., Reno, V.F. & Arantes, C.C. (2013) The vulnerability of Amazon freshwater ecosystems. *Conservation Letters*, doi:10.1111/conl.12008.
- Chang, F. (1998) Fishes of the Tambopata-Candamo reserved zone, southeastern Perú. *Revista Peruana de Biología*, **5**, 15–26.
- Couceiro, S.R.M., Hamada, N., Forsberg, B.R. & Padovesi-Fonseca, C. (2011) Trophic structure of macroinvertebrates in Amazonian streams impacted by anthropogenic siltation. *Austral Ecology*, **36**, 628–637.
- Dangles, O., Crespo-Pérez, V., Andino, P., Espinosa, R., Calvez, R. & Jacobsen, D. (2011) Predicting diversity effects on ecosystem function in natural communities: insights from extreme stream ecosystems. *Ecology*, **92**, 733–743.
- Dobson, M., Magana, A., Mathooko, J.M. & Ndegwa, F.K. (2002) Detritivores in Kenyan highland streams: more

- evidence for the paucity of shredders in the tropics? *Freshwater Biology*, **47**, 909–919.
- Finer, M. & Jenkins, C.N. (2012) Proliferation of hydroelectric dams in the Andean Amazon and implications for Andes-Amazon connectivity. *PLoS ONE*, **7**, 1–9.
- Forero-Medina, G., Terborgh, J., Socolar, S.J. & Pimm, S.L. (2011) Elevational ranges of birds on a tropical montane gradient lag behind warming temperatures. *PLoS ONE*, **6**, e28535.
- Fossati, O., Wasson, J.-G., Héry, C., Salinas, G. & Marín, R. (2001) Impact of sediment releases on water chemistry and macroinvertebrate communities in clear water Andean streams (Bolivia). *Archiv für Hydrobiologie*, **151**, 33–50.
- Freeman, M.C., Pringle, C.M. & Jackson, C.R. (2007) Hydrologic connectivity and the contribution of stream headwaters to ecological integrity at regional scales. *Journal of the American Water Resources Association*, **43**, 5–14.
- Fu, C., Wu, J., Wang, X., Lei, G. & Chen, J. (2004) Patterns of diversity, altitudinal range and body size among freshwater fishes in the Yangtze River basin, China. *Global Ecology and Biogeography*, **13**, 543–552.
- Gomi, T., Sidle, R.C. & Richardson, J.S. (2002) Understanding processes and downstream linkages of headwater systems. *BioScience*, **52**, 905–916.
- Goulding, M., Barthem, R. & Ferreira, E.J.G. (2003) *Smithsonian atlas of the Amazon*. Smithsonian Books, Washington, DC.
- Gray, N.F. (1996) Field assessment of acid mine drainage contamination in surface and ground water. *Environmental Geology*, **27**, 358–361.
- Greathouse, E.A. & Pringle, C.M. (2006) Does the river continuum concept apply on a tropical island? Longitudinal variation in a Puerto Rican stream. *Canadian Journal of Fisheries and Aquatic Sciences*, **63**, 134–152.
- Hall, R.O., Jr, Taylor, B.W. & Flecker, A.S. (2011) Detritivorous fish indirectly reduce insect secondary production in a tropical river. *Ecosphere*, **2**, 135.
- Hardin, C.P. (2006) Human impacts on headwater fluvial systems in the northern and central Andes. *Geomorphology*, **79**, 249–263.
- Harper, M.P. & Peckarsky, B.L. (2006) Emergence cues of a mayfly in a high-altitude stream ecosystem: potential response to climate change. *Ecological Applications*, **16**, 612–621.
- Henley, W.F., Patterson, M.A., Neves, R.J. & Lemly, A.D. (2000) Effects of sedimentation and turbidity on lotic food webs: a concise review for natural resource managers. *Reviews in Fisheries Science*, **8**, 125–139.
- Irons, J.G., III, Osgood, M.W., Stout, R.J. & Pringle, C.M. (1994) Latitudinal patterns in leaf litter breakdown: is temperature really important? *Freshwater Biology*, **32**, 401–411.
- Jacobsen, D. (2000) Gill size of trichopteran larvae and oxygen supply in streams along a 4000-m gradient of altitude. *Journal of the North American Benthological Society*, **19**, 329–343.
- Jacobsen, D. (2004) Contrasting patterns in local and zonal family richness of stream invertebrates along an Andean altitudinal gradient. *Freshwater Biology*, **49**, 1293–1305.
- Jacobsen, D. (2008a) Tropical high-altitude streams. *Tropical stream ecology* (ed. by D. Dudgeon), pp. 219–256. Academic Press, New York.
- Jacobsen, D. (2008b) Low oxygen pressure as a driving factor for the altitudinal decline in taxon richness of stream macroinvertebrates. *Oecologia*, **154**, 795–807.
- Jaramillo-Villa, U., Maldonado-Ocampo, J.A. & Escobar, F. (2010) Altitudinal variation in fish assemblage diversity in streams of the central Andes of Colombia. *Journal of Fish Biology*, **76**, 2401–2417.
- Laraque, A., Bernal, C., Bourrel, L., Darrozes, J., Christophoul, F., Armijos, E., Fraizy, P., Pombosa, R. & Guyot, J.L. (2009) Sediment budget of the Napo River, Amazon basin, Ecuador and Peru. *Hydrological Processes*, **23**, 3509–3524.
- Larson, T., Brehm, G., Navarrete, H., Franco, P., Gomez, H., Mena, J.L., Morales, V., Argollo, J., Blacutt, L. & Canhos, V. (2011) Range shifts and extinctions driven by climate change in the tropical Andes: synthesis and directions. *Climate change and biodiversity in the tropical Andes* (ed. by S.K. Herzog, R. Martinez, P.M. Jørgensen and H. Tiessen), pp. 47–67. Inter-American Institute for Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE), São José dos Campos, São Paulo.
- Li, F., Cai, Q., Jiang, W. & Qu, X. (2012) The response of benthic macroinvertebrate communities to climate change: evidence from subtropical mountain streams in Central China. *International Review of Hydrobiology*, **97**, 200–214.
- Lloyd, D.S., Koenings, J.P. & Laperriere, J.D. (1987) Effects of turbidity in freshwaters of Alaska. *North American Journal of Fisheries Management*, **7**, 18–33.
- Lujan, N.K., German, D.G. & Winemiller, K.O. (2011) Do wood grazing fishes partition their niche?: morphological and isotopic evidence for trophic segregation in Neotropical Loricariidae. *Functional Ecology*, **25**, 1327–1338.
- Maldonado, M., Maldonado-Ocampo, J.A., Ortega, H., Encalada, A.C., Carvajal-Vallejos, F.M., Rivadeneira, J.V., Acosta, F., Jacobsen, D., Crespo, A. & Rivera-Rondón, C.A. (2011) Biodiversity in aquatic systems of the tropical Andes. *Climate change and biodiversity in the tropical Andes* (ed. by S.K. Herzog, R. Martinez, P.M. Jørgensen and H. Tiessen), pp. 276–294. Inter-American Institute for Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE), São José dos Campos, São Paulo.
- McCune, B. & Mefford, M.J. (1999) *PC-ORD. Multivariate analysis of ecological data*. Version 4.0. MjM Software, Gleneden Beach, OR.
- Mol, J.H. & Ouboter, P.E. (2004) Downstream effects of erosion from small-scale gold mining on the instream habitat and fish community of a small Neotropical rainforest stream. *Conservation Biology*, **18**, 201–214.
- Ormerod, S.J., Rundle, S.D., Wilkinson, S.M., Daly, G.P., Dale, K.M. & Juttner, J. (1994) Altitudinal trends in the

- diatoms, bryophytes, macroinvertebrates and fish of a Nepalese river stream. *Freshwater Biology*, **32**, 309–322.
- Ortega, H., Hidalgo, M., Correa, E., Espino, J., Chocano, L., Trevejo, G., Meza, V., Cortijo, A.M. & Quispe, R. (2011) *Lista anotada de los peces de aguas continentales del Perú: Estado actual del conocimiento, distribución, usos y aspectos de conservación*. Ministerio del Ambiente, Dirección General de Diversidad Biológica, Museo de Historia Natural, UNMSM, Lima.
- Rosemond, A.D., Pringle, C.M., Ramírez, A. & Paul, M.J. (2001) A test of top-down and bottom-up control in a detritus-based food web. *Ecology*, **82**, 2279–2293.
- Schaefer, S.A., Chakrabarty, P., Geneva, A.J. & Sabaj Pérez, M.H. (2011) Nucleotide sequence data confirm diagnosis and local endemism of variable morphospecies of Andean astrolepid catfishes (Siluriformes: Astroblepidae). *Zoological Journal of the Linnean Society*, **162**, 90–102.
- Sheldon, K.S., Yang, S. & Tewksbury, J.I. (2011) Climate change and community disassembly: impacts of warming on tropical and temperate montane community structure. *Ecology Letters*, **14**, 1191–1200.
- Swenson, J.J., Carter, C.E., Domec, J.-C. & Delgado, C.I. (2011) Gold mining in the Peruvian Amazon: global prices, deforestation, and mercury imports. *PLoS ONE*, **6**, e18875.
- Thorp, J.H., Delong, M.D., Greenwood, K.S. & Casper, A.F. (2006) The riverine ecosystem synthesis: biocomplexity in river networks across space and time. *River Research and Applications*, **22**, 123–147.
- Tomanova, S., Tadescio, P.A., Campero, M., Van Damme, P.A., Moya, N. & Oberdorff, T. (2007) Longitudinal and altitudinal changes of macroinvertebrate functional feeding groups in neotropical streams: a test of the River Continuum Concept. *Fundamentals and Applied Limnology*, **170**, 233–241.
- Townsend-Small, A., Noguera, J.L., McClain, M.E. & Brandes, J.A. (2007) Radiocarbon and stable isotope geochemistry of organic matter in the Amazon headwaters, Peruvian Andes. *Global Biogeochemical Cycles*, **21**, GB2029.
- Townsend-Small, A., McClain, M.E., Hall, B., Noguera, J.L., Llerena, C.A. & Brandes, J.A. (2008) Suspended sediments and organic matter in mountain headwaters of the Amazon River: results from a 1-year time series study in the central Peruvian Andes. *Geochimica et Cosmochimica Acta*, **72**, 732–740.
- Unmack, P.J., Bennin, A.P., Habit, E.M., Victoriano, P.F. & Johnson, J.B. (2009) Impact of ocean barriers, topography, and glaciation on the phylogeography of the catfish *Trichomycterus areolatus* (Teleostei: Trichomycteridae) in Chile. *Biological Journal of the Linnean Society*, **97**, 876–892.
- Van Damme, P.A., Hamel, C., Ayala, A. & Bervoets, L. (2008) Macroinvertebrate community response to acid mine drainage in rivers of the High Andes (Bolivia). *Environmental Pollution*, **156**, 1061–1068.
- Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R. & Cushing, C.E. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 130–137.
- Vélez-Espino, L.A. (2006) Distribution and habitat suitability index model for the Andean catfish *Astroblepus ubidiai* (Pisces: Siluriformes) in Ecuador. *Revista de Biología Tropical*, **54**, 623–638.
- Verberk, W.C.E.P., Bilton, D.T., Calosi, P. & Spicer, J.I. (2011) Oxygen supply in aquatic ectotherms: partial pressure and solubility together explain biodiversity and size patterns. *Ecology*, **92**, 1565–1572.
- Wang, J., Soininen, J., Zhang, Y., Wang, B., Yang, X. & Shen, J. (2011) Contrasting patterns in elevational diversity between microorganisms and macroorganisms. *Journal of Biogeography*, **38**, 595–603.
- Wantzen, K.M. & Wagner, R. (2006) Detritus processing by invertebrate shredders: a neotropical–temperate comparison. *Journal of the North American Benthological Society*, **25**, 216–232.
- Webster, J.R. & Benfield, E.F. (1986) Vascular plant breakdown in freshwater ecosystems. *Annual Review of Ecology and Systematics*, **17**, 567–594.
- Wetzel, R.G. & Likens, G.E. (1991) *Limnological analyses*, 2nd edn. Springer, New York.
- Young, K. & Leon, B. (1999) *Peru's humid eastern montane forests*. Center for Research on the Cultural and Biological Diversity of Andean Rainforests (DIVA), Copenhagen.

SUPPORTING INFORMATION

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

Appendix S1 Summary of previously published datasets describing elevational–longitudinal gradients in Andean rivers.

BIOSKETCH

Nathan Lujan is interested in the ecological structure, biogeography, taxonomic diversity and evolutionary diversification of herbivorous and detritivorous fishes in tropical rivers.

Author contributions: The project was conceived by N.K.L., K.A.R. and D.J.; fieldwork and data collection were by N.K.L., K.A.R., D.J., V.M.V., V.R.C. and J.A.M.; data analysis and manuscript preparation were by N.K.L., K.A.R., D.J. and K.O.W.

Editor: Richard Ladle