

Convergence of temperate and tropical stream fish assemblages

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The hypothesis of convergence takes the deterministic view that community (or assemblage) structure can be predicted from the environment, and that the environment is expected to drive evolution in a predictable direction. Here we present results of a comparative study of freshwater fish assemblages from headwater streams in four continents (Europe, North America, Africa and South America), with the general objective of testing whether these assemblages display convergent structures under comparable environmental conditions (i.e. assemblage position in the stream longitudinal continuum). We tested this hypothesis by comparing species richness and trophic guilds of those stream fish assemblages represented in available data from multiple sites on each continent. Independent of phylogenetic and historical constraints, fish assemblage richness and trophic structure in the four continents converged along the stream continua to a substantial degree. For the four continents, assemblage richness increased, the proportion of invertivorous species decreased, and the proportion of omnivorous species increased from upstream to downstream, supporting theoretical predictions of the river continuum concept. However, the herbivore/detritivore and piscivore guilds were virtually absent from our small European and North American stream sites, unlike our African and South American stream sites. This divergence can be linked to differences in energy availability between temperate and tropical systems.

The hypothesis of community convergence predicts that under comparable environmental conditions, the structure of phylogenetically unrelated communities should be similar (i.e. the same causes should produce the same effects; MacArthur 1972, Cody and Mooney 1978, Orians and Paine 1983, Schluter 1986). Hence, the hypothesis of convergence supports the deterministic view that community structure can be predicted (at least partly) from the environment because the environment is expected to drive evolution in a predictable direction. If this hypothesis is true, convergence testing could be a powerful method to assess the generality of community patterns observed and of the processes causing those patterns to occur (Lawton 1999, Ben-Moshe et al. 2001). Previous investigators that examined community-level convergence reported mixed results, ranging from total absence of convergence (Price et al. 2000, Verdu et al. 2002, Stephens and Wiens 2004) to partially convergent communities (Schluter 1986, Wine-miller 1991, Schluter and Ricklefs 1993, Losos et al. 1998, Ben-Moshe et al. 2001, Lamouroux et al. 2002, Melville et al. 2006, Irz et al. 2007). Examples of community convergence were mostly restricted to island biotas (includ-

ing lakes and mountain tops), whereas lack of convergence seemed to be the norm for continental communities (Melville et al. 2006).

The degree of community convergence obviously depends on historical contingencies (Ricklefs and Schluter 1993, Melville et al. 2006) but also should be influenced by the degree of constraints exercised by the environment on the communities. Concerning the degree of environmental constraints, rivers or streams offer environmental conditions harsh enough to potentially provide strong selective pressures on aquatic community properties. For example, at the inter-basin scale, fish species richness on different continents has been linked to river size and energy availability (Oberdorff et al. 1995, Guégan et al. 1998) and to biogeographical history (Oberdorff et al. 1997, Tedesco et al. 2005). At the intra-basin scale, fish or macroinvertebrate assemblage structure also displays consistent patterns in species richness and trophic guilds along the size continuum of rivers (Schlosser 1982, Oberdorff et al. 1993, Poff 1997, Usseglio-Polatera et al. 2000, Hoenighaus et al. 2007, Ibañez et al. 2007a, Tomanová et al. 2007). These patterns are usually attributed to changes

in physical conditions of streams or rivers from upstream to downstream areas creating strong constraints on assemblage structure linked to food availability (the river continuum concept; Vannote et al. 1980), habitat spatial heterogeneity (the river habitat template, Townsend and Hildrew 1994), or habitat volume (McGarvey and Hughes 2008). For example, Lamouroux et al. (2002) have found that some morphological traits of fish assemblages in Europe and North America were similarly related to stream environmental conditions such as hydraulics and geomorphology.

Abiotic factors (e.g. stream width, water depth, channel slope, current velocity, and substrate diversity) and associated composite variables (e.g. stream order, distance from sources and basin area) are associated with differing fish assemblage characteristics (Matthews 1998, Tejerina-Garro et al. 2005). Biotic factors (e.g. predation, competition, and disease) have also been reported to influence local fish assemblages (Matthews 1998, Tejerina-Garro et al. 2005).

Comparative studies are needed to ascertain the extent to which patterns in assemblage structure observed along longitudinal gradients are representative of streams or rivers as a whole. Such studies are based on the premise that under a particular set of selective forces (i.e. habitat constraints) specific assemblage traits will be selected (Townsend and Hildrew 1994). Here we present results from a comparative study of freshwater fish assemblages from headwater streams in four continents (Europe, North America, Africa and South America) with the general objective of testing whether these assemblages display convergent structures. To do so, we analyzed fish assemblages at the local (site) scale and asked whether the longitudinal position of sites was a primary factor organizing assemblage structure among those streams. By assemblage structure, we mean the number of species, the total density of individuals (total number of individuals collected m^{-2}) and the proportion (both in terms of richness and density of individuals) of each trophic guild in the assemblage. While many other functional assemblage attributes could have been used to detect convergence patterns (e.g. morphological traits, reproductive and life history strategies) we restricted our analysis to the ones directly available from the literature and for which there were predicted trends along the stream continuum (i.e. trophic guilds; Vannote et al. 1980).

We hypothesized that despite zoogeographic, historical and climatic differences in our headwater streams, species richness, total density of individuals and proportions of trophic guilds would 1) respond to the same physical gradients whatever their continental origin, and 2) that these responses would be similar in shape.

Material and methods

Physical and biological data used in this study were collected in 48 sites of several headwater streams from Africa (Africa; 10 Gabonian stream sites), South America (South America; 15 Bolivian sites), North America (North America; 8 Middle Appalachian sites) and Europe (Europe; 15 French sites). Data for Africa, South America, Europe, and North America were extracted, respectively, from Ibañez et al. (2007a), Tedesco et al. (2007) and Ibañez et al. (2007b), the French Office National de l'Eau et des

Milieux Aquatiques (ONEMA), and the Environmental Monitoring and Assessment Program (EMAP, U.S. EPA). Detailed descriptions of the different methodologies employed in the four continents (including sampling and habitat description methods) are given in Oberdorff et al. (2001), Peck et al. (2006), Ibañez et al. (2007a, b) and Tedesco et al. (2007).

Environmental factors

Two geomorphological variables were used to describe local environmental conditions: mean stream width (m) and mean stream depth (m). Two other variables were used to describe the site spatial position in the stream continuum: distance from sources (km) and surface area of the site's drainage basin (km^2) (Table 1).

Because testing convergence assumes that comparable environments (other than climatic conditions) are present in the different zoogeographic regions studied, the 48 sites were chosen to belong to morphologically comparable streams, to cover a comparable altitudinal gradient, and to display comparable positions in the stream continuum (Table 1). Furthermore, given that disturbed sites could modify the likelihood of detecting convergence, we selected streams that experienced minimal human perturbations, which also explains the relatively small number of sites retained.

Estimating local fish species richness and density of individuals

In France, USA and Bolivia, fishes were collected by electrofishing during the dry season (Table 2). Single pass electrofishing without block nets was employed in France and the USA, but two pass electrofishing with block nets was used in Bolivia. Consequently, only results from the first pass in Bolivia were used so that sampling effort across those three regions was comparable. In Africa, fish were collected during the dry season through use of the ichthyotoxin, rotenone. Although rotenone is not fully comparable to electrofishing, it usually gives comparable estimates of assemblage richness and structure (Penczak et al. 2003, Glowacki and Penczak 2005). We thus combined the African data with those obtained for the three other regions when analyzing species richness and proportions of each trophic guild (in term of richness but not individual density) present in the assemblages (Table 1, 2). All sites were chosen to encompass complete sets of the characteristic stream form (e.g. pools, riffles and runs) and the sampling distances were sufficient to insure reliable estimates of assemblage richness and structure (Oberdorff et al. 2001, Reynolds et al. 2003, Peck et al. 2006, Ibañez et al. 2007a, b, Tedesco et al. 2007).

Defining fish trophic guilds

Trophic trait information for the fish species of the four continents were collected from the literature and coded similarly. Based on its principal adult food, each species was assigned to one of four trophic groups: invertivore (INV),

Table 1. Mean values of environmental variables for the 48 sampled sites. Also given are site species richness, site number of individuals and regional species richness. Concerning North America and Europe, regional species richness refers to the total number of freshwater species present within each river basin (river flowing into the ocean) where the site is present. In this case, regional species richness was calculated using independent data from the French Office National de l'Eau et des Milieux Aquatiques (ONEMA), and the Environmental Monitoring and Assessment Program (EMAP, U.S. EPA). Concerning African and South American sites, regional species richness is the sum of freshwater species already captured within the hydrological region (part of the river basin) where the site is present. In this case, regional species richness was calculated using data from Ibañez et al. (2007a) and Zubietta et al. (pers. comm.). Regional species richness is thus underestimated for African and South American sites compared to European and North American ones.

Continent	Country	Code	Distance from sources (km)	Surface area of the site's drainage (km ²)	Stream depth (m)	Stream width (m)	Elevation (m)	Area sampled (m ²)	Local species richness	Number of individuals	Regional species richness
South America	Bolivia	SA1	2.0	1.5	0.39	6.0	250	241.8	21	220	65
South America	Bolivia	SA2	10.0	10.5	0.29	6.9	250	270.1	21	279	65
South America	Bolivia	SA3	8.0	12.0	0.27	7.3	250	232.7	17	260	65
South America	Bolivia	SA4	6.0	8.0	0.15	9.4	250	516.1	22	269	65
South America	Bolivia	SA5	4.0	4.5	0.34	9.0	250	289.2	18	178	65
South America	Bolivia	SA6	11.0	19.0	0.36	9.7	250	273.5	17	155	65
South America	Bolivia	SA7	7.5	8.0	0.42	7.3	250	163.9	14	359	65
South America	Bolivia	SA8	9.0	13.0	0.33	8.9	250	281.5	21	170	65
South America	Bolivia	SA9	4.0	6.0	0.29	6.7	250	309.6	17	418	65
South America	Bolivia	SA10	4.0	7.0	0.14	3.8	250	99.4	11	309	65
South America	Bolivia	SA11	2.0	5.0	0.26	6.8	250	336.1	20	448	65
South America	Bolivia	SA12	2.0	3.5	0.36	7.4	250	169.7	19	618	65
South America	Bolivia	SA13	4.5	7.5	0.26	6.7	250	300.2	16	492	65
South America	Bolivia	SA14	2.0	0.8	0.43	4.6	250	125.3	12	83	65
South America	Bolivia	SA15	4.0	3.5	0.16	3.9	250	110.3	17	148	65
Europe	France	EU1	6.0	21.0	0.25	3.7	225	439.0	6	544	51
Europe	France	EU2	4.0	11.0	0.23	2.4	150	313.3	2	132	23
Europe	France	EU3	12.0	41.0	0.23	4.9	175	776.0	6	328	51
Europe	France	EU4	13.0	70.0	0.44	5.2	174	651.3	7	713	11
Europe	France	EU5	17.0	115.0	0.43	6.5	215	1006.2	5	1137	14
Europe	France	EU6	18.0	110.0	0.52	4.4	123	655.6	8	257	51
Europe	France	EU7	7.0	13.0	0.34	4.5	150	600.8	4	272	51
Europe	France	EU8	11.0	37.0	0.22	4.7	120	562.9	5	626	23
Europe	France	EU9	6.0	26.0	0.21	2.5	190	335.2	5	299	11
Europe	France	EU10	16.0	86.0	0.41	6.8	75	791.1	8	204	11
Europe	France	EU11	9.0	29.0	0.28	4.2	50	520.3	5	358	17
Europe	France	EU12	17.0	89.0	0.33	7.4	45	529.2	7	298	18
Europe	France	EU13	5.0	7.0	0.15	2.8	245	362.5	4	412	16
Europe	France	EU14	5.0	10.0	0.32	3.4	60	402.0	3	618	11
Europe	France	EU15	15.0	75.0	0.15	5.0	55	673.7	6	1281	16
North America	USA	NA1	5.0	10.7	0.22	4.4	428	655.5	4	198	91
North America	USA	NA2	2.0	2.9	0.17	4.1	462	607.5	2	30	91
North America	USA	NA3	12.3	48.5	0.26	8.5	213	1280.3	10	356	91
North America	USA	NA4	13.8	41.7	0.12	4.4	365	653.3	9	252	61
North America	USA	NA5	8.1	34.7	0.33	8.0	308	1200.5	5	315	61
North America	USA	NA6	22.5	46.2	0.43	9.7	316	1448.1	10	106	61
North America	USA	NA7	10.0	24.5	0.20	5.9	410	885.6	11	430	65
North America	USA	NA8	0.9	1.8	0.19	3.4	482	517.0	4	71	50
Africa	Gabon	AF1	1.0	1.6	0.30	1.0	510		8		76
Africa	Gabon	AF2	0.9	1.2	0.20	1.0	490		16		76
Africa	Gabon	AF3	3.0	5.0	0.30	1.5	460		5		76
Africa	Gabon	AF4	2.0	42.0	0.20	1.0	695		10		76
Africa	Gabon	AF5	14.0	65.0	0.35	2.5	365		16		76
Africa	Gabon	AF6	3.0	9.0	0.20	1.5	535		6		76
Africa	Gabon	AF7	2.0	4.2	0.30	3.0	522		6		76
Africa	Gabon	AF8	3.3	7.1	0.60	2.0	536		27		76
Africa	Gabon	AF9	2.0	5.6	0.20	1.5	493		15		76
Africa	Gabon	AF10	6.0	15.0	0.30	3.0	325		17		76

omnivore (OMN), herbivore/detritivore (HER) or piscivore (PIS) as indicated by the literature (Goldstein and Simon 1999, McCormick et al. 2001, Oberdorff et al. 2002, Ibañez et al. 2007a, b, Tedesco et al. 2007), supplemented with information provided in Fishbase: <www.fishbase.org> (Table 2). This trophic guild classification scheme is adopted worldwide and is consistent between continents (Hughes and Oberdorff 1999). It is thus a good working tool for testing potential convergence in trophic patterns

among the four continents, even if the plasticity inherent in the feeding habits of fishes is usually not negligible. Invertivores are defined as species feeding on crustaceans, oligochaetes, mollusks, and insects. Omnivores are species that consistently feed on substantial proportions of both plant and animal material. Herbivores/detritivores are species feeding on plant material, plankton, detritus and algae. Piscivores feed, as adults, primarily on fish. Because adults of some species change food habits slightly depending

Table 2. Fish species and their trophic traits for the study streams.

Africa–Gabon				South America–Bolivia			
Order and family	Genera and species		Trophic code	Order and family	Genera and species		Trophic code
Characiformes				Beloniformes			
Alestiidae	<i>Alestes schoutedeni</i>	Boulenger, 1912	OMN	Belonidae	<i>Potamorhaphis eigenmanni</i>	Miranda-Ribeiro, 1915	INV
	<i>Brycinus kingsleyae</i>	Günther, 1896	OMN	Characiformes			
	<i>Brycinus longipinnis</i>	Günther, 1864	OMN	Anostomidae	<i>Leporinus striatus</i>	Kner, 1858	OMN
Citharinidae	<i>Neolebias trewasae</i>	Poll & Gosse, 1963	INV	Characidae	<i>Acestrorhynchus</i> sp.		PIS
	<i>Nannocharax fasciatus</i>	Günther, 1867	INV		<i>Astyanacinus</i> sp.		OMN
	<i>Nannocharax parvus</i>	Pellegrin, 1906	INV		<i>Astyanax abramis</i>	Jenyns, 1842	OMN
	<i>Nannocharax</i> sp.		INV		<i>Astyanax lineatus</i>	Perugia, 1891	OMN
Hepsetidae	<i>Hepsetus odoe</i>	Bloch, 1794	PIS		<i>Characidium bolivianum</i>	Pearson, 1924	INV
Cyprinodontiformes					<i>Gephyrocharax chaparae</i>	Fowler, 1940	INV
Aplocheilidae	<i>Aphyosemion cameronense</i>	Boulenger, 1903	INV		<i>Hemigrammus cf. belottii</i>	Steindachner, 1882	OMN
	<i>Aphyosemion joergenscheeli</i>	Huber & Radda, 1977	INV		<i>Hemigrammus cf. lunatus</i>	Durbin, 1918	INV
	<i>Aphyosemion ocellatum</i>	Huber & Radda, 1977	INV		<i>Hemibrycon</i> sp.		INV
	<i>Aphyosemion</i> ssp.		INV		<i>Moenkhausia oligolepis</i>	Günther, 1864	INV
	<i>Epiplatys neumanni</i>	Berkenkamp, 1993	INV		<i>Phenacogaster pectinatus</i>	Cope, 1870	INV
	<i>Fundulopanchax batesii</i>	Boulenger, 1911	INV		<i>Serrapinnus</i> sp.		INV
Poeciliidae	<i>Plataplochilus terveri</i>	Huber, 1981	OMN	Curimatidae	<i>Tytocharax cf. madeirae</i>	Fowler, 1913	INV
Cypriniformes					<i>Steindachnerina dobula</i>	Günther, 1868	HER
Cyprinidae	<i>Barbus brazzai</i>	Pellegrin, 1901	INV		<i>Steindachnerina guentheri</i>	Eigenmann & Eigenmann, 1889	HER
	<i>Barbus camptacanthus</i>	Bleeker, 1863	INV		<i>Cyphocharax spiluropsis</i>	Eigenmann & Eigenmann, 1889	HER
	<i>Barbus caudovittatus</i>	Boulenger, 1902	INV	Erythrinidae	<i>Hoplias malabaricus</i>	Bloch, 1794	PIS
	<i>Barbus guirali</i>	Thomiot, 1886	INV	Gasteropelecidae	<i>Carnegiella myersi</i>	Fernandez-Yepey, 1950	INV
	<i>Barbus holotaenia</i>	Boulenger, 1904	INV	Lebiasinidae	<i>Pyrrhulina vittata</i>	Regan, 1912	INV
	<i>Barbusjae</i>	Boulenger, 1903	INV	Parodontidae	<i>Parodon cf. buckleyi</i>	Boulenger, 1887	HER
	<i>Barbus prionacanthus</i>	Mahnert & Géry, 1982	INV	Prochilodontidae	<i>Prochilodus nigricans</i>	Spix & Agassiz, 1829	HER
	<i>Barbus</i> ssp.		INV	Gymnotiformes			
	<i>Labeo annectens</i>	Boulenger, 1903	HER	Gymnotidae	<i>Gymnotus carapo</i>	Linnaeus, 1758	PIS
	<i>Opsaridium ubangiense</i>	Pellegrin, 1901	INV	Perciformes			
	<i>Raiamas buchholzi</i>	Peters, 1876	INV	Cichlidae	<i>Apistogramma</i> sp.		INV
Osteoglossiformes					<i>Cichlasoma boliviense</i>	Kullander, 1983	OMN
Mormyridae	<i>Brienomyrus hopkinsi</i>	Taverne & Thys van den Audenaerde, 1985	INV		<i>Crenicichla cf. semicincta</i>	Steindachner, 1892	OMN
	<i>Brienomyrus kingsleyae kingsleyae</i>	Günther, 1896	INV		<i>Mikrogeophagus altispinosus</i>	Haseman, 1911	OMN
	<i>Brienomyrus sphekodes</i>	Sauvage, 1879	INV		<i>Satanoperca jurupari</i>	Heckel, 1840	INV
	<i>Marcusenius moorii</i>	Günther, 1867	INV	Siluriformes			
	<i>Mastacembelus</i> ssp.		INV	Callichthyidae	<i>Corydoras</i> spp.		OMN
	<i>Paramormyrops gabonensis</i>	Taverne, Thys van den Audenaerde & Heymer	INV		<i>Callichthys callichthys</i>	Linnaeus, 1758	INV
	<i>Petrocephalus simus</i>	Sauvage, 1879	INV	Heptapteridae	<i>Imparfinis cf. stictonotus</i>	Fowler, 1940	INV
Perciformes					<i>Pimelodella</i> spp.		INV
Anabantidae	<i>Microctenopoma nanum</i>	Günther, 1896	INV		<i>Rhamdia quelen</i>	Quoy & Gaimard, 1824	OMN
Channidae	<i>Parachanna</i> sp.		OMN	Loricariidae	<i>Ancistrus</i> spp.		HER
Cichlidae	<i>Chromidotilapia kingsleyae</i>	Boulenger, 1898	OMN		<i>Hypostomus gr. cochliodon</i>	Kner, 1854	HER
	<i>Hemichromis fasciatus</i>	Peters, 1857	PIS		<i>Rineloricaria lanceolata</i>	Günther, 1868	HER
	<i>Divandu albimarginatus</i>	Lamboj & Snoeks, 2000	OMN	Pseudopimelodidae	<i>Microglanis</i> sp.		INV
	<i>Paranochromis gabonicus</i>	Trewavas, 1975	OMN	Trichomycteridae	<i>Ituglanis cf. amazonicus</i>	Steindachner, 1882	INV

Table 2 (Continued)

Africa–Gabon				South America–Bolivia								
Order and family	Genera and species		Trophic code	Order and family	Genera and species		Trophic code					
Siluriformes Amphiliidae	<i>Paranochromis longirostris</i>	Boulenger, 1903	OMN	Synbranchiformes Symbranchidae	<i>Synbranchus marmoratus</i>	Bloch, 1795	PIS					
	<i>Pelvicachromis</i> ssp.		INV									
	<i>Amphilius baudoni</i>	Pellegrin, 1928	INV									
	<i>Amphilius brevis</i>	Boulenger, 1902	INV									
	<i>Amphilius longirostris</i>	Boulenger, 1901	INV									
	<i>Amphilius pulcher</i>	Pellegrin, 1929	INV									
	<i>Phractura brevicauda</i>	Boulenger, 1911	INV									
	<i>Anaspidoglanis macrostoma</i>	Pellegrin, 1909	INV									
	<i>Anaspidoglanis</i> ssp.		INV									
	<i>Parauchenoglanis balayi</i>	Sauvage, 1879	INV									
<i>Parauchenoglanis loennbergi</i>	Fowler, 1958	INV										
<i>Parauchenoglanis pantherinus</i>	Pellegrin, 1929	INV										
<i>Parauchenoglanis</i> ssp.		INV										
Clariidae	<i>Clarias camerunensi</i>	Lönnberg, 1895	OMN									
	<i>Clarias gariepinus</i>	Burchell, 1822	OMN									
	<i>Clarias jaensis</i>	Boulenger, 1909	OMN									
	<i>Clarias longior</i>	Boulenger, 1907	OMN									
	<i>Clarias pachynema</i>	Boulenger, 1903	OMN									
	<i>Clarias platycephalus</i>	Boulenger, 1902	OMN									
Malapteruridae	<i>Malapterurus electricus</i>	Gmelin, 1789	PIS									
Mochokidae	<i>Synodontis albolineatus</i>	Pellegrin, 1924	INV									
	<i>Synodontis batesii</i>	Boulenger, 1907	INV									
Synbranchiformes Mastacembelidae	<i>Mastacembelus niger</i>	Sauvage, 1879	INV									
North America–USA				Europe–France								
Order and family	Genera and species		Trophic code	Genera and family	Genera and species		Trophic code					
Cypriniformes Cyprinidae	<i>Camptostoma anomalum</i>	Rafinesque, 1820	HER	Anguiliformes Anguillidae	<i>Anguilla anguilla</i>	Linnaeus, 1758	INV					
	<i>Clinostomus funduloides</i>	Girard, 1856	INV									
	<i>Exoglossum maxillingua</i>	Lesueur, 1817	INV									
	<i>Margariscus margarita</i>	Cope, 1867	INV									
	<i>Rhinichthys atratulus</i>	Hermann, 1804	INV									
	<i>Rhinichthys cataractae</i>	Valenciennes, 1842	INV									
	<i>Semotilus atromaculatus</i>	Mitchill, 1818	INV									
	<i>Semotilus corporalis</i>	Mitchill, 1817	INV									
	Catostomidae	<i>Catostomus commersonii</i>	Lacepède, 1803					OMN	Gasterosteiformes Gasterosteidae	<i>Gasterosteus aculeatus</i>	Linnaeus, 1758	OMN
		<i>Hypentelium nigricans</i>	Lesueur, 1817					OMN				
Perciformes Percidae	<i>Etheostoma flabellare</i>	Rafinesque, 1819	INV	Perciformes Percidae	<i>Perca fluviatilis</i>	Linnaeus, 1758	INV					
	<i>Etheostoma olmstedii</i>	Storer, 1842	INV									
Centrarchidae	<i>Lepomis auritus</i>	Linnaeus, 1758	INV	Salmoniformes Salmonidae	<i>Salmo trutta</i>	Linnaeus, 1758	INV					
	<i>Lepomis gibbosus</i>	Linnaeus, 1758	INV									
					<i>Thymallus thymallus</i>	Linnaeus, 1758	INV					

Table 2 (Continued)

North America–USA		Europe–France			
Order and family	Genera and species	Trophic code	Genera and family	Genera and species	Trophic code
Salmoniformes Salmonidae	<i>Lepomis macrochirus</i>	INV	Scorpaeniformes Balitoridae	<i>Barbatula barbatula</i> <i>Cottus gobio</i>	Linnaeus, 1758 Linnaeus, 1758
	<i>Lepomis megalotis</i>	INV			
Scorpaeniformes Cottidae	<i>Salvelinus fontinalis</i>	INV	Cottidae		
	<i>Cottus bairdii</i>	INV			
<i>Cottus cognatus</i> <i>Cottus girardi</i>	Girard, 1850 Richardson, 1836 Robins, 1961	INV INV INV			
Siluriformes Ictaluridae	<i>Noturus insignis</i>	INV			

on their position along the stream continuum we adjusted, when necessary, the classification of these species to our headwater streams. For example, *Perca fluviatilis* is usually classified as a piscivore but feeds more on invertebrates when occurring in small streams. One non-native species (*Salmo trutta*) captured in some North American sites was excluded from the data set before analyses.

Statistical analyses

All statistical analyses were performed using SYSTAT® 12. Species richness, total density (number of individuals collected m^{-2}) and all environmental variables were log transformed prior to analysis to improve normality and stabilize variances. Arcsine square root transformations were conducted on all ecological variables that were proportions (i.e. trophic guilds).

Site-scale convergence was first analyzed by testing the respective effects of physical habitat and continents on fish assemblage structure, where a comparable effect of physical habitat among continents indicated convergence (Schluter 1986, Oberdorff et al. 1997, Lamouroux et al. 2002). We used the first principal component (PC1) of two separate PCA's performed on the four log-transformed environmental variables (sites of the four continents together for species richness related variables, and after excluding African sites for species abundance related variables). PC1 provided a rough characterization of longitudinal changes in habitat characteristics. In both cases PC1 was the only axis with an eigenvalue ≥ 1 and it was positively and significantly related to distance from sources, surface area of the site's drainage basin and mean stream width. We then tested for assemblage-level convergence across continents by examining how PC1 and continents (coded as a categorical variable; South America = 1, Africa = 2, North America = 3, Europe = 4) influenced species richness, the total density of individuals and the proportion of each trophic guild in the assemblage. For this purpose, we used complete ordinary least-square multiple regression models (i.e. evaluating all abiotic predictors; PC1, continents, and their interactions). Following Oberdorff et al. (1997) and Lamouroux et al. (2002), convergence was indicated by 1) a significant effect of the habitat variable (PC1) on the dependent biological variable, and 2) the lack of a significant interaction between PC1 and continents (i.e. slopes of the relationships between the biological variables and PC1 not statistically different across continents). A supplementary significant effect of continents in the model highlights the potential influence of contemporary environments (e.g. climate/productivity), historical contingencies and/or phylogenetic conservatism on the relationships (see Schluter and Ricklefs 1993 for a detailed discussion on this topic).

Results

Each of the four continents was dominated by different families (Table 2) and a pairwise comparison of the percentage of shared families between the continents was generally low: 0% for South America vs Europe or North

America, 2.9% for Africa vs South America, 4.4% for Africa vs Europe or North America and 29% for North America vs Europe.

Assemblage richness and trophic structure along the stream continuum

Site species richness increased along the stream continuum gradient (PC1) and this increase was significantly convergent across the four continents (Fig. 1a, Table 3a, 4a). However, the model clearly shows that even if the relationships between species richness and PC1 are similar in shape (i.e. the slopes of the four relationships do not differ, as there is a lack of a significant interaction between PC1 and continents, $p > 0.05$), species richness was overall significantly different between continents (continent effect strongly significant, $p < 0.001$), except between South America and Africa (least square means difference = 0.195, $p > 0.05$; Bonferroni post hoc test) and between North America and Europe (LSM difference = 0.268, $p > 0.05$; Bonferroni post hoc test) (Table 3a, 4a, Fig. 1a). Species richness was highest in South American and African streams, while lowest in North American and European ones.

Analysis of the geographic trends in assemblage trophic structure along the stream continuum (PC1) confirms convergent patterns for invertivores and omnivores (in term of proportion of richness) in the four continents (Table 3a, 4a). However, proportion of invertivores and omnivores were overall significantly different between continents (significant overall effect of continent, $p < 0.001$), except between North America and Europe (LSM differences = 0.163, $p > 0.05$ and = -0.179, $p > 0.05$ for invertivores and omnivores respectively; Bonferroni post hoc test). In all four continents, the proportion of invertivores decreased along the longitudinal gradient while the proportion of omnivores increased (Fig. 1a). However, the proportion of invertivores was higher in North American and European assemblages compared to South American and African assemblages whereas the proportion of omnivores was higher in South American and African assemblages compared to their North American and European counterparts (Fig. 1a, Table 4a).

On the other hand, there was no convergent pattern for herbivores/detritivores or piscivores among the four continents but a significant ($p < 0.001$) overall effect of continent (Table 3a, 4a). Those trophic guilds were virtually absent from European and North American assemblages. But the proportion of herbivores/detritivores was higher in South American than in African assemblages whereas the reverse was true for proportion of piscivores (Fig. 1a, Table 4a).

The same analysis performed on assemblage trophic guilds, but using density of individuals instead of species richness, produced qualitatively similar results (Fig. 1b, Table 3b, 4b). However, in this case, the proportion of invertivores and the proportion of omnivores, respectively, were significantly higher and lower in North American assemblages compared to their European counterparts (Table 4b). No evidence of convergent pattern was found in the variation of total density of individuals along

the stream continuum, despite a slight decrease of total density along the gradient for the three continents (Africa was not included in density analyses). Total densities were statistically similar between South America and Europe (LSM difference = 0.356, $p > 0.05$), but significantly lower for North America compared to Europe (LSM difference = -1.392, $p < 0.0001$) and South America (LSM difference = -1.748, $p < 0.0001$).

Discussion

Phylogeny

Similarities in assemblage structure across continents may simply reflect common evolutionary histories of the fauna because phylogenetically closely related species are more likely to be ecologically similar. However, the percentage of shared families between the four continents varied from 0 for South America vs Europe or North America to 29% for North America vs Europe. Therefore, even if the studied North American and European faunas cannot be considered totally independent, we can be confident that phylogenetic constraints were not strong factors affecting our results.

Comparison of fish assemblage richness and trophic structure across continents

Changes in local assemblage richness have been previously noted along stream continua worldwide, with species richness usually increasing with stream size. This increase is often attributed to a downstream increase in habitat size, habitat diversity, or both (see Terejina-Garro et al. 2005 for a review). Some authors have used reproductive, trophic or morphological traits to explain assemblage structure along the stream continuum (Angermeier and Karr 1983, Oberdorff et al. 1993, 2002, Mérigoux et al. 1998, Goldstein and Meador 2004, Ibañez et al. 2007a). For example Oberdorff et al. (1993, 2002) and Ibañez et al. (2007a), working respectively on temperate and tropical streams, have shown a transition from invertivorous to omnivorous and piscivorous guilds from upstream to downstream areas. Our study confirmed such trends and formally revealed convergent longitudinal patterns in fish assemblage richness and trophic structure (partial convergence in this latter case) between streams of four continents. Specifically, assemblage richness tended to increase along the stream continuum and the percentage of invertivores tended to significantly decrease along the continuum with a parallel significant increase in the percentage of omnivores. In other words, common environmental constraints seemed to influence food availability within streams, which led to trophic constraints on assemblages and ultimately to differing proportions of trophic guilds. However, we found no convergent pattern for herbivorous/detritivorous and piscivorous guilds along the temperate and tropical stream continua. In fact, piscivores and herbivores/detritivores were absent (or rarely present) from the sites sampled in our small European and North American streams and did not display any particular trend along the African and South American stream continua. This last result suggests that a general convergent pattern can be modified by abiotic

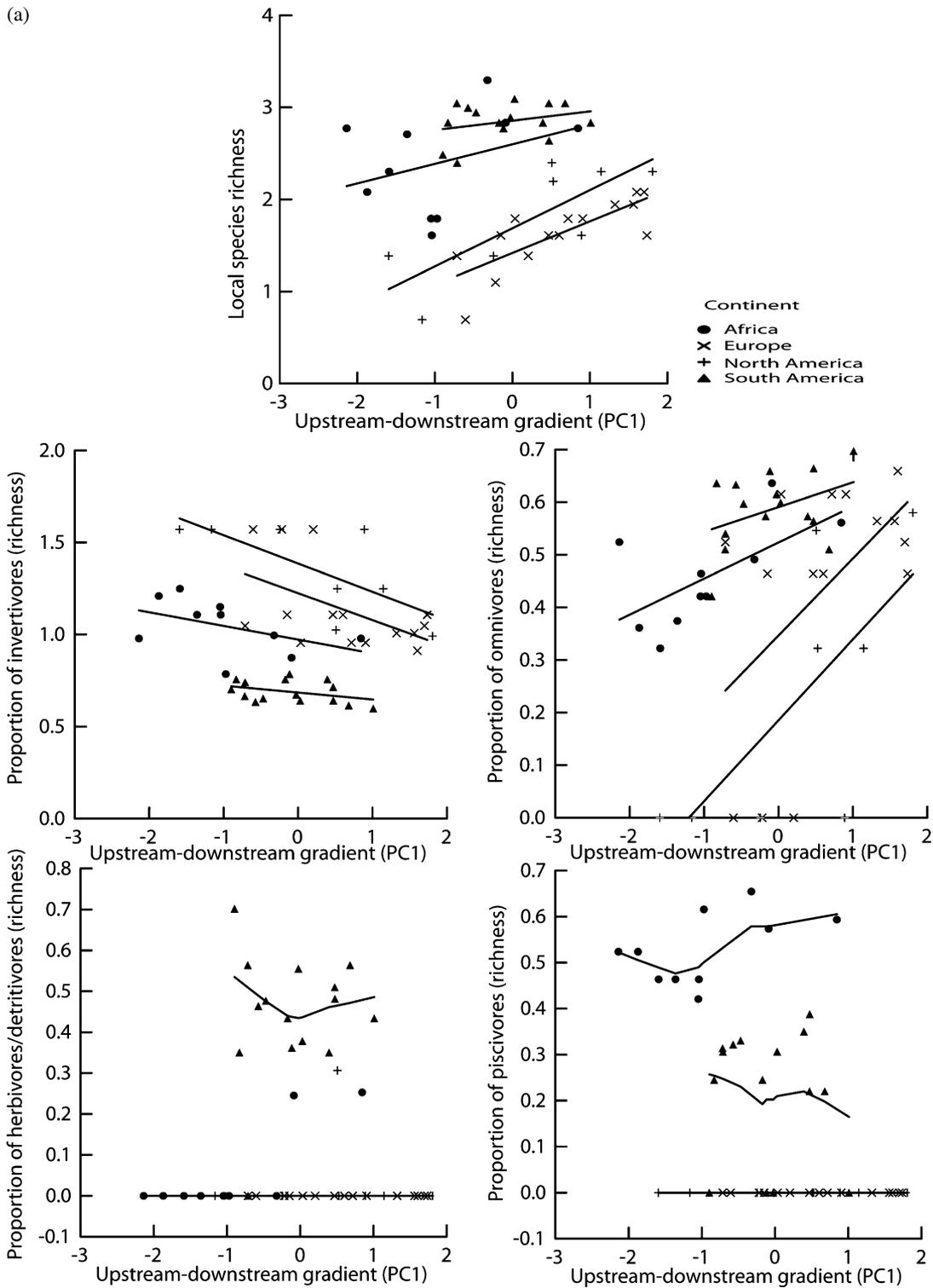


Figure 1. Continued.

conditions. Indeed, with respect to the contemporary environment, climate (which strongly affects available trophic energy to the system; Hawkins et al. 2003) may have influenced our fish assemblages. Temperature and solar energy being higher in the tropics than in temperate areas, we can expect greater energy input in tropical than temperate streams. In particular, there is some evidence that

endogenous primary productivity is higher in tropical streams than in temperate ones for which food webs are mainly initiated by allochthonous production (Davies et al. 2008). Thus, independently of any other environmental constraint, the greater diversity and availability of vegetal material in tropical streams (e.g. particulate organic matter, periphyton and aquatic macrophytes) may explain the

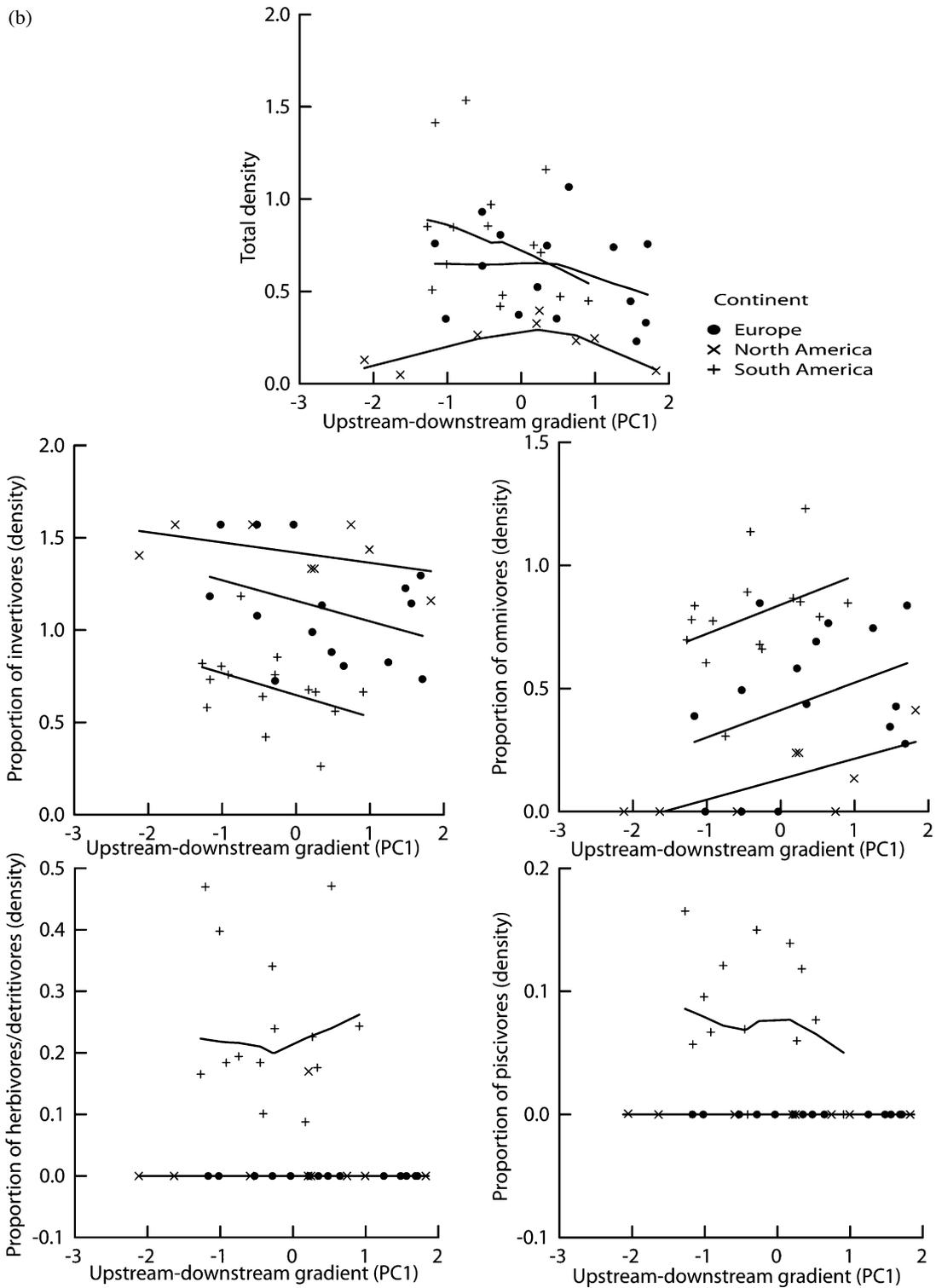


Figure 1. Relationships between each assemblage trait analyzed and the stream continuum described by PC1 (see methods). Relationships are provided for sites of Europe (France, $n = 15$), North America (USA, $n = 8$), Africa (Gabon, $n = 10$) and South America (Bolivia, $n = 15$). Lines are straight lines when relationships were statistically significant and LOWESS trend lines (tension = 0.8) in the other cases. (a) Graphs using species richness data and (b) graphs using density of individuals data (in this latter case, data were available only for Europe, North America and South America). See methods for variable units and transformations.

presence of herbivorous/detritivorous guilds in the African and South American sites studied, as well as their absence in the European and North American sites. A similar trend has been found by Wootton and Oemke (1992) when

comparing tropical (mainly neotropical streams) and temperate (North America) fish assemblages. Furthermore, the presence of herbivores/detritivores within tropical fish assemblages shorten the length of food chains, resulting in

Table 3. Results of covariance models tested for sites in Europe, North America, Africa and South America. Models predict the value of each dependent variable from the position of sites along the stream continuum (represented by PC1) and continent (used as a categorical variable). "PC1 effect" indicates whether the effect of PC1 is significant, "Continent effect" indicates whether the effect of continent is significant, and "PC1 × Continent effect" indicates whether the slopes of the relationships between the dependent variables and PC1 are significantly different (or not) across continents. Values presented in bold are statistically significant. Results are shown for species richness data (a) and individual densities data (b). In this latter case, only streams from Europe, North America and South America are analyzed.

Assemblage traits	PC1 effect p value	Continent effect p value	PC1 × Continent effect p value	R ² complete model
(a)				
Local species richness	0.000	0.000	0.361	0.769
Proportion of invertivores (richness)	0.002	0.000	0.279	0.785
Proportion of omnivores (richness)	0.003	0.000	0.370	0.685
Proportion of herbivores/detritivores (richness)	0.110	0.000	0.317	0.805
Proportion of piscivores (richness)	0.770	0.000	0.557	0.862
(b)				
Total density of individuals	0.372	0.000	0.279	0.572
Proportion of invertivores (density)	0.031	0.000	0.778	0.666
Proportion of omnivores (density)	0.020	0.000	0.933	0.622
Proportion of herbivores/detritivores (density)	0.746	0.000	0.918	0.656
Proportion of piscivores (density)	0.120	0.001	0.271	0.475

direct and relatively efficient conversion of primary production into fish biomass (Winemiller et al. 2008). This may explain, independently of any other environmental constraint, the presence of piscivores observed in the African and South American sites, as well as their absence in the European and North American sites. This does not mean that herbivorous/detritivorous and piscivorous guilds are absent from European and North American streams. Rather they are expected to appear (and actually do appear) further downstream where the amount of available energy is sufficient to maintain viable populations of their constituent species (Matthews 1998, Oberdorff et al. 2002). Our observations of species trophic traits along the stream continuum were also consistent with the predictions provided by the river continuum concept (Vannote et al. 1980) which suggests a longitudinal progression in temperate fish trophic guilds that begins upstream with generalized invertivores and ends in the lower river with omnivores, detritivores, herbivores and piscivores (Schlosser 1987, Oberdorff et al. 1993, 2002, McGarvey and Hughes 2008). The data analyzed also show that after controlling for the effect of the stream continuum, tropical streams average 2.6 times more species than their European or North American counterparts. Part of the reason for this observed trend, independent of contemporary climate, may lie in Pleistocene events where massive river basin extirpations occurred in North America and Europe compared with tropical areas (Mahon 1984, Oberdorff et al. 1997).

Local species richness was not statistically different between African and South American streams or between European and North American ones. This is an unexpected result as local richness is supposed to be positively related, at least partly, to regional richness (Hugueny and Paugy 1995, Griffiths 1997, Oberdorff et al. 1998, Irz et al. 2004). As regional richness (the pool of potential colonists) varied substantially among our studied streams (Table 1) it was logical to expect a significant effect of this factor on local richness. At least three potential explanations may account for this result. 1) The high environmental variability (e.g. variability in the flow regime) and substantial isolation typical of the small headwater streams increase local extinction rates and hinder immigration from downstream

areas (Osborne and Wiley 1992, Taylor and Warren 2001, McGarvey and Hughes 2008). 2) The true size of the regional species pool is overestimated by including species that are unable to colonize the local assemblages studied for morphological, life history, or physiological reasons (pseudo-saturation effect; Cornell and Lawton 1992). 3) Assemblages are truly saturated, which is expected only for strongly interactive assemblages (i.e. competition intensity between species of an assemblage must be strong enough to exclude species). However, this last explanation is unlikely because most previous studies have reported that local fish assemblages are unsaturated rather than the reverse (Hugueny and Paugy 1995, Griffiths 1997, Oberdorff et al. 1998, Irz et al. 2004; but see Angermeier and Winston 1998).

Whatever the continent considered, we found no significant patterns in the total density of individuals collected at sites along the stream continua. However, this result should be taken with caution because one-pass electrofishing poorly estimates the total number of individuals (contrary to species relative abundances) at a site (Angermeier and Smogor 1995, Pusey et al. 1998).

We also noticed that the representation of the different trophic guilds was not proportional among assemblages in the four continents. Invertivores (both in terms of percentage of richness and percentage of density) were more abundant along the temperate stream continuum while omnivores, herbivores/detritivores and piscivores were more common along the tropical stream continuum. This result is in agreement with that of Winemiller (1992) and potentially confirms the possible effect of higher energy input in tropical versus temperate streams.

We examined convergence by testing simultaneously the effects of continent and habitat on assemblage attributes. To do so we compared the slopes of the relationships between habitat and assemblage attributes of the continents. Using this approach as a general test for convergence could be problematic because the power of such a test actually depends on the number of sites involved. For example, increasing the number of sites could lead to minor but significant differences in slopes and ultimately to artificially rejecting the hypothesis of convergence. However, as slopes

Table 4. Assemblage trait values, least square mean pairwise differences (and associated probabilities after Bonferroni post hoc test) between continents, using (a) species richness and (b), density of individuals data. In this latter case, only streams from Europe, North America and South America are analyzed. Numbers in bold represent significant probabilities. AF =Africa, SA =South America, NA =North America and EU =Europe.

Local species richness	AF	EU	NA	SA
(a)				
AF	0.000–1.000			
EU	–1.232– 0.000	0.000–1.000		
NA	–0.965– 0.000	0.268–0.544	0.000–1.000	
SA	0.195–1.000	1.427– 0.000	1.159– 0.000	0.000–1.000
Proportion of invertivores (richness)				
AF	0.000–1.000			
EU	0.310– 0.001	0.000–1.000		
NA	0.511– 0.000	0.163–0.090	0.000–1.000	
SA	–0.174–0.053	–0.501– 0.000	–0.701– 0.000	0.000–1.000
Proportion of omnivores (richness)				
AF	0.000–1.000			
EU	0.140–0.433	0.000–1.000		
NA	–0.078–1.000	–0.179–0.056	0.000–1.000	
SA	–0.197– 0.026	0.229– 0.002	0.447– 0.000	0.000–1.000
Proportion of herbivores/detritivores (richness)				
AF	0.000–1.000			
EU	–0.094–0.507	0.000–1.000		
NA	–0.045–1.000	0.049–1.000	0.000–1.000	
SA	0.368– 0.000	0.461– 0.000	0.413– 0.000	0.000–1.000
Proportion of piscivores (richness)				
AF	0.000–1.000			
EU	–0.539– 0.000	0.000–1.000		
NA	–0.537– 0.000	0.049–1.000	0.000–1.000	
SA	–0.318– 0.000	0.461– 0.000	0.218– 0.000	0.000–1.000
Total density of individuals				
	EU	NA	SA	
(b)				
EU	0.000–1.000			
NA	–1.392– 0.000	0.000–1.000		
SA	0.356–0.514	1.748– 0.000	0.000–1.000	
Proportion of invertivores (density)				
EU	0.000–1.000			
NA	0.267– 0.033	0.000–1.000		
SA	–0.493– 0.000	–0.760– 0.000	0.000–1.000	
Proportion of omnivores (density)				
EU	0.000–1.000			
NA	–0.284– 0.022	0.000–1.000		
SA	0.418– 0.000	0.702– 0.000	0.000–1.000	
Proportion of herbivores/detritivores (density)				
EU	0.000–1.000			
NA	0.001–1.000	0.000–1.000		
SA	0.234– 0.000	0.233– 0.000	0.000–1.000	
Proportion of piscivores (density)				
EU	0.000–1.000			
NA	0.015–1.000	0.000–1.000		
SA	0.065– 0.001	0.05– 0.042	0.000–1.000	

were never different in our study, this potential problem did not affect our results.

In an applied context, considerable effort has been directed towards developing biological indices for assessing stream and river condition on different continents (Hughes and Oberdorff 1999, Karr and Chu 2000). Usually these indices have been based on the index of biotic integrity (IBI) first formulated by Karr (1981) for use in midwestern USA streams. IBIs employ a series of metrics based on assemblage structure (e.g. species richness, trophic composition) that give reliable signals of river condition. The use of functional, rather than taxonomic attributes aids compar-

ison of assemblages extracted from different species pools, which helps explain the successful development of such indices outside the midwest USA. Recently, new multi-metric indices have been developed at regional or continental scales for streams and rivers with different faunas, while maintaining IBI's ecological foundation (Oberdorff et al. 2002, Pont et al. 2006, Whittier et al. 2007). However, the application of IBIs worldwide implies an independent evolution of species with similar ecological characteristics (ecological guilds) in comparable environments in different regions. By formally identifying convergent patterns in stream assemblage richness and structure in comparable

environments of different continents, our study provides support for using such indicators worldwide.

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