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SUJET

**DEGRÉ DE CONVERGENCE ENTRE PEUPELEMENTS DE POISSONS DE COURS D'EAU
TROPICAUX ET TEMPÉRÉS**

Sous la direction de : **Dr. Thierry OBERDORFF**

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A la mémoire de Rosa Luna.

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Résumé

Dans le présent travail nous avons testé l'hypothèse de "convergence" selon laquelle les communautés soumises aux mêmes contraintes environnementales convergent vers une structure commune. Nous avons choisi comme modèle les poissons des cours d'eau tempérés et tropicaux de quatre régions zoogéographiques : Europe (France), Amérique du Nord (USA), Amérique du Sud (Bolivie) et Afrique (Gabon). Pour atteindre notre objectif, des comparaisons locales, régionales et intercontinentales des communautés de poissons ont été menées entre différents sites et entre différents cours d'eau en étudiant leurs caractéristiques écomorphologiques et leur structure trophique. Les résultats montrent que l'organisation locale des communautés résulte de la combinaison de processus locaux et régionaux, abiotiques et biotiques, et s'inscrit par conséquent dans un contexte historique et biogéographique. A l'échelle locale nous avons pu montrer que certaines guildes trophiques peuvent être prédites à partir de quelques attributs morphologiques. Par ailleurs, la richesse des communautés de poissons et leur structure trophique se sont avérées substantiellement convergentes d'une région à l'autre : le pourcentage des espèces invertivores (se nourrissant de façon exclusive d'invertébrés) tend à diminuer le long du gradient longitudinal des cours d'eau étudiés tandis que le pourcentage d'espèces omnivores augmente. Néanmoins, à position égale des sites sur le gradient longitudinal, les guildes herbivores/détritivores et piscivores, présentes dans les cours d'eaux africains et sud-américains, sont pratiquement absentes des cours d'eaux européens et nord-américains étudiés, peut-être en raison de différences en énergie disponible entre les systèmes tempérés et tropicaux. Ces résultats seront certainement utiles aux décideurs pour les aider à mettre en œuvre des plans de conservation et de gestion des systèmes lotiques.

Mots clé : Convergence ; communautés de poissons ; cours d'eau tempérés et tropicaux ; guildes trophiques ; écomorphologie ; gradient longitudinal ; Europe ; Amérique du Nord ; Amérique du Sud et Afrique.

Abstract

This work has tested the assumption of "convergence" according to which communities subjected to the same environmental constraints converge towards a common structure. We chose as a model, fishes of the temperate and tropical streams of four zoogeographical areas: Europe (France), North America (USA), South America (Bolivia) and Africa (Gabon). Hence, ecomorphologic characteristics and trophic structure of fish communities were compared at local, regional and intercontinental scales between various sites and various streams. The results show that local communities' organization depends on the combination of both local and regional and abiotic and biotic processes, relying on a historical and biogeographical context. At the local scale, we have shown that some trophic guilds can be predicted from chosen morphological attributes. In addition, the richness of fish communities and their trophic structure have been proved substantially convergent from one area to the other: the percentage of invertivorous species (exclusively feeding on invertebrates) tends to decrease along the longitudinal gradient of the studied streams while the percentage of omnivorous species increases. Nevertheless, at an equal site position on the longitudinal gradient, the herbivores / detritivorous and piscivorous guilds are present in the African and South American streams, whereas they are barely found in European and North-American studied streams. This might be due to differences in supplied energy between temperate and tropical systems. These results could be useful for the decision makers to implement efficient conservation and management plans of the lotic systems.

Keywords : Convergence; fish community; temperate and tropical streams; trophic guilds; ecomorphology; longitudinal gradient; Europe; North America; South America and Africa.

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1. Démarche d'étude

1.1. Problématique générale

Convergence des espèces et des communautés

Dès le milieu du XIX^{ème} siècle, des discussions émergèrent quant aux phénomènes de convergence et d'évolution des espèces. Ainsi, Darwin (1861) considérait que deux espèces qui appartiennent à deux genres apparentés produisent de nombreuses espèces nouvelles et divergentes. Il pensait que ces nouvelles formes pouvaient en quelque temps être classées à l'intérieur d'un nouveau genre et donc pouvaient converger (Marshall 1971). Le sens de convergence donné par Darwin est plus proche de l'idée actuelle de parallélisme évolutif. C'est bien plus tard que les biologistes se sont demandés si l'évolution indépendante de deux groupes d'espèces habitant des environnements semblables, pouvait être similaire. Un deuxième courant de pensée est venu des systématiciens qui ont décrit un degré souvent étonnant de convergence dans la morphologie parmi des organismes vaguement apparentés et qui exploitent les mêmes ressources (Cody & Mooney 1978; Orians & Paine 1983; Schluter & Ricklefs 1993). A l'heure actuelle, l'hypothèse de convergence est en relation avec le point de vue déterministe : les mêmes causes devraient produire les mêmes effets (Schluter 1986; Samuels & Drake 1997).

Le problème de convergence peut être appréhendé selon deux niveaux : le premier est d'étudier par paire ou par groupe de taxa de différences phylogénétiques connues, qui vivent dans les mêmes genres d'habitat mais dans différentes parties du monde (Blondel *et al.* 1984). En ce qui concerne les caractères biophysiques, biochimiques, physiologiques et le comportement, de nombreuses comparaisons ont été faites sur les plantes et sur les animaux (Karr & James 1975; Cody & Mooney 1978). Pour en citer quelques-uns : sur les plantes (Jousselin *et al.* 2003); sur les oiseaux (Friedmann 1946; Keast 1972; Cody 1973, 1975; Diamond 1975; Schluter 1986); sur les mammifères (Dubost 1968; Kelt *et al.* 1999; Ben-Moshe *et al.* 2001; Jones 2003), sur les lézards (Pianka 1975; Fuentes 1976; Leal *et al.* 2002). et pour les poissons (Moyle & Herbold 1987; Marrero & Winemiller 1993; Norton & Brainerd 1993; Motta *et al.* 1995; Winemiller *et al.* 1995; Hugueny & Pouilly 1999; Knouft 2003).

Le second niveau est d'étudier la communauté complète, qui représente un nouvel intérêt pour les écologistes avec le développement de l'écologie théorique depuis les années 1960 qui pose la question suivante : si les espèces convergent, n'en est-il pas de même des communautés? (Marshall 1971; Schluter & Ricklefs 1993). Plusieurs exemples de convergences des communautés peuvent être trouvés pour les plantes, pour les insectes (Milewski 1979; Medel 1995; Price *et al.* 2000; Davies *et al.* 2003; Meinzer 2003; Wassenaar *et al.* 2005), pour les oiseaux (Cody 1973, 1975; Karr & James 1975; Cody & Mooney 1978; Blondel *et al.* 1984; Schluter 1986; Price *et al.* 2000), pour les mammifères (Brown & Leiberman 1973; Brown 1975; Kelt *et al.* 1999), pour les reptiles (Fuentes 1976; Milewski 1981; Schluter & Ricklefs 1993; Stephens & Wiens 2004; Melville *et al.* 2006) et pour les poissons (Winemiller 1991; Lamouroux *et al.* 2002; Irz *et al.* 2007).

Une étude intéressante a été faite par Losos *et al.* (1998) et examine la radiation adaptative des lézards *Anolis* sur quatre îles des Antilles. Les analyses morphométriques indiquent que au sein de la même espèce se trouve des "morphotype" spécialistes, sur chacune des quatre îles en fonction des caractéristiques d'habitat. L'analyse phylogénétique indique que les "morphotypes" sont apparus indépendamment sur chacune des îles. Ainsi, la radiation adaptative dans des environnements similaires peut prévaloir sur les éventualités historiques pour produire de façon saisissante des résultats évolutifs similaires. (Losos *et al.* 1998).

Alors que les convergences des espèces peuvent, le plus souvent, être facilement expliquées comme une résultante des contraintes identiques (Schluter 1986), celles inhérentes aux communautés paraissent plus complexes car soumises à plusieurs influences.

- La première est d'ordre historique, il faut pouvoir démontrer que les communautés supposées avoir convergé se ressemblent plus entre elles qu'elles ne ressemblent aux communautés ancestrales dont elles sont issues. Ici la démonstration ne peut être qu'indirecte, puisque les communautés ancestrales sont inconnues (Blondel *et al.* 1984; Blondel 1995).
- La deuxième concerne l'évaluation de l'ensemble des communautés qui sont des entités extrêmement complexes. Les écologistes étudient habituellement des parties (guildes) de communautés ou prennent en compte un certain degré de ressemblance (Schluter 1986; Blondel 1995; Ben-Moshe *et al.* 2001). Les associations écologiques

(guildes) (Root 1967) ont souvent été considérées comme des parties maniables qui facilitent l'étude détaillée (Simberloff & Dayan 1991). Par conséquent, la recherche de la convergence au moyen de guildes peut être plus fructueuse que la recherche de convergence entre communautés complètes (Blondel *et al.* 1984; Schluter 1986; Blondel 1995; Ben-Moshe *et al.* 2001).

- Un troisième problème est que la convergence des communautés se base sur l'hypothèse plus générale que les caractéristiques des organismes sont prévisibles à partir de leur environnement. Ceci présuppose que l'hypothèse est souvent biaisée car bien d'autres composantes comme l'hétérogénéité spatiale, la phylogénie et l'histoire, peuvent l'affecter. Il faudra donc prendre ce fait en considération avant toute conclusion sur la convergence des communautés (Orians & Paine 1983; Blondel *et al.* 1984; Schluter 1986; Ricklefs & Schluter 1993; Blondel 1995; Kelt *et al.* 1996; Ricklefs *et al.* 1999; Ben-Moshe *et al.* 2001).

Enfin se pose la question de savoir quelle est l'importance d'étudier la convergence au niveau des communautés? Un des rôles majeurs de l'écologie est d'identifier et d'interpréter des patterns fréquents dans les communautés écologiques. Elucider de tels patterns donne la possibilité de comprendre les principes qui structurent les communautés écologiques, d'appréhender les règles qui les gouvernent et de vérifier si de telles règles sont générales (Lawton 1999). Par ailleurs, chercher à prévoir ces patterns écologiques peut souvent aider à la gestion des ressources (Poff 1997; Oberdorff *et al.* 2002).

Convergence – divergence, les échelles et les “filtres”

D'un point de vue déterministe, les communautés convergent vers une structure commune sous les mêmes conditions (Samuels & Drake 1997). En fait, les patterns de convergence diffèrent selon les échelles que l'on considère. Par exemple, les communautés de divers continents dans des conditions environnementales semblables, laissent apparaître des convergences intéressantes de leur richesse, de leur composition et sur la morphologie des espèces qui les constituent (Samuels & Drake 1997). De telles comparaisons à l'échelle globale forgent les prémisses d'une théorie : les environnements semblables mènent à l'existence de communautés similaires, et ce pour plusieurs raisons. Premièrement, à court terme l'environnement définit les configurations possibles de la communauté. Deuxièmement, à long terme l'environnement mène à un certain niveau de convergence

évolutive parmi des espèces constitutantes (Samuels & Drake 1997). Les études faites entre continents et sous les mêmes conditions, contrôlées ou naturelles, ont montré aussi des divergences (Pianka 1973; Mahon 1984; Leal *et al.* 2002), et/ou différents degrés de convergence (Winemiller 1992; Inouye & Tilman 1995; Samuels & Drake 1997; Orr & Smith 1998; Guo & Ricklefs 2000; Aguirre *et al.* 2002). Ces études laissent envisager une grande gamme de perspectives sur les patterns de convergence et de divergence des communautés qui sont une conséquence de causes multiples interactives produites à différentes échelles spatiales et temporelles (Samuels & Drake 1997). L'organisation locale des communautés est le résultat de la combinaison de processus locaux et régionaux, abiotiques et biotiques et est, par conséquent, limitée dans un contexte historique et biogéographique (Menge & Olson 1990; Ricklefs & Schluter 1993). Poff (1997) explique aussi que les facteurs de l'environnement associés aux différentes échelles spatiales et temporelles peuvent constituer des "filtres" dans lesquels l'espèce appartenant à un pool régional doit passer pour être potentiellement présente dans une localité donnée. La compréhension du fonctionnement des communautés passe donc par l'identification de ces différents filtres. Plusieurs auteurs ont identifié ces filtres à différentes échelles. Par exemple, le climat est fréquemment utilisé pour prédire des modèles de distribution à grande échelle (Inouye & Tilman 1995). Les interactions biotiques (prédation, compétition) et abiotiques sont la deuxième catégorie de facteurs qui limitent la distribution des espèces. Ceux-ci sont le plus souvent utilisés typiquement pour décrire la distribution à petite échelle (Inouye & Tilman 1995). D'autres études incluent les affinités taxinomiques des espèces constitutantes, c'est-à-dire le taux de spéciation pour la région où la communauté locale est implantée, et la facilité de dispersion de nouvelles espèces dans cet habitat (Pearson 1977; Moyle & Herbold 1987; Winemiller 1992; Ricklefs & Schluter 1993; Winemiller & Adite 1997; Bellwood *et al.* 2005).

Il existe, néanmoins, une limite à la ressemblance ou au nombre d'espèces en concurrence pouvant coexister. Le nombre total d'espèces est proportionnel à la gamme totale de l'environnement divisée par la largeur de niche des espèces. Le nombre est réduit par l'abondance inégale de ressources mais augmenté par l'ajout du dimensionnement de la niche (MacArthur & Levins 1967). Cette dynamique peut être rattachée à l'hypothèse richesse/énergie dont une des prédictions est l'augmentation des espèces spécialistes avec une augmentation de l'énergie trophique disponible dans le système, par réduction de la largeur de niche des espèces ou par augmentation de la diversité des ressources et/ou de

l'hétérogénéité de l'habitat (Srivastava & Lawton 1998). Néanmoins, c'est un sujet de discussion car selon l'échelle spatiale considérée, des résultats positives et négatives ont été trouvés en ce qui concerne le lien existant entre la richesse spécifique et l'énergie disponible dans un écosystème (Oberdorff *et al.* 1995; Oberdorff *et al.* 1997; Wittaker 2001; Hawkins *et al.* 2003; Currie *et al.* 2004; Storch *et al.* 2005; Evans *et al.* 2006; Tedesco *et al.* 2007; Whittaker *et al.* 2007).

L'étude de Wainwright *et al.* (2002) sur les poissons de récif coralliens explique la forte diversité locale observée par la diversité de niche des espèces (conditions d'habitat et approche trophique et interactive entre les espèces) qui permet la répartition des ressources entre les spécialistes. On s'attend donc à voir dans ces systèmes de haute biodiversité des évidences sur le phénotype des espèces (adaptées morphologiquement) : diversification de niche et spécialisation écologique (Smith 1982; Winemiller & Adite 1997). Ainsi, les poissons de récifs fournissent de nombreux exemples de morphologies extrêmes (Wainwright *et al.* 2002). La famille des Labridae est un exemple de groupe écologiquement et fonctionnellement varié de poissons de récif corallien, de part leur régime alimentaire et leur large diversité de niches (Wainwright *et al.* 2004; Bellwood *et al.* 2005).

1.2. Les communautés aquatiques

Pourquoi tester l'hypothèse de convergence dans les systèmes aquatiques et sur les communautés des poissons?

Les systèmes aquatiques lenticques et lotiques sont distribués dans tous les continents, ce qui rend possible une comparaison facile. Les avantages d'étudier la convergence sur les communautés de poissons dans les systèmes aquatiques sont :

1. les poissons sont probablement plus divers à tous les niveaux taxinomiques et ont plus d'espèces que tous les autres groupes de vertébrés associés (Matthews 1998; Nonogaki *et al.* 2007). Nelson (2006) a suggéré que le nombre d'espèces de poissons vivants peut atteindre approximativement 32.500 et autour de 13.000 pour ceux d'eau douce.
2. ils colonisent tous les habitats, à l'exception de ceux isolés par des barrières.

3. les poissons ont développé des stratégies larges dans leur cycle vital (histoire de vie) et dans leurs traits écologiques. Par conséquent, il y a suffisamment de variation pour que la sélection naturelle agisse comme une réponse aux conditions de l'environnement, y compris les interactions biotiques (Winemiller 1992; Winemiller & Rose 1992; Matthews 1998).
4. C'est un groupe emblématique auquel on se réfère tant en ce qui concerne l'impact sur l'environnement aquatique que pour les problèmes de biologie de la conservation.
5. Enfin, c'est un groupe largement exploité (pêche, aquaculture) qui permet à de nombreuses populations, souvent défavorisées, d'avoir un apport protéinique minimal.

Hétérogénéité temporelle et spatiale dans les rivières, un aspect à considérer pour l'hypothèse de la convergence

Pour la présente étude, nous avons sélectionné les cours d'eau près de la source. C'est dans ce contexte que nous allons exposer les hypothèses pertinentes pour comprendre le fonctionnement de ces types de systèmes. L'hypothèse de "l'*Habitat Templet*" soutient, par exemple, l'idée de la convergence (Southwood 1977). Dans un cadre de l'hétérogénéité temporelle et spatiale d'habitats dans lequel il existe un continuum multidimensionnel de caractéristiques, l'évolution forge des stratégies biologiques que les organismes adoptent ("Species traits") en fonction de la dimension de l'espace ("Patch size") (Southwood 1977). Cette hypothèse a été développée pour les milieux fluviaux sous le nom de "*River Habitat Templet*" (Townsend & Hildrew 1994) et souligne que, pour un groupe taxinomique donné, la distribution des stratégies biologiques est prévisible en fonction de la variabilité spatio-temporelle du milieu. À partir de cette connaissance, des relevés faunistiques peuvent donc ultérieurement fournir des informations sur les caractéristiques du milieu et son fonctionnement. Plusieurs études portant sur les invertébrés aquatiques confirment cette théorie (Statzner *et al.* 1994; Usseglio-Polatera 1994; Statzner *et al.* 1997; Townsend *et al.* 1997).

Sélection des attributs au niveau des communautés

Pendant au moins trois décennies, les écologistes ont discuté sur les attributs qui peuvent permettre de tester l'hypothèse de convergence entre les communautés aquatiques sur les différents continents (Moyle & Herbold 1987; Winemiller 1992; Norton & Brainerd 1993; Motta *et al.* 1995; Winemiller *et al.* 1995; Winemiller & Adite 1997; Hugueny & Pouilly 1999; Lamouroux *et al.* 2002; Smith & Wilson 2002; Vila-Gispert *et al.* 2002; Knouft 2003). Les communautés sont des entités complexes, et donc difficilement appréhendables dans leur globalité, les écologistes sont alors généralement dans l'obligation de choisir certaines propriétés de ces communautés. Parmi les stratégies biologiques qui décrivent la réponse fonctionnelle des communautés aux conditions environnementales, les plus susceptibles d'être utilisées sont : le régime alimentaire (guildes trophiques), les stratégies démographiques (longévité, fécondité relative, âge de la première reproduction, taille des œufs, style de ponte), l'écophysiologie, les stratégies comportementales mais également la richesse en espèces, la régularité et les distributions relatives d'abondance (Moyle & Herbold 1987; Motta 1988; Poff & Ward 1990; Winemiller 1991, 1992; Marrero & Winemiller 1993; Norton & Brainerd 1993; Motta *et al.* 1995; Winemiller *et al.* 1995; Winemiller & Adite 1997; Hugueny & Pouilly 1999; Ruber & Adams 2001; Lamouroux *et al.* 2002; Knouft 2003).

2. Organisation du mémoire

Le travail présenté permettra de tester l'hypothèse de "convergence", en s'appuyant sur les approches décrites ci-dessus et dans le cadre déterministe, selon le principe que les communautés convergent vers une structure commune sous contraintes des mêmes conditions environnementales. Nous avons choisi comme modèle les poissons de cours d'eau tempérés et tropicaux. Si la structure des communautés est fortement dépendante des conditions environnementales, des convergences adaptatives doivent alors se manifester au sein de communautés non apparentées (phylogénétiquement éloignées) vivant dans des conditions environnementales similaires.

L'hypothèse sera testée sur des données issues de trois continents et quatre régions : Europe (France), Amérique du Nord (USA), Amérique du Sud (Bolivie) et Afrique (Gabon). Ces données ont été obtenues grâce à des recherches bibliographiques (Lévêque &

Paugy 2006; Lee *et al.* 1980; Simon 1999; Oberdorff *et al.* 2002; Paugy *et al.* 2003; Lanoiselée 2004), des collaborations avec le laboratoire de l'EPA (Environmental Protection Agency) de Corvallis aux États-Unis et le laboratoire du Cemagref d'Antony en France, ainsi qu'à des travaux de récoltes sur le terrain dans les rivières de l'Amazonie bolivienne et à l'observation de spécimens conservés au Musée National d'Histoire Naturelle (Tableaux 1 et 2). En ce qui concerne le Gabon, nous n'avons pour l'instant pas obtenu de données morphologiques. Les attributs des communautés qui ont été choisis et étudiés pour cette thèse sont les suivants :

- ✓ la richesse spécifique
- ✓ les guildes trophiques
- ✓ l'écomorphologie

Tableau 1. Informations générales concernant les bassins, le nombre des sites et l'origine des données utilisées dans ce travail de thèse, ainsi que les articles qui correspondent aux données.

Continent	Région	Description de données	N. site	Bassin	Origine de données	Articles concernés
Amérique du Sud	Bolivie	Richesse spécifique et densité	27	Chipiriri (Amazonie bolivienne)	Echantillonnages par pêche électrique (campagne de terrain). 2004 et 2005	Article 1
		Régime alimentaire				
		Morphologie				
		Mesures d'habitat				
		Richesse spécifique et densité	15	Chipiriri (Amazonie bolivienne)	Echantillonnages par pêche électrique (campagne de terrain). 2004	Article 3 et 4
		Régime alimentaire				
		Morphologie				
		Mesures d'habitat				
Europe	France	Données environnementales	15	Loire (4), Orne (1), Touques (1), Risle (1), Cance (1), Sée rousse (1), Sée (1), Douve (1), Siennne (1), Vire (2) et Pre d'Auge (1)	2004	Article 3
		Richesse spécifique et densité			Oberdorff <i>et al.</i> 2002, Fishbase (http://www.fishbase.org)	
		Régime alimentaire			(Lanoiselée 2004) MHNN (table 2)	
		Morphologie				
Amérique du Nord	États - Unis	Données environnementales	8	Cours d'eau des Appalaches	Environmental Protection Agency (EPA). Corvallis, OR, USA. 1993, 1997-1998	Article 3
		Richesse spécifique, densité			Lee <i>et al.</i> (1980), Simon, T. P. (1999), Fishbase (http://www.fishbase.org),	
		Régime alimentaire			Lee <i>et al.</i> (1980). Fishbase (http://www.fishbase.org), MHNN (table 2)	
		Morphologie				
Afrique	Gabon	Données environnementales	52	Ogôoué (32), Nyanga (10), Komo (3), Woleu (3), Ntem (3) et Noya (1)	WWF Gabon, 2001	Article 2
		Richesse spécifique			Lévêque & Paugy, (2006)	
		Régime alimentaire				
		Données environnementales	10	Ogôoué (10)	WWF Gabon, 2001	Article 3
		Richesse spécifique			Lévêque & Paugy, (2006)	
		Régime alimentaire				

Tableau 2. Détails des spécimens du Muséum National d'Histoire Naturelle sur lesquels des mesures morphologiques ont été prises.

Etats - Unis	Référence MNHN	Nombre des individus
<i>Campostoma anomalum</i>	1987-0866	4
<i>Catostomus commersonii</i>	1889-0317	1
	0000-3833	1
	A-2477	1
	0000-3814	1
<i>Cottus bairdii</i>	1905-0529	2
<i>Cottus cognatus</i>	0-4675	1
<i>Etheostoma flabellare</i>	1985-0110	4
<i>Etheostoma olmstedii</i>	0-6781	2
<i>Hypentelium nigricans</i>	0-2865	1
<i>Lepomis gibbosus</i>	1889-0428	1
	0000-4674	2
<i>Lepomis macrochirus</i>	1987-0875	5
<i>Lepomis megalotis</i>	1987-0877	4
<i>Noturus insignis</i>	B-0164	1
	1889-0311	2
	0000-0340	2
<i>Rhinichthys atratulus</i>	1889-0392	1
	1889-0395	2
<i>Rhinichthys cataractae</i>	1905-0523	2
	A-2716	1
<i>Salvelinus fontinalis</i>	A-2437	1
<i>Semotilus atromaculatus</i>	1974-0016	4
<i>Semotilus corporalis</i>	A-1302	1
	B-0131	2
	A-2723	1
France		
<i>Cotus gobio</i>	1986-0913	2
<i>Gasterosteus aculeatus</i>	0000-6664	2
	0000-0681	1
<i>Pungitius pungitius</i>	1925-0170	2
	0000-7106	1
<i>Thymallus thymallus</i>	B-2480	2
	1898-1156	1

Pour atteindre l'objectif de cette thèse, nous avons travaillé à différentes échelles spatiales (locale, régionale et continentale). Nous nous sommes basés sur le fait que l'organisation locale des communautés résulte de la combinaison de processus et de pressions sélectives d'une série d'effets locaux, régionaux et physiologiques, par conséquent, limités par un groupe d'éléments dans un contexte historique et biogéographique. Pour illustrer ces processus et identifier les "filtres" à différentes échelles des systèmes aquatiques, nous présentons la figure 1, qui est une synthèse de plusieurs auteurs (Tonn 1990; Tonn *et al.* 1990; Poff 1997; Samuels & Drake 1997; Chan 2001; Jackson *et al.* 2001; Bunn & Arthington 2002). L'échantillonnage lors de notre étude a été effectué à l'échelle d'un site de pêche (portion d'un cours d'eau). Les approches comparatives ont été menées entre plusieurs sites d'un même cours d'eau (approche locale), plusieurs sites sur différents cours d'eau (approche régionale) et plusieurs sites sur différents cours d'eau de différents continents (approche inter-continentale).

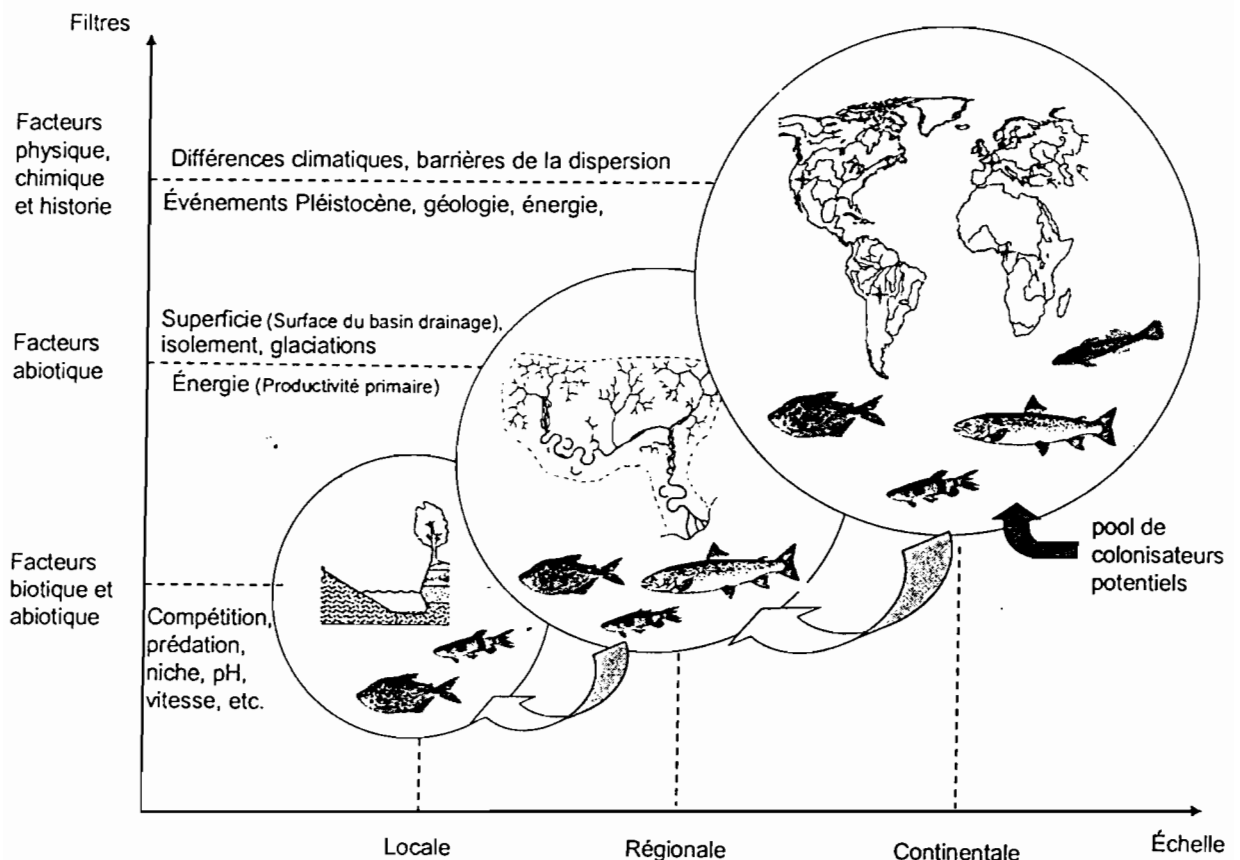


Figure 1. Illustration des effets de filtres qui s'opèrent sur les caractéristiques et la structure de la communauté des poissons, à différentes échelles spatiales et temporelles.

2.1. Hypothèses à tester selon les différentes échelles spatiales

Article 1 (A1) : nous cherchons à comprendre les relations qui peuvent exister au sein de différents peuplements de poissons entre le régime alimentaire, la morphologie et les caractéristiques de l'habitat. Cette hypothèse "écomorphologique" sera testée sur différentes stations du même bassin.

Article 2 (A2) : les facteurs environnementaux sont-ils responsables de la variation de la richesse spécifique locale et de la structuration trophique des poissons entre cours d'eau appartenant à différents bassins d'une même région ?

Article 3 et 4 (A3 et A4) : les structures des poissons (écomorphologiques et trophiques) observées dans quatre régions zoogéographiques à travers le monde (qui appartiennent aux continents européen, nord et sud américains et africains) convergent-elles dans des conditions environnementales semblables? Les divergences constatées peuvent-elles s'expliquer par des facteurs historiques et/ou énergétiques (énergie trophique disponible dans le milieu)?

3. Facteurs environnementaux.

3.1. Facteurs environnementaux et convergences écomorphologiques des communautés de poissons - Approche intra – bassin.

Les résultats obtenus sur les relations entre facteurs environnementaux et les communautés de poissons dans de petits cours d'eau forestiers de l'Amazonie bolivienne (A1) montrent que, indépendamment de la phylogénie, certaines guildes trophiques peuvent être grossièrement prévisibles à partir de quelques attributs morphologiques (Figure 2) (i.e. longueur relative de l'intestin, longueur standard et orientation de la bouche). Cela étant, ce lien entre le régime alimentaire et les caractéristiques morphologiques reste assez faible. Cela suggère que même si la morphologie limite les possibilités d'utilisation des ressources, cette limite est assez souple pour permettre aux espèces de s'adapter, jusqu'à un certain point, à différentes conditions biotiques ou abiotiques locales (filtres locaux voir figure 1).

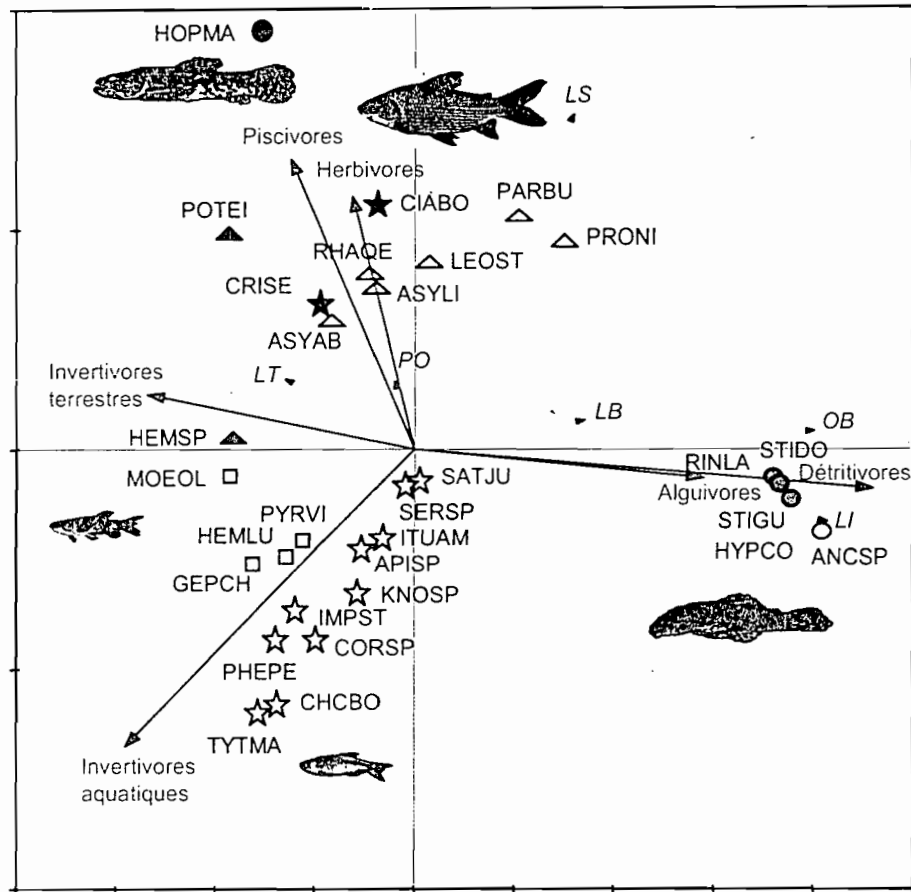


Figure 2. Résultats d'une RDA (Redundancy Analysis) liant le régime alimentaire des espèces à la morphologie : algivores (cercle ouvert), détritviores (cercle fermé gris), invertivores aquatiques (étoile ouverte), invertivores terrestres (triangle fermé), invertivores généralistes (carré), omnivores (étoile fermée), herbivores (triangle ouvert) et piscivores (cercle fermé). En bleu les descripteur morphologiques LS= Longueur standard, PO= position d'oeil, LT= Longueur de la tête, LB = Largeur de la bouche, OB= Orientation de la bouche, LI= Longueur de l'intestin (d'après A1).

L'interaction entre les questions d'échelle spatiale et le rôle des facteurs biotiques et abiotiques dans la structuration des communautés de poissons a été déterminée. Plusieurs modèles de communautés de poissons d'eau douce répondant à l'environnement ont été identifiés à travers les continents. Pour les facteurs biotiques par exemple, la prédation semble avoir des effets importants sur les communautés de poissons grâce à des mécanismes directs et indirects par lesquels les prédateurs peuvent structurer les communautés de poissons (Jackson *et al.* 2001). Ces effets forts pour les prédateurs, peuvent affecter le choix de l'habitat de l'espèce proie (Power *et al.* 1985; Gilliam & Fraser

2001). Cela peut mener les communautés de poissons présents dans les pools et les rapides à se déplacer vers des secteurs qui présentent moins de risque de prédation ou dans lesquels les prédateurs ont plus de difficulté d'attaque (Schlosser & Angermeier 1990). Ils peuvent choisir des habitats différents quand les prédateurs ne sont pas présents. Quand les espèces proie changent leur choix d'habitat pour réduire le risque de prédation, ils peuvent modifier leur trait de vie et ainsi réduire leur performance (Jackson *et al.* 2001). Jackson & Harvey (1989) et Tonn (1990) ont proposé que cette série de filtres, qui soustraient des espèces de la faune globale (potential fish fauna) jusqu'à ce que l'espèce ait trouvé un site particulier pour s'installer (figure 1), joue un rôle fondamental dans la structuration locale de la communauté et sur l'importance des interactions biotiques et abiotiques.

Dans notre cas, on a pu observer que même si la morphologie peut limiter les patterns dans l'utilisation des ressources, ces limites sont assez larges pour permettre à la plupart des poissons de changer leurs ressources alimentaire en réponse aux conditions biotiques et abiotiques locales. On trouve un exemple intéressant avec les espèces de genre *Astyanax* proches phylogénétiquement et morphologiquement comparables, connues pour leur plasticité alimentaire (Ringuelet 1943; Grosman *et al.* 1996; Gonzo *et al.* 1998; Barros 2004) mais qui se sont adapté dans un habitat semblable sur différents fleuves avec des régimes alimentaires similaires (Fritz 1974).

La compétition est un autre facteur biotique. Il n'existe pas de consensus concernant le rôle de compétition interspécifique dans la structuration de communautés de poissons à l'intérieur d'un cours d'eau (Ross 1986; Dunson & Travis 1991; Resetařits 1997; Matthews 1998). La variabilité de l'environnement dans les systèmes lotiques est discutable, si les adaptations comportementales, morphologiques et physiologiques ne sont pas plus importantes que les interactions dues à la compétition (Grossman *et al.* 1998). La plupart des études suggèrent une ségrégation de niche plutôt qu'une exclusion compétitive. C'est maintenant un fait établi que la compétition peut être importante, mais seulement lorsqu'il existe une variété d'autres paramètres comme les facteurs physiques et chimiques, la distribution des unités d'habitat "patchiness", les perturbations abiotiques, la prédation, et l'importance d'un continuum de la communauté dans les équilibres dynamiques (Magnan *et al.* 1994; Blondel 1995; Matthews 1998; Jackson *et al.* 2001).

Nous avons constaté que la disposition d'une espèce à une large dimension trophique est liée en partie à sa morphologie. En effet, les contraintes morphologiques agissant sur une espèce déterminent son potentiel de niche trophique. Néanmoins, la place réalisée semble dépendre également en partie de l'environnement (disponibilité de nourriture et variabilité entre les habitats). Ce fait soutient l'importance de la spécialisation alimentaire dans la ségrégation des niches trophiques (échelle fine) parmi les espèces, comme une explication probable de la haute diversité locale des espèces dans les peuplements néo-tropicaux (voir article 4).

En revanche, nous n'avons pas pu mettre en évidence de lien significatif entre la morphologie des espèces et les caractéristiques d'habitat. Ce dernier résultat s'explique peut être par la très forte homogénéité physique des sites échantillonnés.

3.2. Facteurs environnementaux et convergences des communautés de poissons - Approche Régionale

Nous avons examiné les patterns de structure des communautés de poissons le long du continuum amont-aval de plusieurs cours d'eau du Gabon (A2). Les résultats ont montré que la composition de ces communautés s'organise le long de ce continuum.

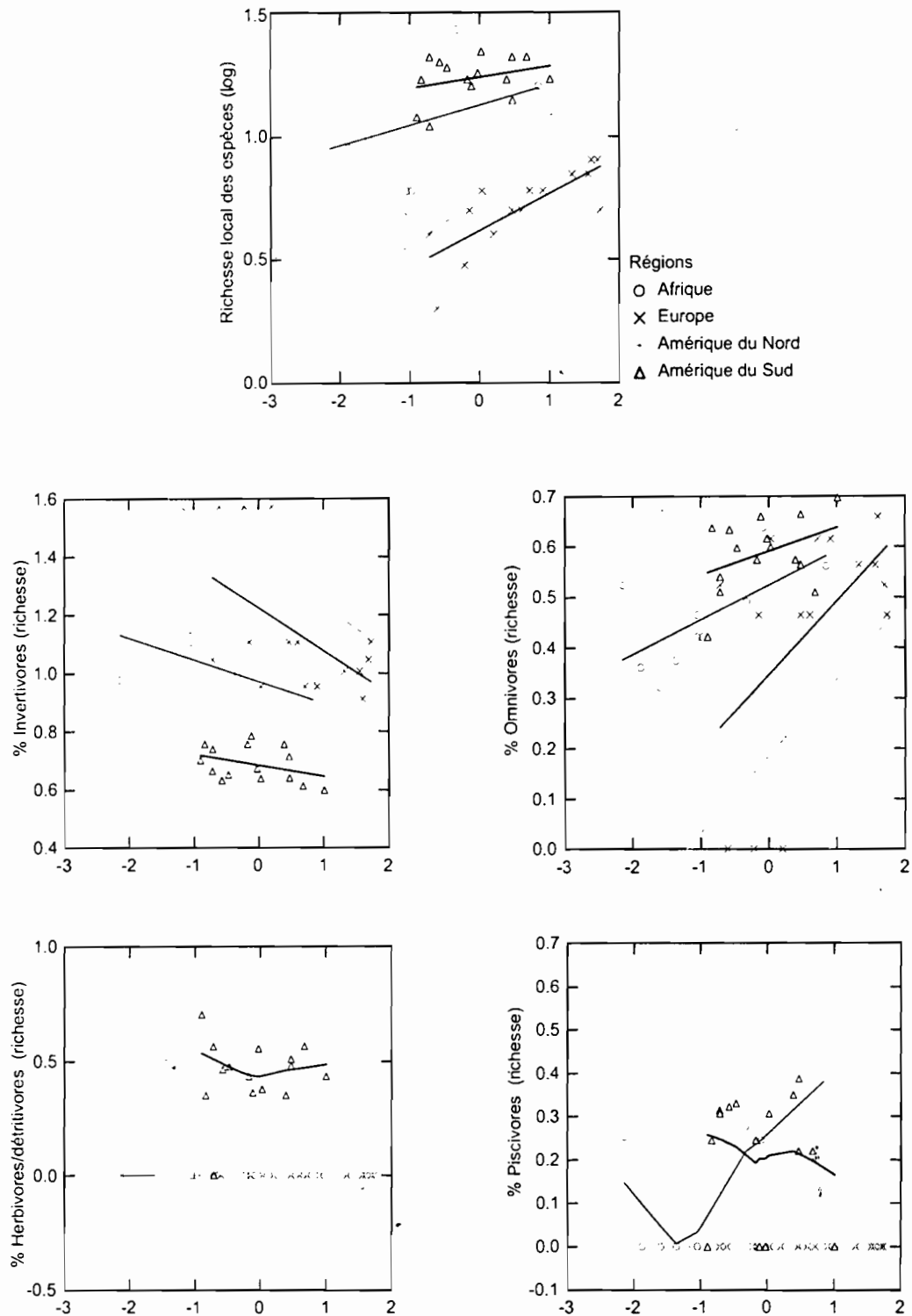
Vannote *et al.* (1980) explique que dans un système lotique, les variables physiques présentent généralement un gradient continu de conditions physiques d'amont en aval. La variation du gradient permet d'obtenir une série de réponses sur le comportement des populations, ayant comme résultat, d'une part, un continuum d'ajustements biotiques, et d'autre part, la constitution d'un modèle de chargement, de transport, d'utilisation, et de stockage de la matière organique sur la longueur d'une rivière, (River Continuum Concept RCC). Ces interactions entre l'environnement physique et la base d'énergie organique (matière organique allochtone et autochtone) résultent d'un modèle prévisible de structure de la communauté d'amont en aval (Oberdorff *et al.* 1993) : une augmentation de la richesse spécifique des communautés de l'amont vers l'aval et un changement de la structure trophique de ces communautés qui devraient être dominées à l'amont par les espèces invertivores et à l'aval par les espèces herbivores/détritivores, omnivores et piscivores (Schlosser 1987; Oberdorff *et al.* 1993; 2002).

Nos résultats paraissent corroborer cette hypothèse. Ils indiquent une augmentation générale de la richesse des espèces de l'amont vers l'aval et la transition d'invertivores à omnivores, herbivores/détritivores et piscivores tout au long du gradient longitudinal. Il existe plusieurs similitudes entre les modèles obtenus et ceux observés dans d'autres cours d'eau tempérés et tropicaux (Morin & Naiman 1990; Oberdorff *et al.* 1993; Kamdem Toham & Teugels 1998; Inoue & Nunokawa 2002; Oberdorff *et al.* 2002; Pouilly *et al.* 2006). Cela suggère une convergence potentielle des communautés de poissons le long des gradients environnementaux dans les systèmes aquatiques tropicaux et tempérés.

3.3. Facteurs environnementaux et convergence des communautés de poissons - Approche inter - continentale.

Les résultats de notre étude comparative entre des communautés de poissons d'eau douce en conditions environnementales semblables dans quatre régions zoogéographiques à travers le monde (A3) montrent que, indépendamment des contraintes phylogénétiques et historiques, la richesse et la structure trophique de la communauté de poisson convergent, à un degré substantiel, le long du continuum longitudinal des cours d'eau.

Pour les quatre régions, la richesse de la communauté a tendance à augmenter le long du gradient longitudinal des rivières. Cependant, bien que la tendance soit sensiblement la même, la richesse enregistrée dans les quatre régions est différente (Figure 3, 4 et 5). Ce dernier résultat pourrait être lié au fait qu'un modèle convergent général peut être modifié par des conditions abiotiques. En effet, en ce qui concerne l'environnement contemporain, le climat (qui affecte fortement l'énergie trophique disponible au système; (Hawkins *et al.* 2003) a pu influencer nos communautés de poissons. Une version de l'hypothèse énergie/espèces (Wright 1983) propose que des limites à la diversité (dans la limite du nombre d'espèce et de guildes fonctionnelles) soient fixées par la quantité d'énergie traversant la chaîne trophique (par exemple la diversité des herbivores est limitée par la production primaire, et ainsi de suite le long de la chaîne alimentaire). D'après cette hypothèse, et toutes choses étant égales par ailleurs, une augmentation de disponibilité d'énergie devrait donc mener à une augmentation significative des spécialistes et des



Position des sites dans les nvières le long de gradient longitudinal (PC1). Position des sites dans les rivières le long de gradient longitudinal (PC1).

Figure 3. Relation entre la richesse locale des espèces et le pourcentage de chaque guildes trophique (% de la richesse) et la position des sites le long du gradient longitudinal. PC1 correspond au premier axe d'une analyse en composantes principales (ACP) effectuée sur les variables environnementales (d'après A3).

espèces prédatrices supérieures (Abrams 1995; Srivastava & Lawton 1998). La température et l'énergie solaire étant plus élevées dans les zones tropicales que dans les zones tempérées, nous pouvons nous attendre à une plus grande énergie trophique dans les cours d'eau tropicaux comparés aux tempérés. Les études précédentes qui analysent la structure des communautés de poissons dans les cours d'eau tropicaux semblent soutenir cette hypothèse (voir A2 et A4).

Nos observations des traits trophiques des espèces le long du gradient longitudinal des cours d'eau sont également conformes aux prévisions fournies par le cadre théorique du River Continuum Concept (RCC) (Vannote *et al.* 1980), qui suggère une progression longitudinale des guildes trophiques de poissons, débutant en amont par les invertivores et terminant à l'aval par les omnivores, les détritivores, les herbivores et les piscivores (Schlosser 1987; Oberdorff *et al.* 1993; 2002). Ces analyses prouvent également, que mis à part l'effet du gradient longitudinal, les cours d'eau tropicaux sont toujours plus riches en espèces que leurs équivalents européens ou nord-américains. Indépendamment du climat contemporain, cette tendance peut-être en partie expliquée par les extinctions massives au cours du Pléistocène, qui ont touché l'Amérique du Nord et l'Europe, plus que les secteurs tropicaux (Mahon 1984; Oberdorff *et al.* 1997).

Nous avons également noté que la représentation des différentes guildes trophiques n'était pas proportionnelle dans les communautés de nos différentes régions zoogéographiques (Figure 4). Les invertivores (en pourcentage de la richesse et du pourcentage de la densité) étaient davantage représentés le long du gradient longitudinal des cours d'eau tempérés tandis que les omnivores, les herbivores/détritivores et les piscivores étaient davantage représentés le long du gradient longitudinal des cours d'eau tropicaux. Ce résultat est en accord avec celui obtenu par Winemiller (1992) et confirmerait l'effet possible d'une énergie trophique plus élevée (ressources disponibles) et d'une longueur de chaîne trophique plus importante dans les cours d'eau tropicaux.

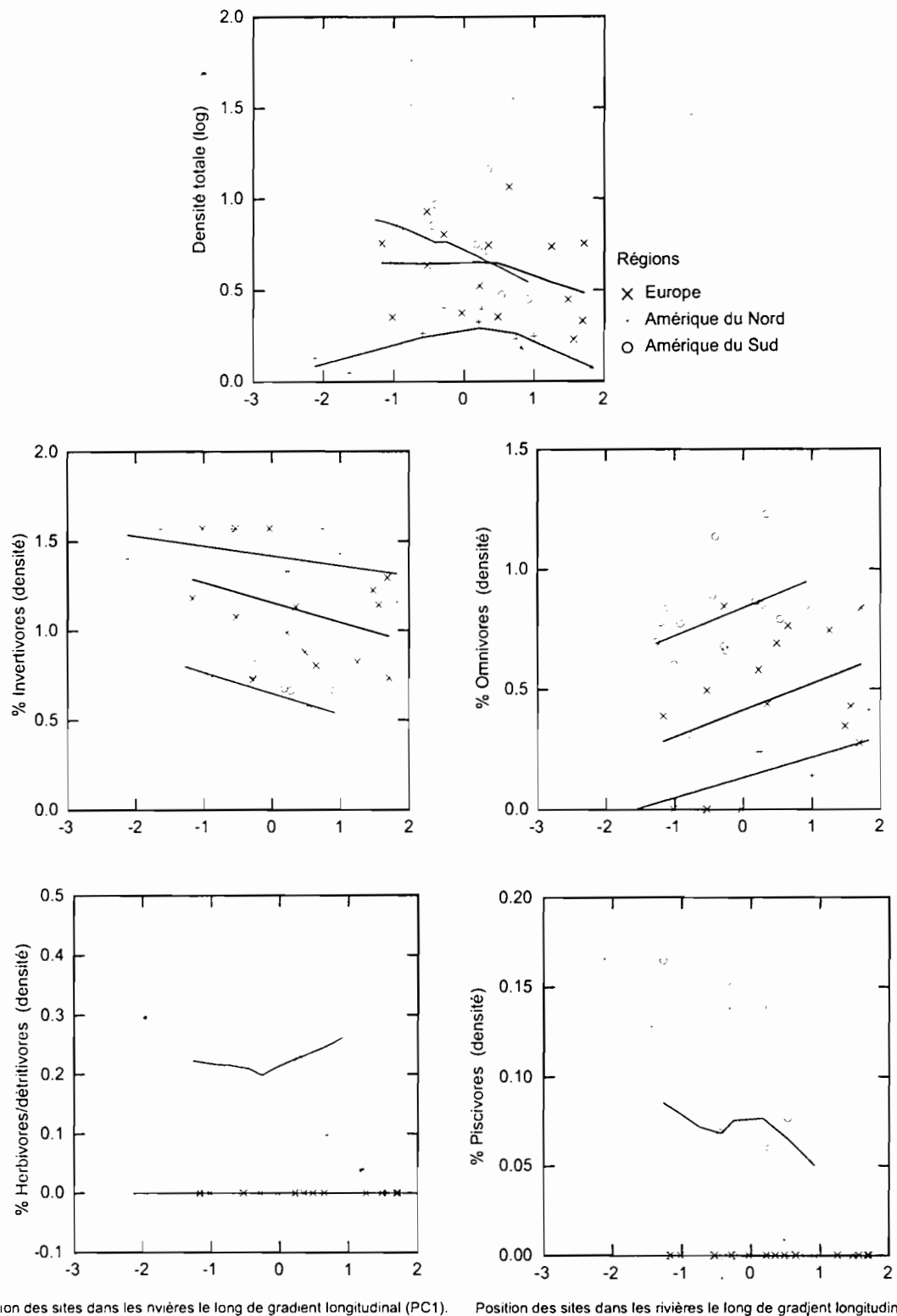


Figure 4. Relations entre la densité totale et les pourcentages des différentes guildes trophiques et la position des sites le long du gradient longitudinal. PC1 correspond au premier axe d'une analyse en composantes principales (ACP) effectuée sur les variables environnementales (d'après A3).

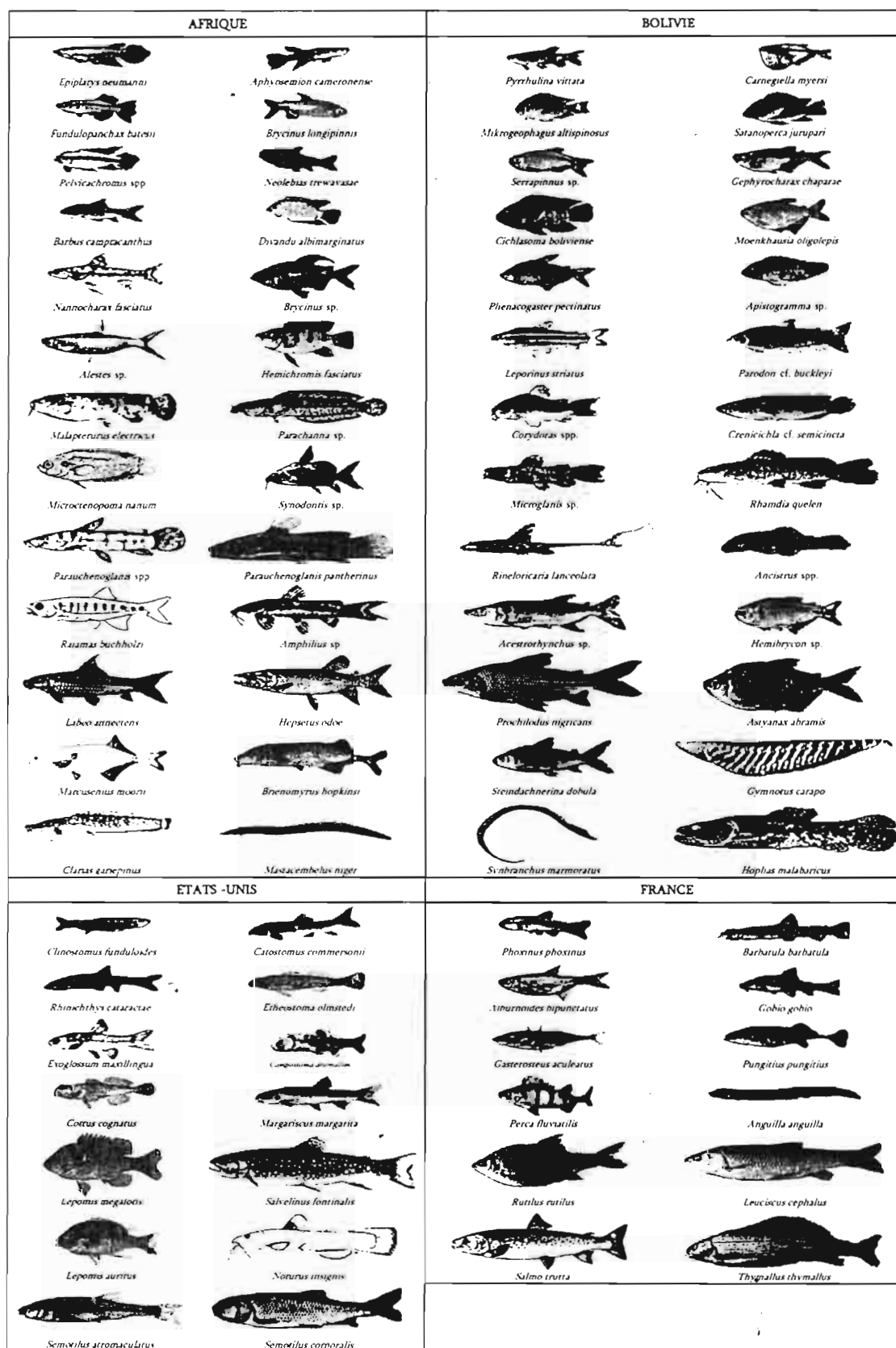


Figure 5. Diversité morphologique des poissons dans les cours d'eau de nos quatre régions zoo - géographiques (Afrique, Bolivie, Etats – Unis et France). Les photos proviennent de Fishbase, Universidad Mayor de San Simon – ULRA et Paugy *et al.* 2003.

4. Conclusion et perspectives

Cette thèse a permis d'aborder différentes questions relatives à l'hypothèse de convergence qui, d'un point de vue déterministe, explique que la structure de la communauté peut être envisagée en fonction de l'environnement et conduit à l'évolution dans une direction prévisible. Elle fournit un outil approximatif pour identifier des filtres d'habitats qui peuvent opérer sur la distribution et la structuration des communautés à différentes échelles et permet d'expliquer comment les facteurs environnementaux associés aux échelles spatiales et temporelles agissent sur la distribution des espèces, et de leurs traits fonctionnels (morphologie et régime trophique).

Les résultats nous ont permis d'intégrer plusieurs approches de l'écologie générale telles que celles concernant la biogéographie et l'écologie fonctionnelle et les résultats obtenus renforcent certaines études précédentes qui ont suggéré des convergences potentielles des communautés de poissons le long d'un gradient environnemental dans des systèmes lotiques, tropicaux ou tempérés.

Mettre en évidence la convergence est une méthode puissante pour généraliser des patterns observés localement, et, de façon optimiste, identifier les processus qui engendrent ces patterns. D'un point de vue de la recherche écologique appliquée (qui cherche à prédire des patterns de distribution et d'abondance en fonction des contraintes de l'environnement) et de la conservation, ces résultats accentuent la nécessité d'évaluer tous les types d'habitats le long du gradient longitudinal des systèmes lotiques, afin d'intégrer toutes les variations des communautés liées aux facteurs environnementaux. Ce type de résultats constitue donc un excellent outil fournis aux décideurs pour les aider à mettre en œuvre des plans de conservation et de gestion des systèmes lotiques.

L'intérêt fondamental de cette étude se trouve dans l'acquisition de données sur les différentes guildes qui permettent d'analyser les communautés selon un aspect fonctionnel (diversité des stratégies biologiques). Il devient ainsi possible de dégager des lois générales des communautés en réponse aux contraintes environnementales indépendantes de la composition spécifique.

Une littérature vaste a été consacrée au développement d'indicateurs biologiques, adaptés régionalement, pour l'estimation de cours d'eau et l'intégrité des rivières sur les différents continents (Hughes & Oberdorff 1999; Karr & Chu 2000). Ces indicateurs biologiques suivent habituellement la méthodologie de l'indice d'intégrité biotique (Index of Biotic Integrity IBI) formulée par (Karr 1981). L'IBI emploie une série de paramètres basés sur la structure de la communauté : par exemple la richesse spécifique ou encore la composition trophique. Cela donne des signaux fiables des conditions de "santé" de la rivière. L'emploi de cet outil, au détriment des attributs taxinomiques, permet de faire la comparaison des différentes communautés extraites de différents pools d'espèces. Cependant, l'application de l'IBI à l'échelle mondiale implique une évolution indépendante des espèces avec des caractéristiques écologiques semblables (associations écologiques) dans des environnements similaires en différentes régions. En identifiant formellement un degré substantiel de convergence dans la richesse et dans la structure trophique des communautés des cours d'eau étudiés, le présent travail appuie l'emploi de tels indicateurs à larges échelles spatiales (Article 5).

5. References

- Abrams P.A. (1995) Monotonic or unimodal diversity-productivity gradients : what does competition theory predict? *Ecology*, 76, 2019-2027
- Aguirre L.F., Herrel A., van Damme R. & Matthysen E. (2002) Ecomorphological analysis of trophic niche partitioning in a tropical savannah bat community. *Proceedings of the Royal Society of London Series B - Biological Sciences*, 269, 1271-1278
- Barros S.E. (2004) Alimentación de *Astyanax abramis* (Characiformes : Characidae) en el Embalse Cabra Corral, Salta, Noroeste de Argentina. *Revista Aquatic*, 20, 88-96
- Bellwood D.R., Wainwright P., Fulton C.J. & Hoey A.S. (2005) Functional versatility supports coral reef biodiversity. *Proc. R. Soc. Lond B.*, 273, 101-107
- Ben-Moshe A., Dayan T. & Simberloff D. (2001) Convergence in Morphological Patterns and Community Organization between Old and New World Rodent Guilds. *The American Naturalist*, 158, 484-494
- Blondel J. (1995) *Biogéographie Approche écologique et évolutive*. MASSON, Paris, Milan, Barcelone.
- Blondel J., Vuilleumier F., Marcus L. & Terouanne E. (1984) Is there ecomorphological convergence among mediterranean bird communities of Chile California, and France? In : *Evolutionary Biology* (ed. Hecht MK, Wallace, B. & Prance, G. T.), pp. 141-213
- Brown J. & Leiberman G. (1973) Resource utilization and coexistence of seed-eating desert rodents in sand-dune habitats. *Ecology*, 54, 788-797
- Brown J.H. (1975) Geographical ecology of desert rodents. In : *Ecology and Evolution of communities* (eds. Cody ML & Diamond JM), pp. 315-341, Cambridge, Massachusetts
- Bunn S. & Arthington A. (2002) Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, 30, 492-507
- Chan M.D. (2001) Fish ecomorphology : Predicting habitat preferences of stream fishes from their body shape. In, p. 251. Faculty of the Virginia Polytechnic Institute and State University., Virginia
- Cody M.L. (1973) Character convergence. *Annu. Rev. Ecol. Syst.*, 4, 189-211
- Cody M.L. (1975) Towards a theory of continental species diversities : Bird distributions over Mediterranean habitat gradients. In : *Ecology and Evolution of communities* (eds. Cody ML & Diamond J.M.), pp. 214-257. Belknap Press, Cambridge
- Cody M.L. & Mooney H.A. (1978) Convergence versus non convergence in mediterranean - climate ecosystems. *Ann. Rev. Ecol. Syst.*, 9, 265 - 321
- Currie D.J., Mittelbach G.G., Cornell H.V., Field R., Guégan J.-F., Hawkins B.A., Kaufman D.M., Kerr J.T., Obérdorff T., O' Brien E. & Turner J.R.G. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology letters*, 7, 1121-1134
- Davies R.G., Eggleton P., Jones D.T., Gathorne-Hardy F.J. & Hernandez L.M. (2003) Evolution of termite functional diversity : analysis and synthesis of local ecological and regional influences on local species richness. *Journal of biogeography*, 30, 847-877
- Diamond J.M. (1975) Assembly of species communities. In : *Ecology and evolution of Communities* (eds. Cody ML & Diamond JM), pp. 342-444. Harvard University Press, Cambridge, Massachusetts
- Dubost G. (1968) Les niches écologiques des forêts tropicales sud-américaines et africaines, sources de convergences remarquables entre rongeurs et artiodactyles. *Terre vie*, 22, 3-28

- Dunson W.A. & Travis J. (1991) The role of abiotic factors in community organization. *American Naturalist*, 138, 1067-1091
- Evans K.L., Jackson S.F., Greenwood J.J.D. & Gaston K.J. (2006) Species traits and the form of individual species - energy relationships. *Proceedings of the royal society B*, 273, 1779 -1787
- Friedmann H. (1946) Ecological counterparts in birds. *Sci. Monthly*, 43, 395-398
- Fritz E.S. (1974) Total diet comparison in fishes by Spearman rank correlation coefficients. *Copeia*, 1, 210-214
- Fuentes E.R. (1976) Ecological convergence of lizard communities in Chile and California. *Ecology*, 57, 3-17
- Gilliam J.F. & Fraser D.F. (2001) Movement in corridors : Enhancement by predation threat, disturbance, and habitat structure. *Ecology*, 82, 258-273
- Gonzo G.M., Matinez V., Vera R. & Santos D. (1998) Utilización de recursos y estructura en gremios de comunidades de peces en rios de bajo orden. *Bol. Soc. Biol.*, 69, 131-140
- Grosman M.F., Gonzalez Castelain J.R. & Usunoff E.J. (1996) Trophic niches in an Argentine pond as a way to assess functional relationships between fishes and other communities. *Water SA*, 22, 345-350
- Grossman G.D., Ratajczak R.E., Crawford M. & Freeman M.C. (1998) Assemblage organization in stream fishes : Effects of environmental variation and interspecific interactions. *Ecological Monographs*, 68, 395-420
- Guo Q.F. & Ricklefs R.E. (2000) Species richness in plant genera disjunct between temperate eastern Asia and North America. *Botanical Journal of the Linnean Society*, 134, 401-423
- Hawkins B.A., Field R., Cornell H.V., Curri D.J., Guégan J.-F., Kaufman D.M., Kerr J.T., Mittelbach G.G., Oberdorff T., O'Brien E.M., Porter E.E. & Turner J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, 84, 3105-3117
- Hughes R.M. & Oberdorff T. (1999) Applications of IBI concepts and metrics to waters outside the United States and Canada. In : *Assessing the sustainability and biological integrity of water resource quality using fish communities* (ed. Simon TP), pp. 79-93. CRC Press, Boca Raton, Florida
- Hugueny B. & Pouilly M. (1999) Morphological correlates of diet in a assemblage of West African freshwater fishes. *Journal of Fish Biology*, 54, 1310-1325
- Inoue M. & Nunokawa M. (2002) Effects of longitudinal variations in stream habitat structure on fish abundance : an analysis based on subunit-scale habitat classification. *Freshwater Biology*, 47, 1594-1607
- Inouye R.S. & Tilman D. (1995) Convergence and divergence of old - field vegetation after 11 yr of nitrogen addition. *Ecology*, 76, 1872-1887
- Irz P., Michonneau F., Oberdorff T., Whittier T.R., Lamouroux N., Mouillot D. & Argiller C. (2007) Fish community comparisons along environmental gradients in lakes of France and Northeast U. S. A. *Global ecology and biogeography*, 16, 350-366
- Jackson D.A. & Harvey H.H. (1989) Biogeographic associations in fish assemblages : Local vs. regional processes. *Ecology*, 70, 1472-1484
- Jackson D.A., Peres-Neto P.R. & Olden J.D. (2001) What controls who is where in freshwater fish communities-the roles of biotic, abiotic, and spatial factors. *Can. J. fish. aquat. sci.*, 58, 157-170
- Jones M.E. (2003) Convergence in ecomorphology and guild structure among marsupial and placental carnivores. In : *Predators with Pouches. The Biology of Carnivorous Marsupials* (eds. Jones ME, Dickman C & Archer M), 504 p. CSIRO PUBLISHING, Collingwood Victoria

- Jousselin E., Rasplus Y. & Kjellberg F. (2003) Convergence and coevolution in a mutualism : evidence from a molecular phylogeny of *Ficus*. *Evolution*, 57, 1255-1269
- Kamdem Toham A. & Teugels G.G. (1998) Diversity patterns of fish assemblages in the lower Ntem River Basin (Cameroon), with notes on potential effects of deforestation. *Arch. Hydrobiol.*, 141, 421-446
- Karr J.R. (1981) Assessment of biotic integrity using fish communities. *Fisheries*, 6, 21-27
- Karr J.R. & Chu E.W. (2000) Sustaining living rivers. *Hydrobiologia*, 422, 1-14
- Karr J.R. & James F.C. (1975) Eco-morphological configurations and convergent evolution in species and communities. In : *Ecology and evolution of communities* (eds. Cody ML & Diamond JM), pp. 258-291. Belknap Press, Cambridge, Massachusetts, USA.
- Keast A. (1972) Ecological opportunities and dominant families, as illustrated by the neotropical Tyrannidae (Aves). In : *Evolutionary Biology* (eds. Dobzhansky T, Hecht MK & Steere WC), pp. 229-277. Appleton-Century-Crofts, New York
- Kelt D.A., Brown J.H., Heske E.J., Marquet P.A., Morton S.R., Reid J.R.W. & Shenbrot G. (1996) Community structure of desert small mammals comparisons across four continents. *Ecology*, 77, 746 - 761
- Kelt D.A., Rogovin K., Shenbrot G. & Brown J.H. (1999) Patterns in the structure of Asian and North American desert small mammal communities. *Journal of Biogeography*, 26, 825-841
- Knouft J.H. (2003) Convergence, divergence, and the effect of congeners on body size ratios in stream fishes. *Evolution*, 57, 2374-2382
- Lamouroux N., Poff N.L. & Angermeier P.L. (2002) Intercontinental convergence of stream fish community traits along geomorphic and hydraulic gradients. *Ecology*, 83, 1792-1807
- Lanoiselée C. (2004) Diversité fonctionnelle des communautés de poissons de plans d'eau. In : *Université Paul Sabatier*, pp. 1-33. Université Paul Sabatier, Toulouse
- Lawton J.H. (1999) Are there general laws in ecology? *Oikos*, 84, 177-192
- Leal M., Knox A.K. & Losos J.B. (2002) Lack of convergence in aquatic Anolis lizards. *Evolution*, 56, 785-791
- Lee D., Gilbert C.R., Hocutt C.H., Jenkins R.E., McAllester D.E. & Stauffer J.R. (1980) *Atlas of North American freshwater fishes*. North Carolina state Museum of natural History edn, Caroline.
- Lévêque C. & Paugy D. (2006) *Les poissons des eaux continentales africaines*. IRD Editions edn, Paris.
- Losos J.B., Jackman T.R., Larson A., de Queiroz K. & Rodriguez-Schettino L. (1998) Contingency and determinism in replicated adaptive radiations of Island Lizards. *Science*, 279, 2115 - 2118
- MacArthur R. & Levins R. (1967) The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist*, 101, 377-385
- Magnan P., Rodriguez M.A., Legendre P. & Lacasse S. (1994) Dietary variation in a freshwater fish species : Relative contributions of biotic interactions, abiotic factors and spatial structure. *Canadian Journal of Fisheries and Aquatic Sciences*, 51, 2856-2865
- Mahon R. (1984) Divergent Structure in Fish Taxocenes of North Temperate Streams. *Can. J. Fish Aquatic*, 41, 330-350
- Marrero C. & Winemiller K.O. (1993) Tube-snouted gymnotiform and mormyrid fishes : convergence of a specialized foraging mode in the teleosts. *Environmental Biology of Fishes*, 38, 299-309
- Marshall N.B. (1971) *Explorations in the life of fishes*. Harvard University Press, Cambridge, Massachusetts, USA.

- Matthews W.J. (1998) *Patterns in freshwater fish ecology*. Chapman & Hall, New York.
- Medel R.G. (1995) Convergence and historical effects in harvester ant assemblages of Australia, North America, and South America. *Biological journal of the Linnean Society*, 55, 29-44
- Meinzer F.C. (2003) Functional convergence in plant responses to the environment. *Oecologia*, 134, 1-11
- Melville J., Harmon L.J. & Losos J.B. (2006) Intercontinental community convergence of ecology and morphology in desert lizard. *Pro. R. Soc. B.*, 273, 557-563
- Menge B.A. & Olson A.M. (1990) Role of scale and environmental factors in regulation of community structure. *Trends in Ecology and Evolution*, 5, 52-57
- Milewski A.V. (1979) A climatic basis for the study of convergence of vegetation structure in Mediterranean Australia and southern Africa. *J. Biogeog.*, 6, 293-299
- Milewski A.V. (1981) A comparison of reptile communities in relation to soil fertility in the mediterranean and adjacent arid parts of Australia and southern Africa. *J. Biogeog.*, 8, 493-503
- Morin R. & Naiman R.J. (1990) The relation of stream order to fish community dynamics in Boreal forest watersheds. *Polskie Archiwum Hydrobiologii*, 37, 135-150
- Motta P.J. (1988) Functional morphology of the feeding apparatus of ten species of Pacific butterflyfishes (Perciformes, Chaetodontidae) : an ecomorphological approach. *Environmental Biology of Fishes*, 22, 39-67
- Motta P.J., Clifton K.B., Hernandez P. & Eggold B. (1995) Ecomorphological correlates in ten species of subtropical sea grass fishes : diet and microhabitat utilization. *Environmental Biology of Fishes*, 44, 37-60
- Moyle P.B. & Herbold B. (1987) Life-history patterns and community structure in stream fishes of western North America : comparisons with Eastern North America and Europe. In : *Community and evolutionary ecology of North American stream fishes* (eds. Matthews WJ & Heins DC), pp. 25-32. University of Oklahoma Press, Norman, London
- Nelson J.S. (2006) *Fishes of the World*. Fourth edition. John Wiley and Sons, Inc., Canada.
- Nonogaki H., Nelson J.A. & Patterson W.P. (2007) Dietary histories of herbivorous loriciid catfishes : evidence from $\delta^{13}C$ values of otoliths. *Environmental biology of fishes*, 78, 13-21
- Norton S.F. & Brainerd E.L. (1993) Convergence in the feeding mechanics of ecomorphologically similar species in the centrarchidae and Cichlidae. *Journal of experimental Biology*, 176, 11-29
- Oberdorff T., Guilbert E. & Lucchetta J.-C. (1993) Patterns of fish richness in the Seine River basin, France. *Hydrobiologia*, 259, 157-167
- Oberdorff T., Guegan J.-F. & Hugueny B. (1995) Global scale patterns of fish species richness in rivers. *Ecography*, 18, 345-352
- Oberdorff T., Hugueny B. & Guégan J.-F. (1997) Is there an influence of historical events on contemporary fish species richness in rivers? Comparisons between Western Europe and North America. *Journal of Biogeography*, 24, 461-467
- Oberdorff T., Pont D., Hugueny B., Belliard J., Berrebi D., Thomas R. & Porcher J.P. (2002) Adaptation et validation d'un indice poisson (FBI) pour l'évaluation de la qualité biologique des cours d'eau français. *Bull. Fr. Pêche Piscic.*, 365/366, 405-433
- Orians G.H. & Paine R.T. (1983) Convergent evolution at the community level. In : *Coevolution* (eds. Futuyma DJ & Slatkin M), pp. 431-458. Sinauer, Sunderland
- Orr M. & Smith T. (1998) Ecology and speciation. *Tree*, 13, 502-506
- Paugy D., Lévêque C. & Teugels G.G. (2003) *Poissons d'eaux douces et saumâtres de l'Afrique de l'Ouest*. IRD Editions, Paris.

- Pearson D.L. (1977) A pantropical comparison of bird community structure on six lowland forest sites. *The Condor*, 79, 232-244
- Pianka E.R. (1973) The structure of lizard communities. *Annual Rev. Ecol. Syst.*, 4, 53-74
- Pianka E.R. (1975) Niche relations of desert lizards. In : *Ecology and Evolution of Communities* (eds. Cody ML & Diamond JM), pp. 292-314. Harvard University Press, Cambridge, Massachusetts
- Poff N.L. (1997) Landscape filters & species traits : Towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society*, 16, 391-409
- Poff N.L. & Ward J.V. (1990) The physical habitat template of lotic systems : recovery in the context of historical pattern of spatio-temporal heterogeneity. *Environmental Management*, 14, 629-646
- Pouilly M., Barrera S. & Rosales C. (2006) Changes of taxonomic and trophic structure of fish assemblages along an environmental gradient in the Upper Beni watershed (Bolivia). *Journal of Fish Biology*, 68, 137-156
- Power M.E., Matthews W.J. & Stewart A.J. (1985) Grazing minnows, piscivorous bass and stream algae : dynamics of a strong interaction. *Ecology*, 66, 1448-1456
- Price T., Lovette I., Bermingham E., Gibbs L. & Richman A. (2000) The imprint of history on communities of North American and Asian Warblers. *The American Naturalist*, 156, 354-367
- Resetarits F.J. (1997) Interspecific competition and qualitative competitive asymmetry between two benthic streams fishes. *Oikos*, 78, 428-439
- Ricklefs R.E., Latham R.E. & Qian H. (1999) Global patterns of tree species richness in moist forests : distinguishing ecological influences and historical contingency. *Oikos*, 86, 369-373
- Ricklefs R.E. & Schluter D. (1993) Species diversity : Regional and historical influences. In : *Species diversity in ecological communities, historical and geographical perspectives* (ed. Ricklefs RES, D.), p. 414. The University of Chicago Press, Chicago
- Ringuelet R. (1943) *Piscicultura del pejerrey o aterinicultura*. Suelo Argentino. Buenos Aires.
- Root R.B. (1967) The niche exploitation pattern of the blue-gray gnatcatcher. *Ecological Monographs*, 37, 317-350
- Ross S.T. (1986) Resource partitioning in fish assemblages : a review on field studies. *Copeia*, 1986, 352-388
- Ruber L. & Adams D.C. (2001) Evolutionary convergence of body shape and trophic morphology in cichlids from Lake Tanganyika. *J. Evol. Biolo.*, 14, 325 - 332
- Samuels C. & Drake J. (1997) Divergent perspectives on community convergence. *Tree*, 12, 427- 432
- Schlosser I.J. (1987) A conceptual framework for fish communities in small warm water streams. In : *Community and Evolutionary Ecology of North American Stream Fishes* (eds. Matthews W.J. & Heins D.C.), pp. 17-24. University of Oklahoma Press, Norman
- Schlosser I. J. & Angermeier P.L. (1990) The influence of environmental variability, resource abundance, and predation on juvenile cyprinid and centrarchid fishes. *Pol. Arch. Hydrobiol.*, 37, 265-284
- Schluter D. (1986) Test for similarity and convergence of finch communities. *Ecology*, 67, 1073-1085
- Schluter D. & Ricklefs R.E. (1993) Convergence and the Regional Component of Species Diversity. In : *Species diversity in ecological communities, historical and*

- geographical perspectives* (ed. Ricklefs RE), pp. 230-240. The University of Chicago Press, Chicago
- Simberloff D. & Dayan T. (1991) The guild concept and the structure of ecological communities. *Annual Review of Ecology and Systematics*, 22, 115-143
- Simon T.P. (1999) *Assessing the Sustainability and Biological Integrity of Water Resources Using Fish Communities*. CRC Press LLC. London, New York, Washington, D. C.
- Smith B. & Wilson J.B. (2002) Community convergence : Ecological and evolutionary. *Folia Geobotanica*, 37, 171-183
- Smith E. (1982) Niche Breadth, Resource availability, and inference. *Ecology*, 63, 1675-1681
- Southwood T.R.E. (1977) Habitat, the templet for ecological strategies? *J. Anim. Ecol.*, 46, 337-365
- Srivastava D.S. & Lawton J.H. (1998) Why more productive sites have more species : An experimental test of theory using tree-hole communities. *The American Naturalist*, 152, 510-529
- Statzner B., Hoppenhaus K., Arens M.-F. & P. R. (1997) Reproductive traits, habitat use and templet theory : a synthesis of world-wide data on aquatic insects. *Freshwater Biology*, 38, 109-135
- Statzner B., Resh V.H. & Roux A.L. (1994) The synthesis of long-term ecological research in the context of concurrently developed ecological theory : design of a research strategy for the Upper Rhône River and its Floodplain. *Freshwater Biology*, 31, 253-263
- Stephens P.R. & Wiens J.J. (2004) Convergence, divergence and homogenization in the ecological structure of Emydidi Turtle communities : the effects of phylogeny and dispersal. *The American Naturalist*, 164, 244-254
- Storch D., Evans K.L. & Gaston K.J. (2005) The species-area-energy relationship. *Ecology letters*, 8, 487-492
- Tedesco P., Ibañez C., Moya N., Bigorne R., Camacho J., Goitia E., Hugueny B., Maldonado M., Rivero M., Tomanova S., Zubieta J. & Oberdorff T. (2007) Local-scale species-energy relationships in fish assemblages of some forested streams of the Bolivian Amazon. *Comptes Rendus Biologies*, 330, 255 - 264
- Tonn W.M. (1990) Climate change and fish communities : a conceptual framework. *Transactions of the American Fisheries Society*, 119, 337-352
- Tonn W.M., Magnuson J.J., Rask M. & Toivonen J. (1990) Intercontinental comparison of small-lake fish assemblages : The balance between local and regional processes. *American Naturalist*, 136, 345-375
- Townsend C.R., Doledéc S. & Scarsbrook M.R. (1997) Species traits in relation to temporal and spatial heterogeneity in streams : a test of habitat templet theory. *Freshwater Biology*, 37, 367-387
- Townsend C.R. & Hildrew A.G. (1994) Species traits in relation to habitat templet for river systems. *Freshwater Biology*, 31, 265-275
- Usseglio-Polatera P. (1994) Theoretical habitat templet, species traits, and species richness : aquatic insects in the Upper Rhone River and its floodplain. *Freshwater Biology*, 31, 417-437
- 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
- Vila-Gispert A., Moreno-Amich R. & García-Berthou E. (2002) Gradients of life-history variation : an intercontinental comparison of fishes. *Reviews in Fish Biology and Fisheries*, 12, 417-427

- Wainwright P.C., Bellwood D.R. & Westneat M.W. (2002) Ecomorphology of locomotion in labrid fishes. *Environmental biology of fishes*, 65, 47-62
- Wainwright P.C., Bellwood D.R., Westneat M.W., Grubich J.R. & Hoey A.S. (2004) A functional morphospace for the skull of labrid fishes : patterns of diversity in a complex biomechanical system. *Biol. J. Linn. Soc.*, 82, 1-25
- Wassenaar T.D., van Aarde R.J., Pimm S.L. & Ferreira S.M. (2005) Community convergence in disturbed subtropical dune forests. *Ecology*, 86, 655-666
- Whittaker R.J., Nogués-Bravo D. & Araújo M.B. (2007) Geographical gradients of species richness : a test of the water-energy conjecture of Hawkins et al. (2003) using European data for five taxa. *Global ecology and biogeography*, 16, 76-89
- Winemiller K.O. (1991) Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. *Ecological Monographs*, 61, 343-365
- Winemiller K.O. (1992) Ecomorphology of freshwater fishes. *National geographic research and exploration*, 8, 308-327
- Winemiller K.O. & Adite A. (1997) Convergent evolution of weakly electric fishes from floodplain habitats in Africa and South America. *Environmental Biology of Fishes*, 49, 175-186
- Winemiller K.O., Kelso-Winemiller L.C. & Brenkert A.L. (1995) Ecomorphological diversification and convergence in fluvial cichlid fishes. *Environmental Biology of Fishes*, 44, 235-261
- Winemiller K.O. & Rose K.A. (1992) Patterns of life history diversification in North American fishes : implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences*, 49, 2196-2218
- Wittaker R.J.W., K.J.; Field, R. (2001) Scale and species richness : towards a general, hierarchical theory of species diversity. *Towards a general theory of diversity*, 28, 453-470
- Wright D.H. (1983) Species-energy theory : an extension of species-area theory. *Oikos*, 41, 496-506

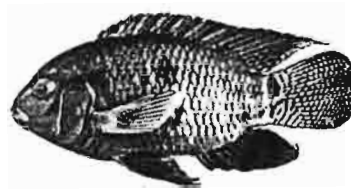
Publications et manuscrits

Article 1

**Dietary –morphological relationships in fish assemblages of small
forested streams in the Bolivian Amazon**

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Cichlasoma boliviense Photo – José Zubieta

Dietary-morphological relationships in fish assemblages of small forested streams in the Bolivian Amazon

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Abstract – We explored the relationships between diet and morphology in 30 fish species from forested tropical streams of the Bolivian Amazon. These species were first assigned to eight broad trophic guilds based on stomach contents analysis. The relationships between diet and morphology were then examined using Redundancy Analysis, after having checked for potential phylogenetical effects. Results show that, independently of any phylogenetic constraints, some of the trophic guilds could be grossly predicted from few relevant morphological attributes (i.e. relative intestinal length, standard length and mouth orientation) and thus suggest a significant link between diet and morphology. In other words, species having similar diet tend to converge to some extent on some morphological attributes. This link was nevertheless rather weak, suggesting that even if morphology may set limits to patterns of resource use, these limits are broad enough to allow fishes changing their choice of prey resources to respond to local biotic and/or abiotic conditions.

Key words: Diet / Morphology / Phylogeny / Convergence / Tropical streams / Fishes / Bolivia

Résumé – Relations entre le régime alimentaire et les caractéristiques morphologiques des peuplements de poissons de petits cours d'eau forestiers de l'Amazonie bolivienne. Nous avons analysé les relations entre le régime alimentaire et la morphologie de 30 espèces de poissons présentes dans de petits cours d'eau forestiers de l'Amazonie bolivienne. Après une analyse de leurs contenus stomacaux, les 30 espèces ont été réparties, dans un premier temps, dans huit grandes guildes trophiques. Dans un deuxième temps, après avoir analysé les éventuelles contraintes phylogénétiques, nous avons examiné, par analyse multivariée, les relations entre le régime alimentaire et la morphologie des espèces. Les résultats montrent que, indépendamment de la phylogénie, certaines des guildes trophiques peuvent être prédites d'après quelques attributs morphologiques (i.e. longueur relative de l'intestin, longueur standard et orientation de la bouche). Cela étant, ce lien entre régime alimentaire et caractéristiques morphologiques reste relativement faible, ce qui suggère que même si la morphologie limite les possibilités d'utilisation des ressources, cette limite est assez large pour permettre aux espèces de s'adapter à différentes conditions biotiques ou abiotiques locales.

1 Introduction

Seeking to test the ecomorphological hypothesis (i.e. particular interactions between the morphology of organisms and their ecology) in fish assemblages, many studies have significantly related diet to several morphological characteristics of species (Gazt 1979; Kotrschal 1989; Wikramanayake 1990;

Winemiller et al. 1995; Piet 1998; Huguény and Pouilly 1999; Xie et al. 2001; Elliott and Bellwood 2003; Pouilly et al. 2003). For instance, in fishes, gut length clearly distinguish algivores, detritivores and herbivores from carnivores (Paugy 1994; Kramer and Bryant 1995; Delariva and Agostinho 2001; Ward-Campbell et al. 2005). However, relationships between diet and morphology are equivocal since other studies found weak and indistinct results rather relating feeding and morphological variables to local environmental factors and

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resource availability (Grossman 1986; Motta 1988; Douglas and Matthews 1992; Winemiller and Adite 1997; Bellwood et al. 2006). Potential large regional changes can be a source of bias explaining these mixed results since feeding and morphological plasticity can be induced by environmental variability (Wainwright et al. 1991; Wimberger 1992; Hegrenes 2001).

Ecological characteristics of organisms can also be related to their shared evolutionary history. Indeed, species sharing a common ancestor cannot be considered independent in a statistical sense, since it is likely that they are quite similar for the features studied (Felsenstein 1985). Significant relationships between diet and morphology can then be spurious by-products of phylogenetic relatedness between species. However, only a few studies have attempted to control for evolutionary distance between species. For instance, Hugueny and Pouilly (1999) and Pouilly et al. (2003) assessed how their results were affected by taxonomic relatedness (as a surrogate of phylogenetic distances) of the species compared. In both cases, when taxonomic relatedness was factored out, relationships between diet and morphology were still significant.

Here we focus on the relationships between diet and morphology within a local assemblage of 30 species from tropical forested headwater streams of the Bolivian Amazon. Using methods dealing with true phylogenetic information, and avoiding potential regional and environmental effects on species plasticity by working at the local level within sites displaying minimal variations in environmental characteristics, we examine the correlations between diet and relevant morphological variables.

2 Methods

Study area

The study was conducted in five tropical, highly forested, headwater tributaries including 27 sites situated in the upper Rio Chiripiri river catchment of the Bolivian Amazon (total area <100 km²). Annual precipitations within the geographical zone vary between 5000 and 6000 mm, with a rank of mean temperatures between 24 and 26 °C (Navarro and Maldonado 2002). The five tributaries originated in the same region, were similar in size and environmental characteristics (i.e. physical and water quality characteristics), and were located between the coordinates 16°40'S, 65°25'W and 17°00'S, 65°15'W at a mean altitude of 270 m. At the basin scale, based on aerial photographs, the percentage of canopy cover along the five tributaries was identical and approximated 100 percent. At the local scale, the 27 sites had overall similar habitat characteristics (mean width 6.95 m (± 2.26 SD), mean depth 0.27 m (± 0.10 m SD) and mean velocity 0.18 m s⁻¹ (± 0.21 SD), same regional species pool, and a slight gradient in canopy cover.

2.1 Fish sampling and habitat description

Electro-fishing was performed during the dry season from June to October 2004. The 27 sample sites (between 21 and 54.9 m long reaches) were chosen to encompass complete sets of the characteristic stream form (e.g. pools and riffles). The

upstream and downstream edges of the sampled area for each site were blocked by closing nets (1 mm mesh size). Two fishing removals were performed by site, applying a constant fishing effort. Fishes were fixed in formaldehyde 4% and brought to laboratory for identification to the species level (or the genus level if systematic knowledge was insufficient), counting and weighing.

For each sampled site three environmental descriptors were measured: mean stream width (m), mean stream depth (m) and mean stream flow velocity (m/s). Width, depth and flow velocity were measured by cross-stream transects at 3–5 m intervals (depending on the stream size), with sampling points spaced 1 m apart (for depth and flow velocity). A detailed description of the methodology is given in Tedesco et al. (2007).

2.2 Fish diet estimation

The 30 species analyzed in the present study represented 97.4% of the total number of individuals captured during the study (10 384 over 10 660 individuals). These species belonged to 13 families and four orders: one family of Belontiiformes, seven families of Characiformes, one family of Perciformes and four families of Siluriformes (Table 1).

Diet estimation was based on stomach contents analysis of adult fishes only. Empty or highly digested stomachs were excluded. The stomach contents were examined with a matting microscope and were separated in five broad categories: substratum (MUD), algae and/or periphyton (ALG), terrestrial vegetation or seeds (VEG), aquatic invertebrate (AIN), terrestrial invertebrates (TIN), and fish (FISH). The substratum category does not correspond to a clearly identified biological feeding resource; but according to Power (1983, 1984), fishes can ingest superficial sediment while consuming biological material associated with the substratum. This category was conserved as an indicator of a particular feeding habitat. We used a binocular microscope for most evaluations and a microscope with a Sedgwick-Rafter for algae and detritus materials. Data for these two last categories are qualitative estimates based on material size.

Several methods have been developed for analyzing fish feeding habits (Hyslop 1980; Michel and Oberdorff 1994). Here, we used a slightly modified version of the dominance method (Frost and Went 1940; Tresierra and Culquichicon 1993). This method is based on the size and abundance of prey in the stomach, where each category of food item is allotted a number of points (from 1 to 4) proportional to the stomach fullness and the points gained by each food item are summed, indicating the amount or "the real" bulk of each item category. The % of occurrence of an item in the diet was estimated by divided the number of stomachs that contained that item by the total number of non-empty stomachs analyzed in that particular species.

2.3 Morphological variables

The morphological variables were selected based on previous works by Gatz (1979); Watson and Balon (1984);

Table 1. Taxonomic classification of the 30 studied species.

Order	Family	Code	Scientific name
Beloniformes	Belontiidae	POTEI	<i>Potamorhaphis eigenmanni</i> Miranda-Ribeiro, 1915
Characiformes	Anostomidae Characidae	LEOST	<i>Leporinus striatus</i> Kner, 1858
		ASYAB	<i>Astyanax abramis</i> (Jenyns, 1842)
		ASYLI	<i>Astyanax lineatus</i> (Perugia, 1891)
		CHCBO	<i>Characidium bolivianum</i> Pearson, 1924
		GEPCH	<i>Gephyrocharax chaparae</i> Fowler, 1940
		HEMLU	<i>Hemigrammus cf. lunatus</i> Durbin, 1918
		HEMSP	<i>Hemibrycon</i> sp.
		KNOSP	<i>Knodus</i> sp.
		MOEOL	<i>Moenkhausia oligolepis</i> (Günther, 1864)
		PHEPE	<i>Phenacogaster pectinatus</i> (Cope, 1870)
		SERSP	<i>Serrapinnus</i> sp.
		TYTMA	<i>Tytocharax cf. madeirae</i> Fowler, 1913
		STIDO	<i>Steindachnerina dobula</i> (Günther, 1868)
		STIGU	<i>Steindachnerina guentheri</i> (Eigenmann & Eigenmann, 1889)
Perciformes	Erythrinidae	HOPMA	<i>Hoplias malabaricus</i> (Bloch, 1794)
	Lebiasinidae	PYRVI	<i>Pyrrhulina vittata</i> Regan, 1912
	Parodontidae	PARBU	<i>Parodon cf. buckleyi</i> Boulenger, 1887
	Prochilodontidae	PRONI	<i>Prochilodus nigricans</i> Spix & Agassiz, 1829
	Cichlidae	APISP	<i>Apistogramma</i> sp.
		CIABO	<i>Cichlasoma boliviense</i> Kullander, 1983
		CRISE	<i>Crenicichla cf. semicincta</i> Steindachner, 1892
		SATJU	<i>Satanoperca jurupari</i> (Heckel, 1840)
Siluriformes	Callichthyidae	CORSP	<i>Corydoras</i> spp.
	Heptapteridae	IMPST	<i>Imparfinis cf. stictonotus</i> (Fowler, 1940)
		RHAQE	<i>Rhandaia quelen</i> (Quoy & Gaimard, 1824)
		ANCSP	<i>Ancistrus</i> spp.
	Loricariidae	HYPKO	<i>Hypostomus gr. cochliodon</i> Kner, 1854
		RINLA	<i>Rineloricaria lanceolata</i> (Günther, 1868)
		ITUAM	<i>Ituglanis cf. amazonicus</i> (Steindachner, 1882)

Winemiller (1991); Kramer and Bryant (1995); Huguency and Pouilly (1999) and Pouilly et al. (2003). Six ecomorphological variables were measured on 5 to 70 individuals for each species, depending on the number of individuals captured (Table 2). Average values of these variables were computed (Table 3).

In order to minimize the influence of body size on the four continuous morphological variables (Table 2), we regressed log-transformed variables against log-Standard Length and used the residuals values for subsequent Redundancy analysis (RDA) (Schneider et al. 1999).

2.4 Phylogenetic effect

The degrees of freedom in statistical tests may be inflated due to phylogenetic bias (non-independence of observations). In order to assess the phylogenetic effect in diet-morphology relationships, we compiled a synthetic evolutionary tree using data from Diogo (2003), Malabarba et al. (1998) and the "Tree of Life Web Project" (1995) (<http://tolweb.org>) that represents phylogenetic relationships among the genera studied (Fig. 1). We then calculated patristic distances between genera from cytochrome b sequences downloaded from GenBank (860 bp; <http://www.ncbi.nlm.nih.gov/Genbank/>) and using the synthetic evolutionary tree as a constraint under

PAUP 4.0b10 (Swofford 2002) through the neighbour-joining method.

Based on the patristic distances, we evaluated the phylogenetic effect on our data set by applying a Moran's *I* statistic (Moran 1948). This autocorrelation index was calculated for 10 classes of patristic phylogenetic distances (Appendix 1). Positive values of Moran's *I* coefficients show that phylogenetically closer species are more similar than the others for the considered character.

The index of Moran is based on average values and is thus not very sensitive to aberrant values and takes the following form:

$$\frac{n}{m} \frac{\sum_i \sum_j W_{ij} (Z_i - \bar{Z})(Z_j - \bar{Z})}{\sum_i (Z_i - \bar{Z})^2}$$

where:

Z_i = average value of the considered variable

i = unit of reference

j = units close to the item "i", defined by the matrix W_{ij}

n = total number of individuals in the sample ($\sum_i i$)

m = total number of pairs of neighbors ($\sum_i i \sum_j W_{ij}$)

W_{ij} = weighing matrix.

Under the hypothesis of phylogenetic inertia we expect a positive autocorrelation between related species, this autocorrelation decreasing toward null values as phylogenetic distance between species increases. When this situation occurs several

Table 2. Description of species traits and the functions they describe.

Functional trait	Code	Function	Reference
Standard length: Distance from the tip of the snout to the last vertebra	SL	No specific function, but could inform on prey size	Hugueny & Pouilly (1999), Chan (2001), Pouilly et al. (2003).
Eye diameter	ED	Inform about the fish visual acuity. Important factor for the search for food.	Gatz (1979), Piet (1998)
Head length: Distance from the tip of the snout to the posterior extension of the operculum	HEAL	Fishes with relatively larger head were found to consume larger prey	Gatz (1979), Watson & Balon (1984)
Mouth width: Horizontal distance measured among limit them ends of the mouth	MOWI	Maximal prey size	Gatz (1979)
Mouth orientation (code): 1 - dorsal; 2 - terminal; 3 - oblique; 4 - ventral	MORI	Method of food acquisition	Gatz (1979)
Gut length: Distance from the beginning of the esophagus to anus	GUTL	Inform on the fish trophic status	Gatz (1979)

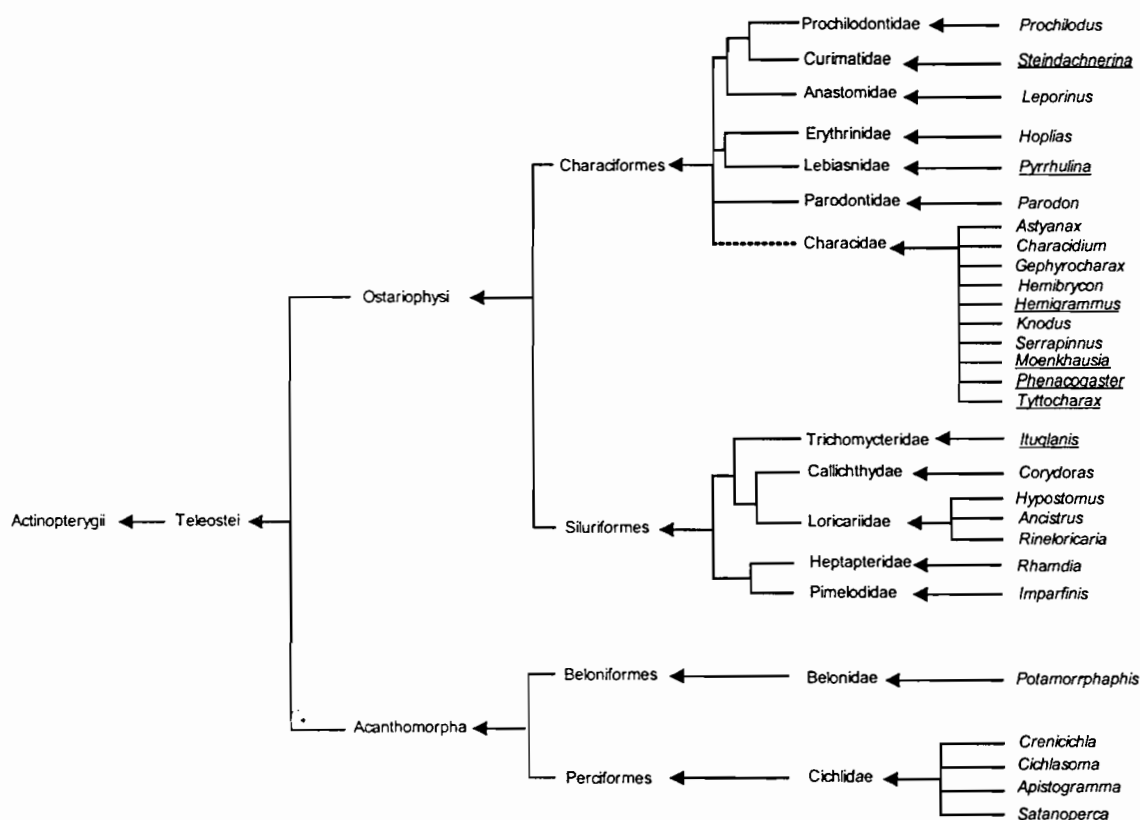


Fig. 1. Hypothetic phylogenetic tree for the 28 genera encountered in our study. The tree is based on compiled data from Diogo (2003), Malabarba et al. (1998) and *The Tree of Life Web Project* (1995) (<http://tolweb.org>). Patristic distances between 21 over the 28 genera were then calculated using cytochrome b sequences available in GenBank. The seven genera not included in the calculation of patristic distances are underlined.

methods are available (Harvey and Pagel 1991) to “remove” the phylogenetic autocorrelation. However, phylogenetic inertia was observed for none of our variables and hence no method accounting for phylogenetic relatedness was used.

2.5 Statistical analyses

Diet breadth was calculated by using Levin’s standardized index: $B_i = \left[\left(\sum_j P_{ij}^2 \right)^{-1} - 1 \right] (n - 1)^{-1}$ where P_{ij} is the proportion of prey j in the diet of predator i and n is the number of

prey categories (Hurlbert 1978). This index ranges from 0 to 1, low values indicating diets dominated by a few prey items (i.e. specialist species), and high values indicating generalist diets (Gibson and Ezzi 1987; Xie et al. 2001; Pouilly et al. 2003).

In order to identify trophic guilds, we used the species – food item matrix (elaborated using our modified version of the dominance method; Table 4) to compute a χ^2 distance between species. Distance values were then clustered using unweighted pair group method of arithmetic averages (UPGMA) algorithm (Legendre and Legendre 1998).

Table 3. Mean values of the six morphological attributes: Standard length (SL; in mm); eye diameter (ED; mm); head length (HEAL; in mm); mouth width (MOWI; mm); mouth orientation (MORI; categorical variable, see Table 2) and gut length (GUTL, mm). Values in parentheses correspond to range values for standard length and to standard deviation values for the other morphological parameters except MORI.

Species	N	SL	ED	HEAL	MOWI	MORI	GUTL
<i>Ancistrus</i> spp.	84	90 (61 - 150)	5 (0.8)	26 (6.5)	14 (4.1)	4	287 (396)
<i>Apistogramma</i> sp.	432	31 (18 - 46)	3 (0.4)	11 (1.8)	3 (0.7)	2	34 (7.3)
<i>Astyanax abramis</i>	499	74 (45 - 109)	6 (0.9)	21 (3.2)	6 (1.2)	1	60 (16.2)
<i>Astyanax lineatus</i>	72	73 (48 - 121)	6 (0.9)	21 (4.6)	6 (1.7)	1	82 (9.3)
<i>Characidium bolivianum</i>	126	52 (29 - 69)	3 (1.6)	13 (1.9)	2 (0.4)	2	26 (3.4)
<i>Cichlasoma boliviense</i>	79	69 (51 - 138)	7 (0.8)	25 (5.6)	8 (2.8)	2	102 (42.7)
<i>Corydoras</i> spp.	109	51 (41 - 65)	3 (0.3)	15 (1.4)	3 (0.6)	3	28 (6)
<i>Crenicichla</i> cf. <i>semicincta</i>	209	89 (60 - 199)	6 (1.2)	33 (10.9)	10 (4.5)	2	86 (43.3)
<i>Gephyrocharax chaparae</i>	79	46 (33 - 55)	3 (0.4)	11 (1)	3 (0.4)	1	27 (4.8)
<i>Hemibrycon</i> sp.	80	62 (42 - 85)	5 (0.8)	16 (3.2)	4 (1.2)	1	58 (11.4)
<i>Hemigrammus</i> cf. <i>lunatus</i>	191	26 (21 - 33)	3 (0.3)	8 (0.6)	2 (0.3)	1	19 (4.6)
<i>Hoplias malabaricus</i>	33	137 (69 - 212)	5 (1)	48 (9.5)	16 (3.9)	1	101 (31.4)
<i>Hypostomus</i> gr. <i>cochliodon</i>	23	55 (34 - 75)	4 (0.6)	16 (3.4)	7 (3)	4	560 (156)
<i>Imparfinis</i> cf. <i>stictionotus</i>	17	36 (26 - 45)	1 (0.2)	9 (1.2)	4 (0.5)	2	16 (2.4)
<i>Iuglanis</i> cf. <i>amazonicus</i>	41	49 (41 - 88)	2 (0.4)	8 (1.2)	4 (0.6)	2	20 (5.6)
<i>Knodus</i> sp.	23	30 (24 - 37)	3 (0.3)	8 (0.7)	2 (0.5)	1	31 (7.2)
<i>Leporinus striatus</i>	96	106 (75 - 148)	6 (0.7)	28 (3.5)	6 (1.6)	3	132 (36.5)
<i>Moenkhausia oligolepis</i>	274	52 (36 - 68)	5 (0.5)	15 (1.8)	4 (0.6)	1	58 (11.3)
<i>Parodon</i> cf. <i>buckleyi</i>	41	97 (63 - 131)	4 (0.8)	21 (3.6)	6 (1.2)	4	115 (15.9)
<i>Phenacogaster pectinatus</i>	269	36 (26 - 49)	3 (0.4)	9 (1.1)	2 (0.3)	1	17 (3.1)
<i>Potamorhaphis eigenmanni</i>	10	164 (142 - 201)	6 (0.1)	61 (7.4)	4 (0.9)	2	66 (8.7)
<i>Prochilodus nigricans</i>	34	169 (137 - 202)	10 (0.8)	53 (5.4)	22 (2.5)	2	579 (235)
<i>Pyrhulina vittata</i>	93	30 (22 - 36)	3 (0.3)	8 (1.1)	2 (0.3)	1	22 (3.8)
<i>Rhamdia quelen</i>	140	120 (67 - 213)	4 (1)	31 (8.7)	16 (5.4)	2	158 (61.4)
<i>Rineloricaria lanceolata</i>	24	88 (71 - 106)	3 (0.3)	14 (1.8)	6 (2.3)	4	272 (58.2)
<i>Satanoperca jurupari</i>	12	85 (71 - 130)	8 (0.5)	32 (6.1)	11 (2.5)	2	93 (20.2)
<i>Serrapinnus</i> sp.	59	28 (24 - 35)	3 (0.2)	7 (0.7)	2 (0.2)	2	25 (3.4)
<i>Steindachnerina dobula</i>	57	98 (58 - 138)	6 (1.3)	28 (6.9)	9 (1.8)	3	1590 (497)
<i>Steindachnerina guentheri</i>	20	75 (55 - 95)	6 (0.8)	21 (3.1)	7 (1.5)	3	1188 (285)
<i>Tyttocharax</i> cf. <i>madeirae</i>	159	15 (11 - 18)	2 (0.3)	4 (0.6)	1 (0.2)	1	7 (1.2)

Table 4. Diet composition and diet breadth (Lewin's index, *B*) of the 30 species studied. The diet composition is expressed as 1) values obtained using the dominance method (DM) and 2) the % of occurrence of each food category in the non-empty stomachs (% OC): Terrestrial invertebrates (TIN); aquatic invertebrate (AIN); algae (ALG); substratum (MUD); terrestrial vegetation or seeds (VEG) and fish (FISH).

Species	Number of stomachs	TIN		AIN		ALG		MUD		VEG		FISH		<i>B</i>
		(DM) (% OC)	(DM) (% OC)	(DM) (% OC)	(DM) (% OC)	(DM) (% OC)	(DM) (% OC)	(DM) (% OC)	(DM) (% OC)					
Piscivorous														
<i>Hoplias malabaricus</i>	17	0	0	1.12	0.47	0	0	0.06	0.06	0.88	0.65	1.65	0.47	0.32
Herbivorous														
<i>Parodon</i> cf. <i>buckleyi</i>	17	0	0	0.06	0.06	0	0	0.24	0.24	1.94	1	0	0	0.01
<i>Leporinus striatus</i>	27	0.27	0.23	0.41	0.32	0.45	0.18	0.23	0.14	3.27	1	0	0	0.03
<i>Prochilodus nigricans</i>	16	0	0	0	0	0.06	0.06	0.5	0.44	1.19	0.94	0	0	0.06
<i>Astyanax lineatus</i>	5	0.8	0.4	0.4	0.2	1.4	0.4	0	0	3.6	1	0	0	0.09
<i>Rhamdia quelen</i>	26	0.73	0.28	0.62	0.36	0.38	0.12	0.54	0.16	2.31	0.88	0.38	0.12	0.12
<i>Astyanax abramis</i>	67	1.24	0.57	0.51	0.32	0.24	0.22	0.18	0.16	2.94	0.91	0	0	0.12
Omnivorous														
<i>Crenicichla</i> cf. <i>semicincta</i>	16	0.63	0.31	1.25	0.38	0	0	0.06	0.06	0.81	0.5	0.56	0.19	0.37
<i>Cichlasoma boliviense</i>	14	1.07	0.29	0.29	0.14	0.64	0.21	0.07	0.07	0.43	0.36	0.64	0.21	0.57
Terrestrial invertivorous														
<i>Potamorhaphis eigenmanni</i>	10	2.7	1	0.1	0.1	0	0	0	0	0	0	0.7	0.2	0.02
General invertivorous														
<i>Hemibrycon</i> sp.	25	3	1	0.5	0.27	0	0	0	0	0.46	0.15	0	0	0.02
<i>Pyrrhulina vittata</i>	29	1.31	0.76	1.79	0.86	0.14	0.03	0	0	0	0	0	0	0.15
<i>Hemigrammus</i> cf. <i>lunatus</i>	25	1.35	0.69	1.92	0.85	0	0	0	0	0	0	0	0	0.14
<i>Gephyrocharax chaparae</i>	28	1.71	0.96	1.86	0.86	0	0	0	0	0.14	0.04	0	0	0.17
<i>Moenkhausia oligolepis</i>	30	2.33	0.97	1.03	0.67	0.7	0.2	0.07	0.03	1.7	0.63	0	0	0.26
Aquatic invertivorous														
<i>Corydoras</i> spp.	22	0	0	3.04	1	0.43	0.3	0	0	0.43	0.17	0	0	0.03
<i>Phenacogaster pectinatus</i>	64	0.78	0.44	2.73	0.98	0.09	0.09	0.03	0.03	0	0.08	0	0	0.04
<i>Imparfinis</i> cf. <i>stictonotus</i>	12	0.67	0.33	2.58	1	0	0	0	0	0	0	0	0	0.03
<i>Serrapinnus</i> sp.	21	0.27	0.23	1.77	1	0.18	0.14	0	0	0	0	0	0	0.02
<i>Knodus</i> sp.	20	0.05	0.05	2.63	0.79	0.32	0.16	0	0	0	0.21	0	0	0.01
<i>Tytocharax</i> cf. <i>madeirae</i>	29	0.24	0.21	3.52	1	0	0	0	0	0	0	0	0	0
<i>Ituglanis</i> cf. <i>amazonicus</i>	10	0	0	2.3	1	0	0	0	0	0	0	0	0	0
<i>Satanoperca jurupari</i>	7	0	0	1.86	1	0	0	0	0	0	0	0	0	0
<i>Characidium bolivianum</i>	29	0.03	0.03	3.53	1	0	0	0	0	0	0	0	0	0
<i>Apistogramma</i> sp.	30	0	0.03	2.47	0.97	0.07	0.07	0	0	0	0	0.07	0.03	0
Mud feeders														
<i>Steindachnerina dobula</i>	25	0	0	0	0	0.88	0.24	3.44	1	0	0	0	0	0.02
<i>Steindachnerina guentheri</i>	8	0	0	0	0	0	0	4	1	0	0	0	0	0
<i>Rineloricaria lanceolata</i>	10	0	0	0	0	0	0	3.67	0.9	0	0	0	0	0
Algivorous														
<i>Hypostomus</i> gr. <i>cochliodon</i>	15	0	0	0	0	4	1	3	1	0	0	0	0	0.16
<i>Ancistrus</i> spp.	17	0	0	0	0	4	1	3	1	0	0	0	0	0.16
Species VEG FISH														

Fish diet/morphology relationships were investigated using Redundancy Analysis (RDA) (CANOCO version 4.0; Ter Braak and Smilauer 1998). RDA is a constrained ordination process (a canonical version of principal component analysis, PCA). The ordination seeks the axes that are best explained by a linear combination of explanatory variables. Each axis is thus a linear combination (i.e. a multiple regression model) of all explanatory variables. Examination of the canonical coefficients (i.e. the regression coefficients of the models) for the explanatory variables on each axis highlights the most important variables in explaining the different axes. When applied to species diet data, the component axes resulting from RDA are interpretable in terms of differences in species' diet. Thus, the component axes in RDA plots represent the distribution of species based on their diet and constrained by the explanatory variables (i.e. the morphological variables expected to

be directly linked to diet). The statistical significance of the diet-morphology correlations extracted from the RDA was estimated by a Monte Carlo permutation test (1000 simulations) (Makarek and Legendre 2002; Legendre et al. 2005).

3 Results

3.1 Diets analysis and trophic guilds

Empty stomachs were found in 11.1% of a total of 840 analyzed individuals. This result varied among orders (Characiformes = 7.4%, Perciformes = 16.6% and Siluriformes = 21.9%), and among species (0% to 67.4%). Arrington et al. (2002) explains this phenomenon by particular life history

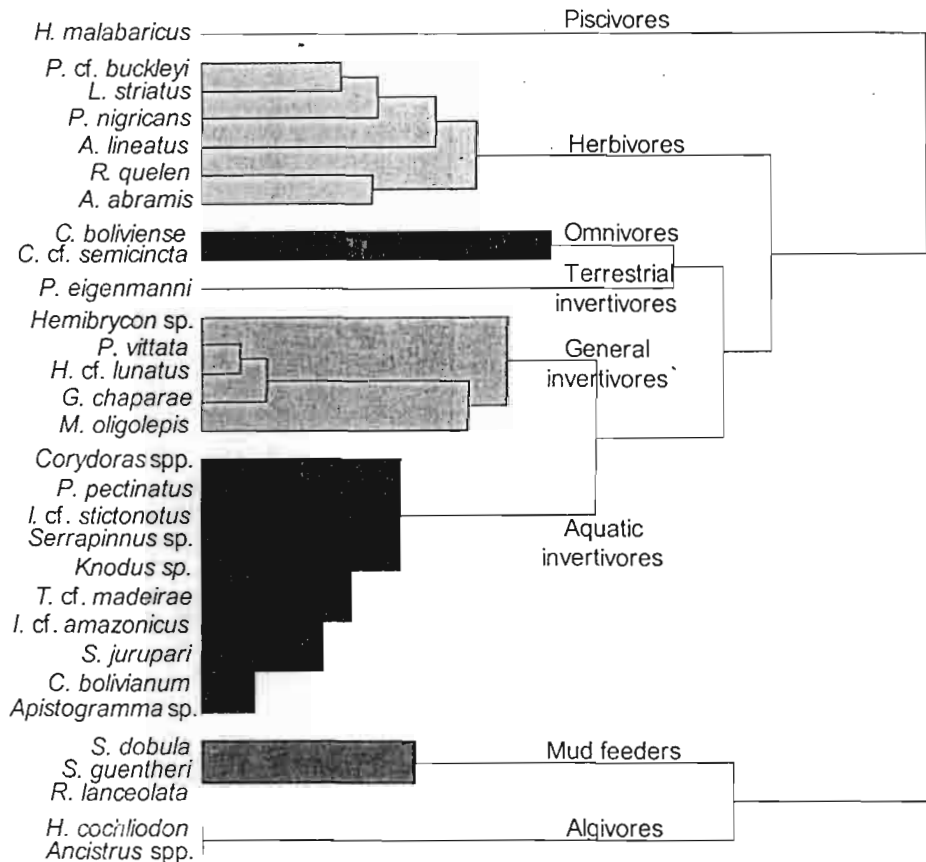


Fig. 2. Cluster analysis (UPGMA) showing trophic distances between the 30 species studied. Eight trophic guilds were distinguished: algivores, mud feeders, aquatic invertivores, general invertivores, terrestrial invertivores, omnivores, herbivores and piscivores.

traits related to diurnal or nocturnal activity of species associated with their trophic levels. Piscivorous species had the greater percentage of empty stomachs (e.g. 46.9% for *Hoplias malabaricus*) and algivorous species the smaller (e.g. 100% of full stomachs for *Ancistrus* spp. and *Hypostomus* gr. *cochliodon*).

Diet composition and abundance varied among the 30 species studied and our cluster analysis allowed us to identify eight broad trophic guilds (Table 4 and Fig. 2). The Piscivore guild was represented by only one species, *Hoplias malabaricus* (3.3% of the total assemblage). Diet breadth (Levin's index, B) showed particularly high generalist tendency for *H. malabaricus* ($B = 0.32$). The Herbivorous guild was represented by six species accounting for 20% of the assemblage: *Prochilodus nigricans*, *Parodon* cf. *buckleyi*, *Leporinus striatus*, *Astyanax lineatus*, *Rhamdia quelen* and *Astyanax abramis*. Diet breadth reflected slight generalist tendency for *R. quelen* ($B = 0.12$) and *A. abramis* ($B = 0.12$) and high specialization tendency for *P. buckleyi* ($B = 0.01$). The other three species ranged between intermediate levels of specialization (B from 0.03 to 0.09). Omnivores were represented by two species (6.6% of the assemblage): *Crenicichla* cf. *semicincta* and *Cichlasoma boliviense*, with generalist tendency ($B = 0.37$ and $B = 0.57$, respectively).

Invertivorous species were the dominant diet group representing 53.3% of the assemblage with 16 species. Our results

distinguished between three groups of terrestrial, generalist and aquatic invertivores. *Potamorhaphis eigenmanni* was found to be a terrestrial invertebrate specialist ($B = 0.02$). Five species (*Pyrrhulina vittata*, *Hemibrycon* sp., *Hemigrammus* cf. *lunatus*, *Gephyrocharax chapare* and *Moenkhausia oligolepis*) fed on both terrestrial and aquatic invertebrates, (B varying between 0.02 and 0.26) and the third group (*Phenacogaster pectinatus*, *Imparfinis* cf. *stictonotus*, *Corydoras* spp., *Serrapinnus* sp., *Knodus* sp., *Tytocharax* cf. *madeirae*, *Ituglanis* cf. *amazonicus*, *Satanoperca jurupari*, *Characidium bolivianum* and *Apistogramma* sp.), specialized on aquatic invertebrates, presented high degree of specialization (B varying between 0 and 0.04).

Three species (representing 10% of the assemblage) belonged to the mud feeder guild: *Steindachnerina dobula*, *Steindachnerina guentheri* and *Rineloricaria lanceolata*. These species showed highly specialized diet, with B values between 0.00 and 0.02. Finally, two species (6.6% of the assemblage) were grouped as algivorous, *Ancistrus* spp. and *Hypostomus* gr. *cochliodon*, with rather generalist tendencies ($B = 0.16$ for both species).

3.2 Phylogenetic constraints

Except for one variable (i.e. gut length; GUTL), Moran's I coefficients showed no significant phylogenetic effect and no

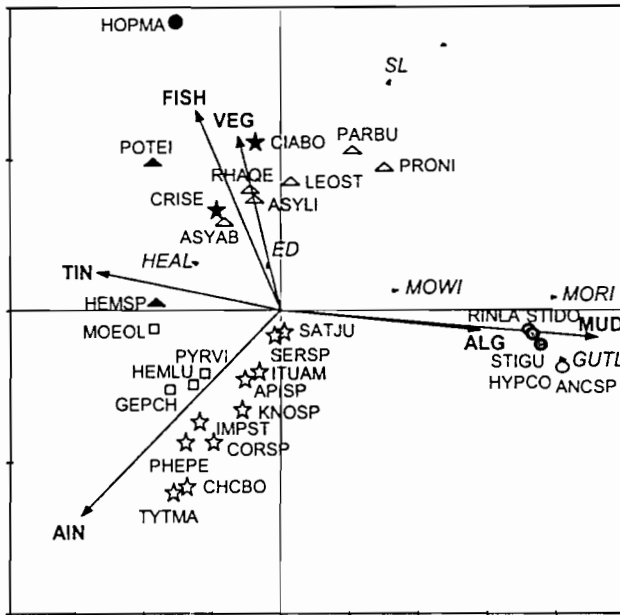


Fig. 3. Redundancy Analysis (RDA) linking species diets to morphology: algivores (open circle), mud feeders (gray closed circle), aquatic invertivores (open star), terrestrial invertivores (closed triangle), general invertivores (square), omnivores (closed star), herbivores (open triangle) and piscivores (closed circle).

regular decrease of autocorrelation with phylogenetic distance. Furthermore, concerning GUTL, the significant autocorrelation was positive instead of negative, as logically expected. Negative values suggest some kind of morphological convergence and in this case using methods to “remove” the phylogenetic effect would eliminate the desired data signal. As a result data in subsequent analyses were kept untransformed. The Moran’s I coefficient matrix including corresponding p values is available on request from the authors.

3.3 Relationship between diet and morphology

The first two axes of the RDA analysis relating diet to associated morphological variables accounted for 54.7% of the variation in species diets and for 95% of the variation explained by morphological variables (Fig. 3, Table 5). The global model was highly significant (Monte Carlo test ($p \neq 0.001$)) (Table 5). Among the 6 morphological variables tested, only 3 were statistically significant ($p < 0.001$): gut length (GUTL), mouth orientation (MORI) and standard length (SL). Axis 1 was positively related to GUTL and MORI while axis 2 was negatively related to SL (Table 5). Axis 1 (Fig. 3) clearly distinguished fish species feeding preferentially on algae and mud (e.g. *Ancistrus* spp., *Steindachnerina guentheri*, *Steindachnerina dobula* and *Rineloricaria lanceolata*) and displaying high relative gut length and an oblique or ventral mouth orientation. Axis 2 mainly separated a group of aquatic invertivores characterized by small size (Fig. 3 bottom-left), and a group of species showing a wide diversity of feeding habits (e.g. herbivorous, terrestrial invertivorous and piscivorous species; Fig. 3 top) and displaying larger body size.

Table 5. Results of redundancy analysis relating diet to associated morphological variables.

Variable	Axis 1	Axis 2
Correlations of food items with ordination axes		
TIN	-0.511	0.096
AIN	-0.553	-0.511
ALG	0.552	-0.049
MUD	0.877	-0.069
VEG	-0.118	0.436
FISH	-0.235	0.500
Summary statistics for ordination axes		
Eigenvalues	0.51	0.089
Diet - morphological correlations	0.953	0.757
Monte Carlo probability for significance of the sum of all eigenvalues (1000 permutations) = 0.0010		

4 Discussion

4.1 Feeding habits and degree of specialization of species

Thirty fish species were classified in eight trophic guilds: mud feeders, algivorous, aquatic invertivorous, general invertivorous, terrestrial invertivorous, omnivorous, herbivorous and piscivorous. Invertivorous species composed the dominant guild of this assemblage. This result is in agreement with the ones already obtained for other tropical (Angermeier and Karr 1983; Bojsen and Barriga 2002; Silva 1993; Uieda et al. 1997; Deus and Petrere-Junior 2003; Pouilly et al. 2006; Ibañez et al. 2007) and temperate forested streams (Schlosser 1982; Rahel and Hubert 1991; Oberdorff et al. 1993, 2002) suggesting a possible convergence in trophic structure between temperate and tropical fish assemblages (Ibañez et al. 2007). Trophic diversity of fish assemblages in such systems may be strongly related to food availability (Angermeier and Karr 1983), which in turn may be influenced by common environmental constraints. The organic energy base in forested headwater streams is essentially allochthonous and mostly comes from riparian vegetation through dead leaves, branches and wood processing by microbial and aquatic invertebrate communities (Wallace et al. 1997; Thompson and Townsend 2005; Tedesco et al. 2007). The energy flux reaching fishes thus strongly reflect the production of invertebrates via availability of terrestrial detritus and to a lesser extend aquatic primary production. It is thus coherent to expect a dominance of the invertivorous guild in these forested streams.

Our study strongly suggests a high degree of diet specialization for species at almost all trophic levels. In fact, if we arbitrarily adopt a quite conservative cut-off level at $B < 0.2$ (Levin’s standardized index) for classifying a species as a specialist, 94% of the invertivorous guild (15 species), 100% of the herbivorous guild (6 species), 100% of mud feeders guild (2 species) and 100% of the algivorous guild (2 species) can be considered specialist feeders. Only omnivorous and piscivorous (only one species for the later) guilds

were represented by more generalist species (this generalist tendency was obviously expected concerning omnivorous species). This result highlights the importance of feeding specialization in the segregation of trophic niches among species, as the probable explanation for the local maintenance of high species diversity in these highly diverse neotropical assemblages is via fine-scale niche partitioning by resource specialists (Tedesco et al. 2007).

4.2 Phylogeny

Although phylogenetic informations for neotropical freshwater fishes were scarce, we tried to account for evolutionary history of taxa by applying true phylogenetic distances available for 70% of the species analyzed (21 over a total of 30 species). No significant effect of phylogeny on species diets and morphology was found for this large subset of species. It is thus, very unlikely, that our final results are altered by spurious phylogenetical effects.

4.3 Relationships between diet and morphology

According to the RDA, fishes belonging to the algivorous and detritivorous guilds displayed large relative gut lengths. This appears to be a highly robust ecomorphological pattern since our finding is in agreement with results found in several other studies dealing with fish assemblages worldwide (Kotrschal 1989; Paugy 1994; Kramer and Bryant 1995; Hugueny and Pouilly 1999; Winemiller and Adite 1997; Delariva and Agostinho 2001; Pouilly et al. 2003; Ward-Campbell et al. 2005). Bowen (1983) working on neotropical fish communities ranked relative intestine development in relation to diet as: carnivorous < omnivorous < herbivorous < detritivorous, which is generally interpreted as reflecting the resistance of different foods to digestion (Herder and Freyhof 2006). Our results are globally in accordance with this proposed scheme, as our ranking of relative intestine development in relation to trophic guilds, based on the RDA, was: invertivorous < piscivorous < herbivorous < algivorous < detritivorous (see Fig. 3). Benthic fishes from the algivorous and mud feeder guilds were also characterized by relatively narrow heads and a ventral (Loricaridae) or oblique (Curimatidae) mouth orientation and this result is again well supported by other studies (Gatz 1979; Watson and Balon 1984; Winemiller et al. 1995; Hugueny and Pouilly 1999; Pouilly et al. 2006). Fishes from the herbivorous and piscivorous guilds generally displayed a large standard length while species from the aquatic invertivorous guild were mostly characterized by their small sizes. These results accord, at least concerning invertivorous and piscivorous guilds, with the general observation that body and prey size are often correlated (Gatz 1979). The association between herbivory and large body size of species is difficult to interpret but has been also reported for other vertebrates such as lizards (Cooper and Vitt 2002).

Then, our results show that, independently of any phylogenetic constraints, some of the trophic guilds can be grossly predicted from few relevant morphological attributes. Such consistent pattern suggests a link between diet and morphology.

In other words, species having similar diet tend to converge to some extent on some morphological attributes. Nevertheless, this link mostly concerns, in our case, three trophic guilds over the six previously defined (i.e. invertivore, algivore and detritivore guilds) and three morphological attributes over the six actually tested (i.e. standard length, relative gut length and mouth orientation). This suggests that even if morphology may limit patterns of resource-use, these limits are broad enough to allow most fishes changing their choice of prey resources in response to local biotic and abiotic conditions. For example, Pouilly et al. (2006) have analyzed the trophic structure of fish species in other neotropical streams of the Beni River basin of the Bolivian Amazon. We compared the trophic status and the diet breath (using Levin's standardized index) of four species common to both studies (i.e. *Characidium bolivianum*, *Crenicichla semicincta*, *Hoplias malabaricus* and *Rhamdia quelen*) (see Appendix 2). The trophic status was similar for two species (*Characidium boliviense* was classified as aquatic invertivore and *Hoplias malabaricus* was classified as piscivore, in both studies) but significantly differed for the two others (*Crenicichla semicincta* was classified as piscivore in the Beni River system and omnivore in our study, and *Rhamdia quelen* was classified as aquatic insectivore in the Beni River system and herbivore in our study). In return, based on Levin's standardized index values, the four species' diet breath was overall similar in both studies (Appendix 2). In the same way, Fritz (1974) working on phylogenetically related species with similar morphology (genus *Astyanax*), showed that within a similar habitat but on different rivers, similar diets were found.

4.4 Conclusion

In summary, we found that the position of a species along the trophic dimension is related partly to its morphology, independently of any phylogenetic effect. In other words, some morphological constraints acting on a species determine its potential trophic niche. Nevertheless, its realized niche seems to depend also partly on the environment (i.e. food availability and its variability between habitats). Among the morphological variables tested here, relative intestinal length and mouth orientation appear the most useful descriptors of diet, with the direction of relative morphological variations reflecting diet quality. These two morphological characters could be thus useful to predict resource use and trophic structure of fish assemblages of forested neotropical streams, where fish species feeding habits information is rather scarce.

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Appendix 1. Matrix of phylogenetic distances (patristic distances) for the 21 genera analyzed.

Genre	<i>Ancistrus</i>	<i>Apistogramma</i>	<i>Astyanax</i>	<i>Characidium</i>	<i>Serrapinnus</i>	<i>Cichlasoma</i>	<i>Corydoras</i>	<i>Crenicichla</i>	<i>Gephyrocharax</i>	<i>Hemibrycon</i>	<i>Hoplias</i>	<i>Hypostomus</i>	<i>Imparfinis</i>	<i>Knodus</i>	<i>Leporinus</i>	<i>Parodon</i>	<i>Potamorhaphis</i>	<i>Prochilodus</i>	<i>Rhamdia</i>	<i>Rineloricaria</i>	<i>Satanoperca</i>
<i>Ancistrus</i>	-	85	106	84	116	112	152	160	155	130	126	165	168	135	124	132	112	124	132	186	148
<i>Apistogramma</i>	63	-	113	91	123	119	159	167	162	137	133	172	175	142	131	139	119	131	139	193	155
<i>Astyanax</i>	64	69	-	88	76	72	112	120	115	90	110	149	152	119	108	116	96	108	116	170	132
<i>Characidium</i>	46	67	56	-	98	94	134	142	137	112	108	147	150	117	106	114	94	106	114	168	130
<i>Serrapinnus</i>	35	41	45	42	-	56	62	70	65	40	120	159	162	129	118	126	106	118	126	180	142
<i>Cichlasoma</i>	62	65	72	50	39	-	92	100	95	70	116	155	158	125	114	122	102	114	122	176	138
<i>Corydoras</i>	58	59	72	60	32	61	-	50	45	54	156	195	198	165	154	162	142	154	162	216	178
<i>Crenicichla</i>	50	61	64	54	43	62	50	-	41	62	164	203	206	173	162	170	150	162	170	224	186
<i>Gephyrocharax</i>	45	61	69	58	31	61	44	41	-	57	159	198	201	168	157	165	145	157	165	219	181
<i>Hemibrycon</i>	52	65	62	54	33	62	54	40	47	-	134	173	176	143	132	140	120	132	140	194	156
<i>Hoplias</i>	52	79	62	58	44	70	76	58	59	58	-	91	94	61	72	80	96	108	116	170	132
<i>Hypostomus</i>	57	72	81	71	46	63	67	61	54	61	75	-	69	60	111	119	135	147	155	209	171
<i>Imparfinis</i>	56	65	70	58	43	62	64	58	63	58	58	69	-	63	114	122	138	150	158	212	174
<i>Knodus</i>	53	72	75	51	44	61	65	57	57	57	61	60	63	-	81	89	105	117	125	179	141
<i>Leporinus</i>	46	69	58	56	45	56	58	54	51	52	66	69	70	67	-	68	94	106	114	168	130
<i>Parodon</i>	64	73	62	70	42	78	74	70	71	68	72	75	78	77	68	-	102	114	122	176	138
<i>Potamorhaphis</i>	54	52	56	61	42	54	55	49	47	50	57	52	59	59	58	52	-	80	88	142	104
<i>Prochilodus</i>	76	77	80	72	54	80	78	80	74	74	80	87	74	81	82	90	53	-	68	122	84
<i>Rhamdia</i>	64	89	94	66	42	80	72	68	66	70	74	77	76	71	74	92	53	68	-	98	60
<i>Rineloricaria</i>	88	109	94	96	60	112	106	98	100	100	96	101	102	99	102	102	75	90	98	-	86
<i>Satanoperca</i>	64	81	76	58	39	72	74	62	62	64	64	83	78	65	72	76	51	66	60	86	-

Appendix 2. Comparison of diet composition (% of occurrence) and diet breadth (Lewin's index, *B*) of four species common to Pouilly et al. (2006) and the present study.

Species	Basin	Trophic	TIN	AIN	ALG	MUD	VEG	FISH	<i>B</i>
<i>Characidium bolivianum</i>	Chapare	AIN	0.03	1	0	0	0	0	0.00
	Beni	AIN	0.07	1	0.13	0.02	0.02	0	0.08
<i>Hoplias malabaricus</i>	Chapare	OMN	0.31	0.38	0	0.06	0.50	0.19	0.37
	Beni	FISH	0.03	0.67	0.05	0.03	0.05	0.38	0.20
<i>Crenicichla semicincta</i>	Chapare	FISH	0	0.47	0	0.06	0.65	0.47	0.32
	Beni	FISH	0	0.29	0	0.43	0.14	0.43	0.36
<i>Rhamdia quelen</i>	Chapare	HER	0.28	0.36	0.12	0.16	0.88	0.12	0.12
	Beni	AIN	0.25	0.96	0	0	0.11	0.14	0.16

References

- Angermeier P.L., Karr J.R., 1983, Fish communities along environmental gradients in a system of tropical streams. *Environ. Biol. Fish.* 9, 117–135.
- Arrington D.A., Winemiller K.O., Loftus W.F., Akin S., 2002, How often do fishes Run on Empty. *Ecology* 83, 2145–2151.
- Bellwood D.R., Wainwright P., Fulton C.J., Hoey A.S., 2006, Functional versatility supports coral reef biodiversity. *Proc. R. Soc. B.* 273, 101–107.
- Bojsen B.H., Barriga R., 2002, Effects of deforestation on fish community structure in Ecuadorian Amazon streams. *Freshw. Biol.* 47, 2246–2260.
- Bowen S.H., 1983, Detritivory in neotropical fish communities. *Environ. Biol. Fishes* 9, 137–144.
- Chan M.D., 2001, Fish ecomorphology: Predicting habitat preferences of stream fishes from their body shape. PhD Thesis. Faculty of the Virginia Polytechnic Institute and State University, USA.
- Cooper W.E., Vitt L.J., 2002, Distribution, extent, and evolution of plant consumption by lizards. *J. Zool.* 257, 487–517.
- Delariva R., Agostinho A., 2001, Relationship between morphology and diets of six neotropical loricariids. *J. Fish Biol.* 58, 832–84.
- Deus C.P., Petrer - Junior M., 2003, Seasonal diet shifts of seven fish species in an Atlantic Rainforest Stream in Southeastern Brazil. *Braz. J. Biol.* 64, 579–588.
- Diogo R., 2003, Catfish morphology, phylogeny and macroevolution: A case study in theoretical phylogeny and macroevolution. Doctoral Thesis. Université de Liège.
- Douglas M.E., Matthews W.J., 1992, Does morphology predict ecology? Hypothesis testing within a freshwater stream fish assemblage. *Oikos* 65, 213–224.
- Elliott J.P., Bellwood D.R., 2003, Alimentary tract morphology and diet in three coral reef fish families. *J. Fish Biol.* 63, 1598–1609.
- Felsenstein J., 1985, Phylogenies and the comparative method. *Am. Nat.* 125, 1–15.
- Fritz E.S., 1974, Total diet comparison in fishes by Spearman rank correlation coefficients. *Copeia* 1, 210–214.
- Frost W.E., Went A.E., 1940, River life survey III. The growth and food of young Salmon. *Proc. R. Ir. Acad.* 46, 53–80.
- Gatz A.J., 1979, Ecological morphology of freshwater stream fishes. *Tulane studies in zoology and botany* 21, 91–124.
- Gibson R.N., Ezzi A., 1987, Feeding relationships of a Demersal fish assemblage on the West Coast of Scotland. *J. Fish Biol.* 31, 55–69.
- Grossman G.D., 1986, Food resource partitioning in a rocky intertidal fish assemblage. *J. Zool.* 1, 317–355.
- Harvey P.H., Pagel M.D., 1991, The comparative method in evolutionary biology. Oxford: Oxford University Press.
- Hegrenes S., 2001, Diet-induced phenotypic plasticity of feeding morphology in the orangespotted sunfish, *Lepomis humilis*. *Ecol. Freshw. Fish.* 10, 35–42.
- Herder F., Freyhof J., 2006, Resource partitioning in a tropical stream fish assemblage. *J. Fish Biol.* 69, 571–589.
- Hugueny B., Pouilly M., 1999, Morphological correlates of diet in an assemblage of West African freshwater fishes. *J. Fish Biol.* 54, 1310–1325.
- Hurlbert S.H., 1978, The measurement of niche overlap and some relatives. *Ecology* 59, 67–77.
- Hyslop E.J., 1980, Stomach contents analysis—a review of methods and their application. *J. Fish Biol.* 17, 411–429.
- Ibañez C., Oberdorff T., Teugels G., Mamononekene V., Lavoué S., Fermon Y., Paugy D., Toham A.K., 2007, Fish assemblages structure and function along environmental gradients in rivers of Gabon Africa. *Ecol. Freshw. Fish.* (doi: 10.1111/j.1600-0633.2006.00222.x).
- Kramer D., Bryant M., 1995, Intestine length in the fishes of a tropical stream: 2. relationship to diet—the long and short of a convoluted issue. *Environ. Biol. Fishes* 42, 129–141.
- Kotrschal K., 1989, Trophic ecomorphology in eastern Pacific blennioid fishes: character transformation of oral jaws and associated change of their biological roles. *Environ. Biol. Fishes* 24, 199–218.
- Legendre P., Legendre L., 1998, Numerical Ecology. Amsterdam: Elsevier.
- Legendre P., Borcard D., Peres-Neto, P., 2005, Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecol. Monogr.* 75, 435–450.
- Makarevich V., Legendre P., 2002, Nonlinear redundancy analysis and canonical correspondence analysis based on polynomial regression. *Ecology* 83, 1146–1161.
- Malabarba L.R., Reis R.E., Vari R.P., Lucena Z.M., Lucena C.A.S. (Eds), 1998, Phylogeny and classification of Neotropical fishes. Edipucrs, Porto Alegre.
- Michel P., Oberdorff T., 1994, Feeding habits of fourteen European freshwater fish species. *Cybiu* 19, 5–46.
- Moran P.A.P., 1948, The interpretation of statistical maps. *J. R. Stat. Soc. B.* 10, 243–251.
- Motta P.J., 1988, Functional morphology of the feeding apparatus of ten species of Pacific butterflyfishes Perciformes, (Chaetodontidae): An ecomorphological approach. *Environ. Biol. Fishes* 22, 39–67.
- Navarro G., Maldonado M., 2002, Geografía Ecológica de Bolivia: Vegetación y Ambientes Acuáticos. Editorial: Centro de Ecología Simón I. Patiño-Departamento de difusión. Cochabamba, Bolivia.
- Oberdorff T., Guilbert E., Luchetta J.C., 1993, Patterns of fish species richness in the Seine River basin, France. *Hydrobiologia* 259, 157–167.

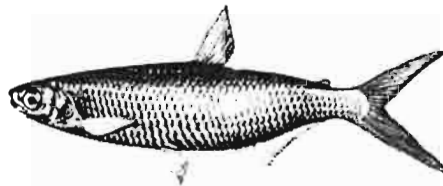
- Oberdorff T., Pont D., Hugueny B., Porcher J.P., 2002, Development and validation of a fish-based index for the assessment of rivers "health" in France. *Freshw. Biol.* 47, 1720-1735.
- Paugy D., 1994, Ecologie des poissons tropicaux d'un cours d'eau temporaire (Baoulé, haut bassin du Sénégal au Mali): Adaptation au milieu et plasticité du régime alimentaire. *Rev. Hydrobiol. Trop.* 27, 157-172.
- Piet G., 1998, Ecomorphology of a size-structured tropical freshwater fish community. *Environ. Biol. Fishes* 51, 67-86.
- Pouilly M., Lino F., Bretenoux G., Rosales C., 2003, Dietary-morphological relationships in a fish assemblage of the Bolivian Amazonian floodplain. *J. Fish Biol.* 62, 1137-1158.
- Pouilly M., Barrera S., Rosales C., 2006, Changes of taxonomic and trophic structure of fish assemblages along an environmental gradient in the Upper Beni watershed Bolivia). *J. Fish Biol.* 68, 137-156.
- Power M.E., 1983, Grazing responses of tropical freshwater fishes to different scales of variation in their food. *Environ. Biol. Fishes* 9, 103-115.
- Power M.E., 1984, The importance of sediment in the grazing ecology and size class interactions of an armored catfish, *Ancistrus spinosus*. *Environ. Biol. Fishes* 10, 173-181.
- Rahel F.J., Hubert W.A., 1991, Fish assemblages and habitat gradients in a Rocky Mountain-Great Plains stream: biotic zonation and additive patterns of community change. *Trans. Am. Fish. Soc.* 120, 319-332.
- Schlosser I.J., 1982, Fish community structure and function along two habitat gradients in a headwater stream. *Ecol. Monogr.* 52, 395-414.
- Schneider C.J., Smith T.B., Larison B., Moritz C., 1999, A test of alternative models of diversification in tropical rainforests: Ecological gradients vs. rainforest refugia. *Proc. Natl. Acad. Sci. USA* 96, 13869-13873.
- Silva C.P.D., 1993, Alimentação e distribuição espacial de algumas espécies de peixes do igarapé do Candirú, Amazonas. Brasil. *Acta Am.* 23, 271-285.
- Swofford D.L., 2002, PAUP. Phylogenetic Analysis Using Parsimony. Sunderland, M. A. Sinauer Associates.
- Tedesco P.A., Ibañez C., Moya N., Bigorne R., Camacho J., Goitia E., Hugueny B., Maldonado M., Rivero M., Tomanová S., Zubietta J.P., Oberdorff T., 2007, Local scale species-energy relationships in tropical fish assemblages of some forested streams of the Bolivian Amazon. *C.R. Biol.* 330, 255-264.
- Ter Braak C.J.F., Smilauer P., 1998, CANOCO reference manual and user's guide to CANOCO for Windows: software for canonical community ordination. Version 4. Microcomputer Power, Ithaca, New York, USA.
- Thompson R.M., Townsend C.R., 2005, Energy availability, spatial heterogeneity and ecosystem size predict food-web structure in streams. *Oikos* 108, 137-148.
- Tresierra A., Culquichicón Z.G., 1993, *Biología pesquera*. Ed. Universitaria. Trujillo, Perú.
- Uieda V.S., Buzzato P., Kikushi R.M., 1997, Partilha de recursos alimentares em peixes em um riacho de serra do Sudeste do Brasil. *Nat. Acad. Bras. Ci.* 69, 243-252.
- Wainwright P.C., Oseberg C.W., Mittelbach G.G., 1991, Trophic polymorphism in the pumpkinseed sunfish (*Lepomis gibbosus* Linnaeus): effects of environment on ontogeny. *Funct. Ecol.* 5, 40-55.
- Wallace J.B., Eggert S.L., Meyer J.L., Webster J.R., 1997, Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science* 277, 102-104.
- Ward-Campbell B.M.S., Beamish F.W.H., Kongchaiya C., 2005, Morphological characteristics in relation to diet in five coexisting Thai fish species. *J. Fish Biol.* 67, 1266-1279.
- Watson D.J., Balon E.K., 1984, Ecomorphological analysis of fish taxocenes in rainforest stream of northern Borneo. *J. Fish Biol.* 25, 371-384.
- Wikramanayake E.D., 1990, Ecomorphology and biogeography of a tropical stream fish assemblage: Evolution of assemblage structure. *Ecology* 71, 1756-1764.
- Wimberger P.H., 1992, Plasticity of fish body shape. The effects of diet, development, family and age in two species of *Geophagus* (Pisces, Cichlidae). *Biol. J. Linn. Soc.* 45, 197-218.
- Winemiller K.O., 1991, Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. *Ecol. Monogr.* 61, 343-365.
- Winemiller K.O., Kelso-Winemiller L.C., Brenkert A.L., 1995, Ecomorphological diversification and convergence in fluvial cichlid fishes. *Environ. Biol. Fishes* 44, 235-261.
- Winemiller K.O., Adite A., 1997, Convergent evolution of weakly electric fishes from floodplain habitats in Africa and South America. *Environ. Biol. Fishes* 49, 175-186.
- Xie S., Cut Y., Li Z., 2001, Dietary-morphological relationships of fishes in Liangzi Lake, China. *J. Fish Biol.* 58, 1714-1729.

Article 2

**Fish assemblage structure and function along environmental
gradients in rivers of Gabon (Africa)**

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Alestes sp. Photo - Paugy & Leveque (2003)

Fish assemblages structure and function along environmental gradients in rivers of Gabon (Africa)

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Abstract – We examined patterns in fish species assemblages structure and function along environmental gradients in rivers of Gabon. Species presence–absence data from 52 sites were first analysed by canonical correspondence analysis. Results showed that the position of sites along the upstream–downstream gradient, together with elevation and water conductance were the most important predictors of local fish assemblage composition. Assemblage richness and trophic structure were further investigated using regression tree analysis. Results revealed a general increase in species richness from upstream to downstream areas and a transition from insectivorous to omnivorous, herbivorous and piscivorous species along this longitudinal gradient. There were several similarities between these previous patterns and those observed in other temperate streams suggesting a potential convergence in fish assemblage along environmental gradients in tropical and temperate riverine systems. From a conservation standpoint, these results highlight the need to evaluate all habitat types along rivers longitudinal gradient to integrate the full spectrum of species assemblages within conservation plans.

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Key words: fish assemblages; richness; trophic structure; rivers; Gabon

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Introduction

The accelerating rate of extinction of plants and animals because of anthropogenic impacts in ecosystems is a world-wide crisis (Myers et al. 2000). The problem is particularly severe in freshwater habitats, which are among the world's most threatened ecosystems (Sala et al. 2000), with a projected extinction rate of about five times greater than the average species extinction rate for terrestrial fauna. To mitigate these projected losses, it is vital to develop a deeper understanding of the factors and processes that determine aquatic diversity at different spatial scales. Only when this understanding is achieved we will be

able to predict the effects of global climatic changes, habitat loss and fragmentation on the maintenance of aquatic biodiversity. Concerning riverine fishes, while a considerable proportion of species is concentrated in the tropics (Guégan et al. 1998), relatively little is known about the patterns of assemblage composition and distribution within and among rivers under natural conditions (Lewis et al. 2006; Lévêque 2006). This scarcity of data for most tropical rivers precludes accurate prediction of effects of human-induced perturbations on these systems. Indeed, existing models of the structure of riverine fish assemblages are still largely based on patterns observed in temperate areas (see Tejerina-Garro et al. 2005 for a review) and there

is thus an urgent need for field data in tropical species rich areas to assess the generality of the patterns previously observed in temperate rivers.

To further the understanding of tropical river assemblages we undertook an exploratory study to give a qualitative description of the ecological factors that are most important in determining the patterns of fish distribution and assemblage structure in streams and rivers of Gabon (west-central Africa). We focused on two main characteristics of assemblage structure: species richness and trophic traits.

Longitudinal changes in local assemblage richness have long been noted along the length of temperate streams and rivers (see Matthews 1998 for a review). The local assemblage richness usually increases along the upstream-downstream gradient. This increase is often attributed to a downstream increase in habitat size, habitat diversity or both (e.g., measured as a function of stream width, volume, stream discharge, stream order, drainage basin area, stream depth, current velocity and substrate composition) (Sheldon 1968; Gorman & Karr 1978; Horwitz 1978; Schlosser 1982; Balon et al. 1986; Rahel & Hubert 1991; Paller 1994; Belliard et al. 1997; Oberdorff et al. 2001; Grenouillet et al. 2004). The studies conducted in tropical systems reveal patterns that generally agree with patterns from temperate regions but were most often spatially limited to a single stream or river (Bussing & Lopez 1977; Sydenham 1977; Angermeier & Karr 1983; Hugueny 1990; Winemiller & Leslie 1992; Mèrigoux et al. 1998; Ibarra & Stewart 1989; Tito de Moraes & Lauzanne 1994; Mazzoni & Lobon-Cervia 2000).

To address explicitly the potential role of environmental factors on the functional aspect of fish assemblages, some authors have used different ecological attributes of species (i.e., reproductive, trophic or morphological traits) to explain assemblage structure (Angermeier & Karr 1983; Schlosser 1987; Oberdorff et al. 1993, 2002; Chipps et al. 1994; Belliard et al. 1997; Mèrigoux et al. 1998; Kamdem-Toham & Teugels 1998; Lamouroux et al. 2002). Concerning trophic traits, Oberdorff et al. (1993, 2002) working on temperate rivers, have shown longitudinal trends in fish trophic groups and a few similar studies conducted in tropical streams seem to confirm such trends (Angermeier & Karr 1983; Kamdem-Toham & Teugels 1998; Pouilly et al. 2006), thus suggesting possible convergence in trophic structure between temperate and tropical assemblages.

Our main objectives in this study, therefore, were to: (i) examine the longitudinal patterns of faunal composition exhibited by fishes in different river basins of Gabon and (ii) determine the main environmental factors responsible for the variation in local

assemblage richness and trophic structure at this relatively large spatial scale. Our intention was to look for potential patterns of similarity in fish assemblage attributes (i.e., species richness and trophic guilds) between temperate and tropical rivers. In other words we wanted to assess broadly the degree of convergence in these assemblage traits from temperate and tropical systems.

Methods

Regional description and choice of sites

On a continental scale, Gabon belongs to the ichthyogeographical province of lower-Guinea which contains all of the western hydrographical systems between the Cross basin in the north and the Congolese basin in the south (Roberts 1975; Lavoué et al. 2004; Lévêque & Paugy 2006). This province is characterised by both a high diversity (more than 500 species reported) and a high level of endemism (around 54%: Teugels & Guégan 1994; Stiassny et al. in press). Most of the country is covered in dense equatorial rain forests, which are actually threatened by timber exploitation and burn agriculture (Kamdem-Toham & Teugels 1998).

The interior of Gabon rises in a series of steps to the Central African Plateau. In the north, the Crystal Mountains enclose the valleys of the Woleu and Ntem rivers as well as the Ivindo River Basin. In southern Gabon, the coastal plain is dominated by granite hills and almost the entire country is situated on the Ogoe River with its two major tributaries, the N'Gounie and Ivindo Rivers.

The study was conducted in 52 sites within the six major river basins of Gabon (i.e., the Ogoe Basin (32 sites; total drainage area of the basin 205,000 km²), the Nyanga Basin (10 sites; total drainage area of the basin 20,062 km²), the Ntem Basin (four sites; total drainage area of the basin 31,000 km²), the Komo Basin (three sites; total drainage area of the basin 7900 km²), the Mbini Basin (three sites; total drainage area of the basin 13,694 km²) and the Noya Basin (one site; total drainage area of the basin 8500 km²); (Fig. 1). Originally, the sampling design was conceived to get a representative picture of fish assemblages across all Gabonian river systems. Unfortunately, we were unable to reach this goal mostly because a majority of the sites originally preselected on geographical maps were not physically accessible. We are thus conscious that some of the river basins analysed here are highly under-sampled, which slightly weakens the generality of the patterns noticed. However, as the sampling effort was fairly proportional to the size of each drainage basin, we feel confident about the representativeness of our findings.

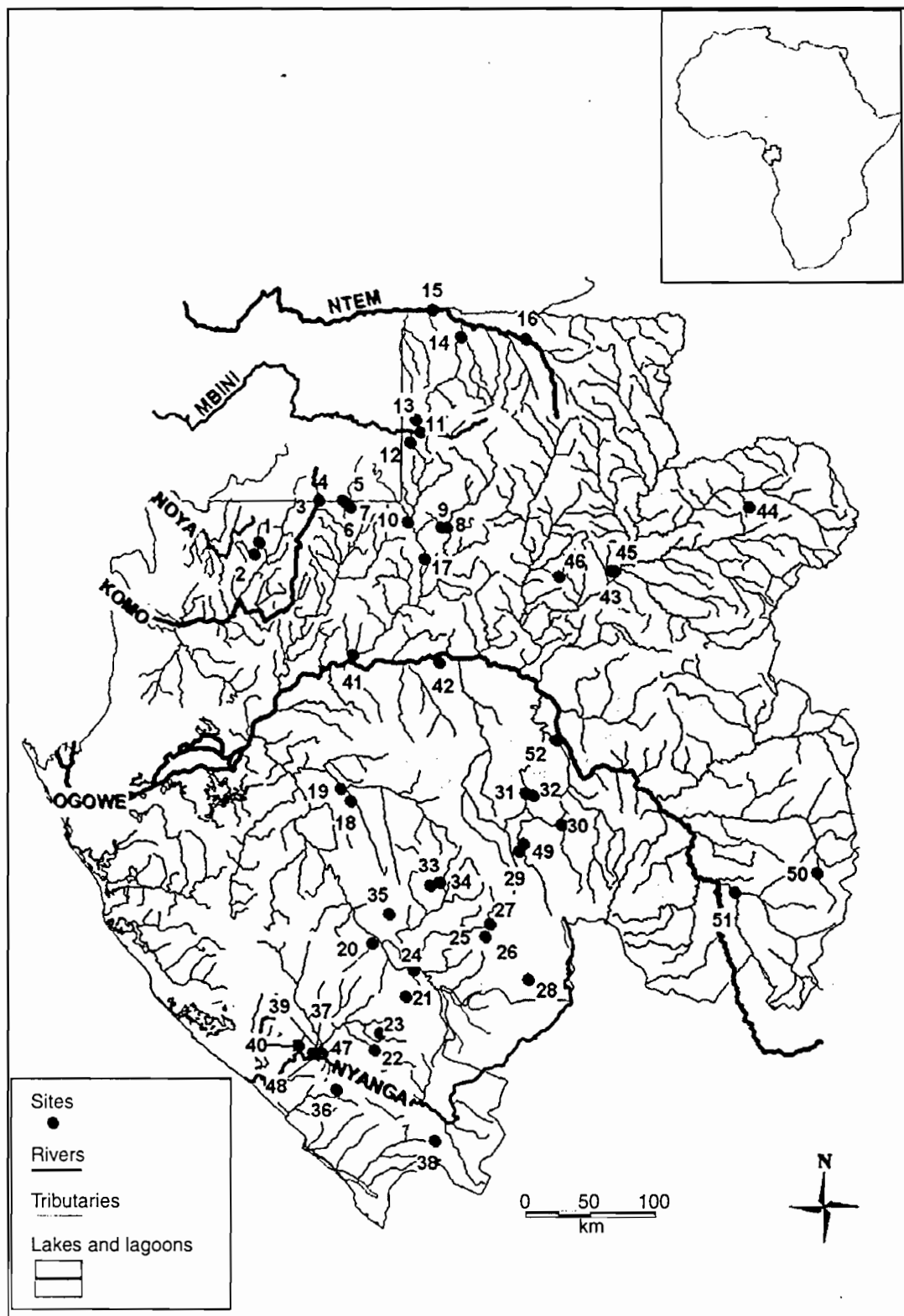


Fig. 1. Map of Gabon showing sites location (see Appendix 1 for sites description).

Fish assemblages were sampled between February and October 2001 following a standardised protocol. Depending on river width and depth two different sampling techniques were used. For small streams (mean width ≤ 10 m, mean depth = 1 m), as water conductivity (*CON*) was too low to employ electrofishing, we used the ichthyotoxin sampling method. Length of stream sampled was typically around 100 m and covered all habitat types in the vicinity (e.g., riffles, runs and pools). For each site, both edges of the sampled area were blocked by closing nets (1 mm mesh size). Liquid rotenone was poured out around 10 m upstream of the first (upstream) blocking net. Rotenone dilution was calculated following Finlayson et al. (2000) and its concentration in water was kept more or less constant for at least 1 h. Potassium permanganate, simultaneously with the ichthyotoxin, was poured out below the second blocking net to eliminate the effect of the later downstream of the sampled site.

Although this last sampling technique is passive and consequently may not have yielded a complete inventory of all species, we combined these data with those obtained for small streams as our purpose here was only to give a qualitative picture of fish assemblages structure along environmental gradients in rivers of Gabon. Fishes were fixed in a 10% formalin solution and brought to the laboratory for identification of the species or genus level (Stiassny et al. in press).

Besides the geographical position measured with a GPS 12XL *Garmin*, a total of nine variables were used to describe environmental conditions at each of the 52 sites. As factors that influence fish distribution may operate at different spatial scales (see Tejerina-Garro et al. 2005 for a review) we included in the analyses sets of environmental variables differing in spatial coverage. Six geomorphological and chemical variables were used to describe local environmental conditions. These variables were elevation (*ELE*, m), stream gradient (*STG*; visually assessed in four categories: very steep, steep, moderate and slight), mean stream width (*STW*, m), mean stream depth

Mean depth was measured by cross-stream transects at 3–5 m intervals (depending on the stream size), with sampling points spaced 1 m apart. The variables *ELE*, *DIS*, and *SAD* were estimated using a geographic information system developed by World Wildlife Fund (WWF) Gabon.

The adult feeding habits of all collected species were drawn from the literature (available on request) at the genera or species level when available. Each species was assigned into trophic groups as invertivorous, omnivorous, herbivorous/detritivorous and piscivorous based on its principal adult food as indicated by the literature (Paugy & Lévêque 2006) supplemented with informations provided in *Fishbase*: <http://www.fishbase.org>.

Multidimensional statistical analysis

Seventy-eight species that were captured at more than 5% of the 52 sites were used in the multidimensional analysis. Species captured at <5% of the sites were omitted from canonical correspondence analysis (CCA) because rare species typically have a minor influence on results of multivariate statistics and can be perceived as outliers in ordinations (Gauch 1982). Environmental variables were log-transformed when necessary prior to analysis. Associations between fish assemblages (presence-absence) and environmental variables were quantified by using CCA (CANOCO version 4.5; Ter Braak & Smilauer 2002). CCA is a nonlinear ordination technique especially designed for direct analysis of the relationships between multivariate ecological data sets (Ter Braak & Smilauer 2002). Significance tests for the general model relating assemblage structure to environmental variables were based on Monte Carlo permutation tests (1000 permutations). The environmental variables entering the CCA were selected using the forward selection of CANOCO (Monte Carlo tests, 1000 permutations).

Assemblage structure was also analysed based on species richness and species trophic composition. We

used here the total number of species actually captured during the study. Species trophic composition was calculated as the proportion richness (i.e., the number of species in each trophic group divided by the total number of species).

We used regression tree analysis (RTA), a binary partitioning technique (Breiman et al. 1984) to predict species richness and species composition from the 10 environmental variables described above. Regression trees were only recently recognised as powerful tools for modelling ecological data (De'ath & Fabricius 2000) and used in aquatic ecology (Magnuson et al. 1998; Rathert et al. 1999; Olden & Jackson 2002; Hershey et al. 2005). The approach is robust to nonlinear data and interactions among variables, and accepts categorical and continuous variables. For each partition, RTA selects the variable that minimises the residual sum of squares (RSS) of the two subgroups, relative to the parent group. The values of the selected explanatory variable over each subset define a splitting threshold, and the mean of the dependent variable values in each subgroup is the predicted value for this subgroup. This process is recursively and independently continued on each subgroup, checking all divisions and variables, until additional splits provide minor further reduction in the RSS. Splitting was stopped when nodes contained <5 sites. To determine the optimal size of each tree, the mode of 50 repeated cross-validations using the one standard-error rule was used. RTA analyses were performed using SYSTAT 11.

Results

A total of 238 species of fishes were collected (Appendix 1), of which more than 50% were present at only one site. Cyprinids were the most abundant taxon with 22% of the species, followed by cichlids (16%), mormyrids (11%) and alestiids (10%). The remaining 41% were members of 22 different families. According to Stiassny et al. in press, we sampled during this study around 70% of strictly freshwater fish species known to be present in Gabonian rivers.

We can thus consider that our sample is fairly representative of the global structure of the potential fish fauna expected in this area.

General trends in the distribution of species

Correlation coefficients among continuous numeric environmental variables are shown in Table 1. The two variables reflecting sites spatial position along the longitudinal gradient (i.e., *SAD* and *DIS*) were highly correlated ($r = 0.978$, $P < 0.001$), as expected. These two variables were also highly and positively correlated with the two local habitat variables *DEP* and *STW*, reflecting the increase in habitat size and volume along the upstream–downstream gradient.

The CCA for all samples combined showed the overall relationships between species distribution and environmental variables (Table 1, Fig. 2). Among all the environmental variables initially included in the analysis, only six were significantly related to assemblage structure and CCA components 1 and 2 together explained 57.3% of the total variation in distribution among sites of the 78 retained species. The CCA showed that the first axis was mainly related to the *SAD*, the fishing method (*FIM*) and (*ELE*), thus reflecting the samples position along the longitudinal gradient. Along axis 2, variation was mainly related to the *CON*, the *FIM* used and the sites belonging to the Nyanga Basin. Following the first two CCA components, four main groups of species were distinguished. The first one, (e.g., *Amphilius baudoni*, *Fundulopanchax batesii*, *Aphyosemion cameronense*, *Clarias jaensis*, *Matacembelus niger*, *Neolebias trewavasae*, *Microctenopoma nanum*, *Clarias camerunensis*, *Barbus camptacanthus*, *Amphilius pulcher*, *Epiplatys neumanni*, *Clarias platycephalus*, *Clarias pachynema* and *Barbus brazzaei*), with high positive scores, was representative of upstream areas. The second one, with positive scores on axis 1 and negative scores on axis 2, and constituted by species like *Paranochromis gabonicus*, *Paramormyrops gabonensis* and *Anaspis doglanis macrostoma*, was more typical of elevated upstream areas. The third group, (e.g., *Pollimyrus*

Table 1. Pearson's correlations between continuous environmental variables for the 52 sites analysed.

	<i>SAD</i> (Ln)	<i>DIS</i> (Ln)	<i>ELE</i> (Ln)	<i>STW</i> (Ln)	<i>DEP</i> (Ln)	<i>CON</i> (Ln)	pH
<i>SAD</i> (Ln)	1.000						
<i>DIS</i> (Ln)	0.978*	1.000					
<i>ELE</i> (Ln)	-0.398	-0.392	1.000				
<i>STW</i> (Ln)	0.853*	0.846*	-0.220	1.000			
<i>DEP</i> (Ln)	0.725*	0.756*	-0.012	0.875*	1.000		
<i>CON</i> (Ln)	0.230	0.237	-0.654*	0.056	-0.093	1.000	
pH	0.222	0.252	-0.581*	0.128	0.016	0.713*	1.000

* $P < 0.001$.

CON, conductivity; *DEP*, depth; *DIS*, distance; *ELE*, elevation; *SAD*, surface area of the drainage; *STW*, stream width.

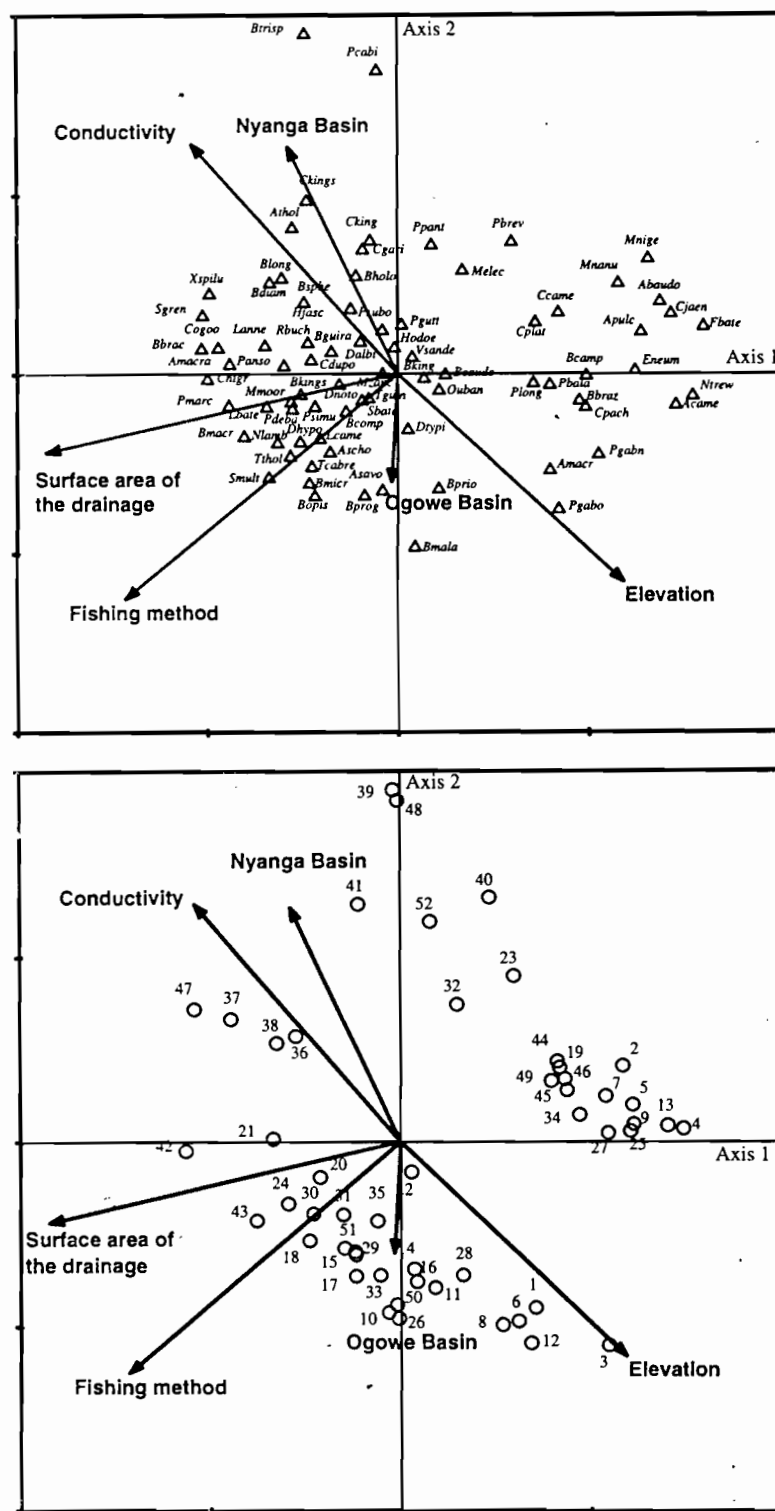


Fig. 2. Canonical correspondence analysis ordination plots showing species and sites distribution in relation to significant environmental variables (see Appendices 1 and 2 for sites and species code).

marchei, *Bryconaethiops macrops*, *Chrisichthys nigrodigitatus*, *Brienomyrus brachyistius*, *Schilbe grenfelli*, *Schilbe multitaeniatus*, *Labeo batesii*,

Tilapia tholloni, *Alestes schoutedeni* and *Brycinus opisthotaenia*), with negative scores on components 1 and 2, was representative of downstream sites sampled

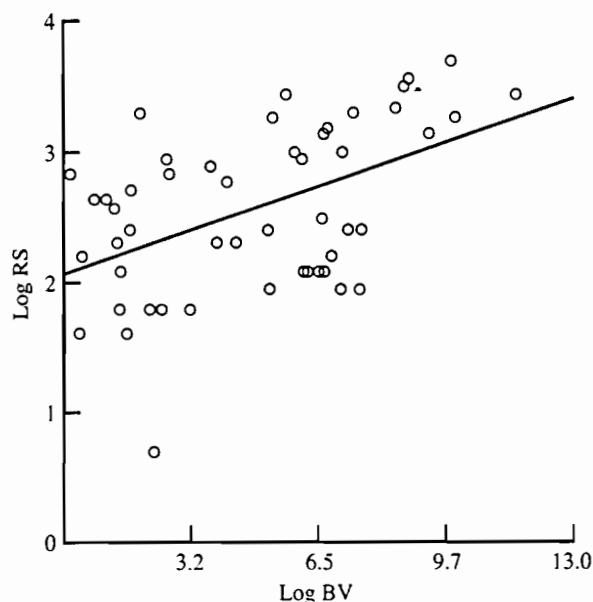


Fig. 3. Effects of stream size (i.e., surface area of the drainage) on local species richness.

with gill nets. The fourth group, (e.g., *Schilbe grenfelli*, *Xenochorax spilurus*, *Brycinus longipinnis* and *Alestes tholloni*) with negative scores on axis 1 and positive scores on axis 2, was representative of downstream areas of the Nyanga Basin having higher conductance waters.

Local assemblage richness

Figure 3 shows a significant positive relationship between local species richness (LSR) and the sites position within the upstream-downstream gradient (i.e., *SAD*) ($R = 0.454$, $P = 0.001$).

The RTA divided LSR into three-node tree using variables *SAD* and *pH* as the decision criteria and explained 67.5% of the variation in LSR. *SAD* was most important (45.2% of the total variation), and *pH* explained a further 22%. LSR was first split according to $SAD \leq 4900 \text{ km}^2$ (Fig. 4). Cell with $SAD > 4900 \text{ km}^2$ had a mean richness of 30.9 species. Cells with $SAD < 4900 \text{ km}^2$ had a mean richness of 13.2 species, and were further split into two groups for which *pH* was ≤ 7.5 . Mean richness in these groups was 20.3 and 10.3 respectively. The RTA thus predicted that LSR would be greater downstream compared with upstream areas and that LSR would be more species poor in acidic waters.

Local assemblage trophic structure

Results of the RTAs for local assemblages trophic structure are shown in Fig. 5(a-d). Concerning the

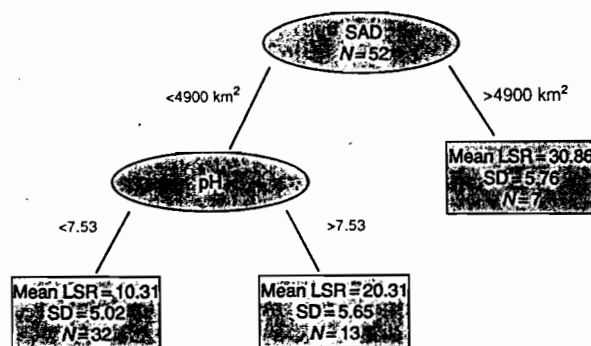


Fig. 4. Regression tree analysis for local species richness (LSR). Ovals show variables used as decision points, and values of decision criteria are indicated along diagonal lines. Rectangles show nodes used in tree construction. Also given are the mean LSR and standard deviation values for each node.

invertivorous guild (Fig. 5a) the RTA divided percentage of invertivorous (%INV) species into three-node tree using variables *STW* and *SAD* as the decision criteria and explained 52.4% of the variation in %INV. *STW* was most important (43.2% of the total variation), and *SAD* explained only a further 9.3%. The %INV was first split according to $STW \leq 5 \text{ m}$. Cell with $STW < 5 \text{ m}$ had a mean %INV species of 67.2. Cells with $STW > 5 \text{ m}$ had a mean %INV of 45.3, and were further split into two groups for which *SAD* was $\leq 210 \text{ km}^2$. Mean percentage in these groups was 13.3 and 10.7 respectively. The RTA thus predicted that the %INV species would be greater upstream compared with downstream areas.

Concerning the omnivorous guild (%OMN) (Fig. 5b) the RTA divided %OMN into three-node tree using variables *DIS* and *CON* as the decision criteria but explained only 23.2% of the variation in %OMN. *DIS* was most important (18.1% of the total variation), and *CON* explained a further 5.1%. The %OMN was first split according to $DIS \leq 50 \text{ km}$. Cell with $DIS < 50 \text{ km}$ had a mean %OMN of 27.7. Cells with $DIS > 50 \text{ km}$ had a mean %OMN of 37.8, and were further split into two groups for which *CON* was $\leq 35 \text{ } \mu\text{s}$. Mean percentage in these groups was 42.1 and 33.8 respectively. The RTA thus predicted that the percentage of omnivorous species would be greater downstream compared with upstream areas and greater in waters having low conductance.

Concerning the herbivorous guild (Fig. 5c) the RTA divided percentage of herbivorous (%HER) species into three-node tree using variables *STW* and *pH* as the decision criteria and explained 50.5% of the variation in %HER. *STW* was most important (38.9% of the total variation), and *pH* explained a further 11.7%. The %HER was first split according to $STW \leq 5 \text{ m}$. Cell with $STW < 5 \text{ m}$ had a mean %HER of 2.2. Cells with $STW > 5 \text{ m}$ had a mean %HER of 16.6, and were

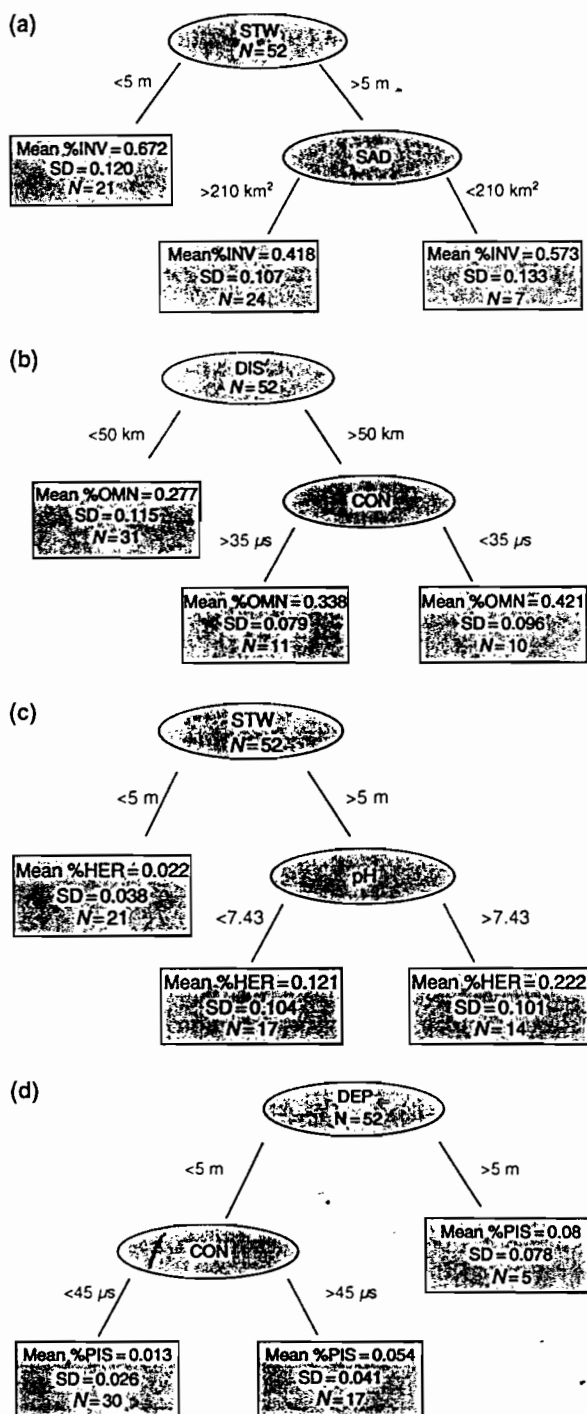


Fig. 5. Regression tree analysis for %INV (a), %OMN (b), %HER (c) and %PIS (d) (see legend Fig. 4 for explanations and text for abbreviations).

further split into two groups for which pH was ≤ 7.43 . Mean percentage in these groups was 12.1 and 22.2 respectively. The RTA thus predicted that the percentage of herbivorous/detritivorous species would be greater downstream compared with upstream areas and would decrease in acidic waters.

Concerning the piscivorous guild (Fig. 5d) the RTA divided percentage of piscivorous (%PIS) species into three-node tree using variables *DEP* and *CON* as the decision criteria and explained 30.0% of the variation in %PIS. *CON* was most important (18.0% of the total variation), and *DEP* explained a further 12.0%. The %PIS was first split according to $DEP \leq 5$ m. Cell with $DEP < 5$ m had a mean %PIS of 2.8%. Cells with $DEP > 5$ m had a mean %PIS of 8.0%, and were further split into two groups for which *CON* was $\leq 45 \mu S$. Mean percentage in these groups was 1.3 and 5.4 respectively. The RTA thus predicted that the %PIS species would be greater in deep areas and in waters of higher conductance.

To strengthen these findings we performed a re-run of RTA analyses using only the sites sampled by rotenone ($N = 21$) and obtained similar trends in species richness and trophic composition patterns (results not shown but available from the authors on request).

Discussion

Sampling issues

The fact that '*FIM*' had a significant influence on both axis 1 and 2 of the CCA suggests that using two different sampling methods in the same analysis may introduce some uncontrolled assemblages composition variability to our data. To grossly evaluate this variability we compared two pairs of similar sites (i.e., sites having similar mean stream width and belonging to the same river basin) in which either rotenone (sites 39, 40) or gill nets (sites 36, 38) were used. The mean number of species captured was respectively 29 (rotenone sampling) and 24 (gill nets sampling), suggesting that both sampling techniques were quite comparable in term of capture efficiency. In return, the percentage of similarity in assemblages composition between the two pairs of sites (number of species common to each pair of sites/total number of species captured) was only 23% (10/44). Even if part of this variability could be attributed to differences in environmental characteristics between the sites (particularly mean stream depth), we can assume that mixing the two sampling methods in our analyses did introduce some uncontrolled variability in assemblage composition. However, an important point that should be noted here is that, in all our RTA analyses, the *FIM* (rotenone vs. gill nets) never entered as a significant variable in explaining either LSR or fish assemblages trophic structure. This last result suggests that even if our sampling methods introduce variability in assemblage composition, they however do not influence significantly species richness and trophic composition patterns.

Species distribution in Gabonian rivers

The 'sites' position along the upstream–downstream gradient (i.e., the *SAD* upstream of the site) and to a lesser extent elevation and *CON* were the most important descriptors of local fish assemblage composition in our study (taking apart the *FIM*, see above).

Fish assemblages among Gabonian rivers seem to change smoothly along environmental gradients, but there appears to be a slight faunal break between upstream and downstream habitats (i.e., zonation; Appendix 3A, B). Longitudinal patterns of species addition and/or replacement have long been noted along the length of temperate and tropical streams and rivers (see Tejerina-Garro et al. 2005 for a review). These longitudinal patterns have been attributed to temperature and other habitat requirements or dispersal boundaries (Huet 1959; Gorman & Karr 1978; Horwitz 1978; Balon et al. 1986; Rahel & Hubert 1991; Belliard et al. 1997; Kamdem-Toham & Teugels 1998; Matthews & Matthews 2000). In our study, results of the ordination analysis suggest the presence of four main assemblages: assemblages typical of elevated headwaters with low conductance (mostly representative of the upper Ogowe Basin); assemblages typical of less elevated headwaters with higher conductance; assemblages typical of lowland waters with low conductance (mostly representative of the Ogowe Basin); assemblages typical of lowland waters with higher conductance (mostly representative of the Nyanga Basin). Taking apart the processes acting at the intra-basin scale, our results also highlight the strong role of river basins themselves in defining local assemblages composition (Matthews 1998). In our ordination analysis both the Ogowe and the Nyanga basins display significant effects on species presence/absence. This result was expected as the absence of migration between rivers over large temporal scales implies that extinction and speciation processes are specific of each river basin. For example, a recent

work realised in the Ogowe basin (Gabon) shows that *in situ* speciation of fish species belonging to the Mormyridae family has greatly contributed to the high degree of endemism (around 30%) occurring in this basin (Sullivan et al. 2002).

Consequently, complete answers in the explanation of local fish assemblage distribution must address the relative importance of regional scale (basin scale) processes, which determine the species available to occur locally, and small-scale processes, which should limit the number of species that actually occur locally (Angermeier & Winston 1998).

Local assemblage richness

According to the RTA, *SAD* basin and *pH* were the most important descriptors of LSR in our study. The increase in local fish species richness with increasing stream size (e.g., *SAD*) is one of the most well-known patterns in riverine fish assemblages (Fig. 3). The rise in species richness is generally attributed to an absolute increase in available habitat, an increase in habitat heterogeneity, and a decrease in environmental fluctuations from upstream to downstream resulting in increased within habitat specialisation (see Matthews 1986; Tejerina-Garro et al. 2005 for reviews). In upstream areas (*SAD* <4900 km²) species richness was around two times less in acidic catchments than in circumneutral ones. This pattern has already been observed in temperate (Townsend et al. 1983; Turnpenny et al. 1987; Peterson & Gale 1991) and tropical (Lowe-McConnell 1991) rivers and is generally attributed to physiological stress and/or lower productivity levels in these types of systems (e.g., lack of primary production and aquatic insects).

Local assemblage trophic structure

In the present study, proportion of omnivores and herbivores/detritivores increased with river size,

Table 2. Results of canonical correspondence analysis for fish assemblages of Gabon.

Variable	Axis 1	Axis 2	Axis 3
Correlations of environmental variables with ordination axes			
Ogowe	-0.015	-0.303	0.008
<i>SAD</i>	-0.921	-0.214	-0.083
<i>FIM</i>	-0.716	-0.627	0.056
<i>CON</i>	-0.542	0.637	0.005
Nyanga	-0.289	0.627	0.458
<i>ELE</i>	0.593	-0.576	-0.102
Summary statistics for ordination axes			
Eigenvalues	0.511	0.224	0.196
Species–environment correlations	0.906	0.903	0.757

Refer Appendices 1 and 2 for sites and species code. Variables significant at $P < 0.05$ are shown in bold. Monte Carlo probability for significance of the sum of all eigenvalues (1000 permutations) = 0.001.

CON, conductivity; *ELE*, elevation; *FIM*, fishing method; *SAD*, surface area of the drainage.

whereas proportion of invertivores declined downstream. Furthermore, if we consider that depth is also a good surrogate for stream size (Table 1) then, proportion of piscivores also increased downstream. Apart from stream size, water conductance and pH also seem to influence assemblage trophic structure. Proportion of herbivores/detritivores decreased in acidic waters, proportion of piscivores increased with water conductance while proportion of omnivores decreased.

There are several similarities between the longitudinal changes in assemblage trophic structure that occurred in our study and those observed in other temperate and tropical streams (Morin & Naiman 1990; Lowe-McConnell 1991; Oberdorff et al. 1993, 2002; Chipps et al. 1994; Kamdem-Toham & Teugels 1998; Pouilly et al. 2006). For example Oberdorff et al. (1993, 2002) working on French rivers showed a transition from insectivorous to omnivorous and piscivorous species from upstream to downstream areas. In a similar way, Lowe-McConnell (1991) suggested some general tendencies in African rivers like a higher abundance of surface-eating insectivores and omnivores consuming riparian allochthonous material in the upper course, and the presence of herbivores and benthic detritivores in the lower course. Kamdem-Toham & Teugels (1998) working on small streams of the lower Ntem river basin (West Central Africa) confirmed these patterns. More recently, a study of several streams in the upper Amazon Basin found that trophic composition of local assemblages became more diverse at lower altitudes, with a decrease in the relative number of invertivorous species and an increase in the relative number of detritivorous, algivorous and piscivorous species (Pouilly et al. 2006).

Similarities in these patterns between temperate and tropical rivers suggest that trophic diversity of fish assemblages may be related in part to food availability (Lotrich 1973; Angermeier & Karr 1983) and that food availability may be influenced, in turn, by common environmental constraints along the longitudinal gradient shared by these rivers.

The river continuum concept (RCC) hypothesises that those interactions between the physical environment and the organic energy base (allochthonous and autochthonous organic matter) result in a predictable pattern of riverine assemblage structure from upstream to downstream areas (Vannote et al. 1980; Minshall et al. 1985). While the original RCC dealt only minimally with fish, it seems logical to expect also a gradual change in fish assemblage structure along some downstream continuum if streams lack abrupt thermal or geological transitions (Oberdorff et al. 1993; Matthews 1998). In other words, if the RCC hypothesis is correct we should expect convergence in the trophic structure of fish assemblages for temperate

and tropical rivers. Our results seem to corroborate this hypothesis. Nevertheless, our study was only exploratory and if we are to advance further in testing convergence, then we should aim for studies that formally compare fish assemblages of different regions and/or continents.

Although there are major uncertainties in identifying and quantifying the appropriate habitat features that represent selective forces on biotic assemblages (Poff 1997), we do believe that convergence testing is a powerful method to assess the generality of some patterns observed locally, and hopefully of the processes causing these patterns.

From a conservation standpoint, these results highlight the need to evaluate all habitat types along the river longitudinal gradient to integrate the full spectrum of species assemblages within conservation plans. Position of the site within the watershed, site elevation, stream width, stream depth, water pH and water conductance appear to be the most influential factors in shaping species assemblages, and should be taken into consideration when defining aquatic habitat types for conservation planning and integrated river basin management.

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References

- Angermeier, P.L. & Karr, J.R. 1983. Fish communities along environmental gradients in a system of tropical streams. *Environmental Biology of Fishes* 9: 117–135.
- Angermeier, P.L. & Winston, M.R. 1998. Local versus regional influences on local diversity in stream fish communities of Virginia. *Ecology* 79: 911–927.
- Balon, E.K., Crawford, S.S. & Lelek, A. 1986. Fish communities of the upper Danube River (Germany, Austria) prior to the new Rhein-Main-Donau connection. *Environmental Biology of Fishes* 15: 243–271.
- Belliard, J., Boët, P. & Tales, E. 1997. Regional and longitudinal patterns of fish community structure in the Seine River basin, France. *Environmental Biology of Fishes* 50: 133–147.
- Breiman, L., Friedman, J.H., Olshen, R.A. & Stone, C.J. 1984. *Classification and regression trees*. Belmont, CA, USA: Wadsworth International Group.
- Bussing, W.A. & Lopez, M.I. 1977. Distribución y aspectos ecológicos de los peces de las cuencas hidrográficas de

- Arenal Bebedero y Tempisque, Costa Rica. *Revista de Biología Tropical* 25: 13–37.
- Chippis, S.R., Perry, W.B. & Perry, S.A. 1994. Fish assemblages of the central Appalachian Mountains: an examination of trophic groups abundance in nine West Virginia streams. *Environmental Biology of Fishes* 40: 91–98.
- De'ath, G. & Fabricius, K.E. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology* 81: 3178–3192.
- Finlayson, B.J., Schmick, R.A., Cailteux, R.L., DeMong, L., Horton, W.D., McClay, W., Thompson, C.W. & Tichacek, G.J. 2000. Rotenone use in fisheries management. Administrative and technical guidelines manual. American Fisheries Society, Bethesda, Maryland, USA.
- Gauch, H.G. Jr. 1982. Multivariate analysis in assemblage ecology. New York: Cambridge University Press, pp. 298.
- Gorman, O.T. & Karr, J.R. 1978. Habitat structure and stream fish communities. *Ecology* 59: 507–515.
- Grenouillet, G., Pont, D. & Hérissé, C. 2004. Within-basin fish assemblage structure: the relative influence of habitat versus stream spatial position on local species richness. *Canadian Journal of Fisheries and Aquatic Sciences* 61: 93–102.
- Guégan, J.F., Lek, S. & Oberdorff, T. 1998. Energy availability and habitat heterogeneity predict global riverine fish diversity. *Nature* 391: 382–384.
- Hershey, A.E., Beaty, S., Fortino, K., Keyse, M., Mou, P.P., O'Brien, W.J., Ulseth, A.J., Gettel, G.A., Lienesch, P.W., McDonald, M.E., Mayer, C.H., Miller, M.C., Richards, C., Schuldt, J.A. & Whalen, S.C. 2005. Effect of landscape factors on fish distribution in arctic Alaskan lakes. *Freshwater Biology* 51: 39–55.
- Horwitz, R.J. 1978. Temporal variability patterns and the distribution patterns of stream fishes. *Ecological Monographs* 48: 307–321.
- Huet, M. 1959. Profiles and biology of Western European streams as related to fish management. *Transaction of the American Fisheries Society* 88: 155–163.
- Hugueny, B. 1990. Richesse des peuplements de poissons dans le Niandan (haut Niger, Afrique) en fonction de la taille de la rivière et de la diversité du milieu. *Revue Hydrobiologie Tropicale* 23: 351–364.
- Ibarra, M. & Stewart, D.J. 1989. Longitudinal zonation of sandy beach fishes in the Napo river basin, Eastern Ecuador. *Copeia* 2: 364–389.
- Kamdem-Toham, A. & Teugels, G.G. 1998. Diversity patterns of fish assemblages in the Lower Ntem River basin (Cameroun), with notes on potential effects of deforestation. *Archives Hydrobiologie* 141: 421–426.
- Lamouroux, N., Poff, N.L. & Angermeier, P.L. 2002. Inter-continental convergence of stream fish community traits along geomorphic and hydraulic gradients. *Ecology* 83: 1792–1807.
- Lavoué, S., Hopkins, C.D. & Kamdem Toham, A. 2004. The *Petrocephalus* (Pisces, Osteoglossomorpha, Mormyridae) of Gabon, Central Africa, with the description of a new species. *Zoosystema* 26: 511–535.
- Lévêque, C. 2006. River and stream ecosystems of the northwestern Africa. In: Cushing, C.E., Cummins, K.W. & Minshall, G.W., eds. *River and stream ecosystems of the world*. CA, USA: University of California Press, pp. 519–536.
- Lévêque, C. & Paugy, D. 2006. Les poissons des eaux continentales africaines: diversité, écologie, utilisation par l'homme. Paris, France: IRD Éditions, pp. 564.
- Lewis, W.M. Jr., Hamilton, S.K. & Saunders, J.F. III. 2006. Rivers of northern South America. In: Cushing, C.E., Cummins, K.W. & Minshall, G.W., eds. *River and stream ecosystems of the world*. CA, USA: University of California Press, pp. 219–256.
- Lotrich, V.A. 1973. Growth, production, and community composition of fishes inhabiting a first-, second-, and third-order stream of eastern Kentucky. *Ecological Monographs* 43: 377–397.
- Lowe-McConnell, R.H. 1991. *Ecological studies in tropical fish communities*. New York: Cambridge University Press, pp. 382.
- Magnuson, J.J., Tonn, W.M., Banerjee, A., Toivonen, J., Sanchez, O. & Rask, M. 1998. Isolation versus extinction in the assembly of fishes in small northern lakes. *Ecology* 79: 2941–2956.
- Matthews, W.J. 1986. Fish faunal 'breaks' and stream order in the eastern and central United States. *Environmental Biology of Fishes* 17: 81–92.
- Matthews, W.J. 1998. *Patterns in freshwater fish ecology*. New York, NY: Chapman and Hall, pp. 784.
- Matthews, E.M. & Matthews, W.J. 2000. Geographic, terrestrial and aquatic factors: which most influence the structure of stream fish assemblages in the midwestern United States? *Ecology of Freshwater Fish* 9: 9–21.
- Mazzoni, R. & Lobon-Cervia, J. 2000. Longitudinal structure, density and production of a neotropical stream fish assemblage: the river Ubatuba in the Serra do Mar, southeast Brazil. *Ecography* 23: 588–602.
- Mérigoux, S., Ponton, D. & Mérona, B. 1998. Fish richness and species-habitat relationships in two coastal streams of French Guiana, South America. *Environmental Biology of Fishes* 51: 25–39.
- Minshall, G.W., Cummins, K.W., Petersen, R.C., Cushing, C.E., Bruns, D.A., Sedell, J.R. & Vannote, R.L. 1985. Developments in stream ecosystem theory. *Canadian Journal of Fisheries and Aquatic Sciences* 42: 1045–1055.
- Morin, R. & Naiman, R.J. 1990. The relation of stream order to fish community dynamics in boreal forest watersheds. *Polish Archives Hydrobiology* 37: 135–150.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.
- Oberdorff, T., Guilbert, E. & Luchetta, J.C. 1993. Patterns of fish species richness in the Seine River basin, France. *Hydrobiologia* 259: 157–167.
- Oberdorff, T., Pont, D., Hugueny, B. & Chessel, D. 2001. A probabilistic model characterizing riverine fish communities of French rivers: a framework for environmental assessment. *Freshwater Biology* 46: 399–415.
- Oberdorff, T., Pont, D., Hugueny, B. & Porcher, J.P. 2002. Development and validation of a fish-based index for the assessment of rivers 'health' in France. *Freshwater Biology* 47: 1720–1735.
- Olden, J.D. & Jackson, D.A. 2002. A comparison of statistical approaches for modeling fish species distributions. *Freshwater Biology* 47: 1976–1995.

- Paller, M.H. 1994. Relationships between fish assemblage structure and stream order in South Carolina coastal plain stream. *Transactions of the American Fisheries Society* 123: 150–161.
- Paugy, D. & Lévêque, C. 2006. Régimes alimentaires et réseaux trophiques. In: Lévêque, C. & Paugy, D., eds. *Les poissons des eaux continentales Africaines: Diversité, écologie, utilisation par l'homme*. Paris, France: IRD Éditions, pp. 191–215.
- Peterson, R.H. & Gale, D. 1991. Fish species associations in riffle habitat of streams of varying size and acidity in New Brunswick and Nova Scotia. *Journal of Fish Biology* 38: 859–871.
- Poff, N.L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* 16: 391–409.
- Pouilly, M., Barrera, S. & Rosales, C. 2006. Changes of taxonomic and trophic structure of fish assemblages along an environmental gradient in the Upper Beni watershed (Bolivia). *Journal of Fish Biology* 68: 137–156.
- Rahel, F.J. & Hubert, W.A. 1991. Fish assemblages and habitat gradients in a Rocky Mountain–Great Plains stream: biotic zonation and additive patterns of community change. *Transactions of the American Fisheries Society* 120: 319–332.
- Rathert, D., White, D., Sifneos, J.C. & Hughes, R.M. 1999. Environmental correlates of species richness for native freshwater fish in Oregon, USA. *Journal of Biogeography* 26: 257–274.
- Roberts, T.R. 1975. Geographical distribution of African freshwater fishes. *Zoological Journal of the Linnean Society* 57: 249–319.
- Sala, O.E., Chapin, F.S. III., Armesto, J.J., Berlow, R., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.H. 2000. Global biodiversity scenarios for the year 2100. *Science* 287: 1770–1774.
- Schlosser, I.J. 1982. Fish community structure and function along two habitat gradients in a headwater stream. *Ecological Monographs* 52: 395–414.
- Schlosser, I.J. 1987. A conceptual framework for fish communities in small warm water streams. In: Matthews, W.J. & Heins, D.C., eds. *Community and evolutionary ecology of North American stream fishes*. Norman, OK, USA: University of Oklahoma Press, pp. 17–24.
- Sheldon, A.L. 1968. Species diversity and longitudinal succession in stream fishes. *Ecology* 49: 193–198.
- Stiassny, M.L.S., Teugels, G.G. & Hopkins, C.D. (in press). The fresh and brackish water fishes of the Lower Guinea, West Central Africa. Paris, France: IRD Éditions; Tervuren, Belgium: MRAC.
- Sullivan, J.P., Lavoué, S. & Hopkins, C.D. 2002. Discovery and phylogenetic analysis of a riverine species flock of African electric fishes (Mormyridae: Teleostei). *Evolution* 56: 597–616.
- Sydenham, D.H.J. 1977. The qualitative composition and longitudinal zonation of the fish fauna of the river Ogun. *Revue de Zoologie Africaine* 91: 974–996.
- Tejerina-Garro, F., Maldonado, M., Ibañez, C., Pont, D., Roset, N. & Oberdroff, T. 2005. Effects of natural and anthropogenic environmental changes on riverine fish assemblages: a framework for ecological assessment of rivers. *Brazilian Archives of Biology and Technology* 48: 91–108.
- Ter Braak, C.J.F. & Smilauer, P. 2002. *CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5)*. Ithaca, NY: Microcomputer Power.
- Teugels, G.G. & Guégan, J.F. 1994. Diversité biologique des poissons d'eau douce de la Basse Guinée et de l'Afrique Centrale. In: Teugels, G.G., Guégan, J.F. & Albaret, J., eds. *Diversité biologique des poissons d'eau douce et saumâtres d'Afrique*. Tervuren, Belgium: Annales du Musée Royal de l'Afrique Centrale, Sciences zoologiques, pp. 67–85.
- Tito de Moraes, L. & Lauzanne, L. 1994. Zonation longitudinale des peuplements ichtyques avant mise en eau de la retenue de Petit-Saut (Guyane française). *Revue Hydrobiologie Tropicale* 27: 467–483.
- Townsend, C.R., Hildrew, A.G. & Francis, J. 1983. Community structure in some southern English streams: the influence of physiochemical factors. *Freshwater Biology* 13: 521–544.
- Turnpenny, A.W.H., Sadler, K., Aston, R.J., Milner, A.G.P. & Lynam, S. 1987. The fish populations of some streams in Wales and northern England in relation to acidity and associated factors. *Journal of Fish Biology* 31: 415–434.
- 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.
- Winemiller, K.O. & Leslie, M.A. 1992. Fish assemblages across a complex, tropical freshwater/marine ecotone. *Environmental Biology of Fishes* 34: 29–50.

Appendix 1. Total species list

Order and family	Species	Species code†
Characiformes		
Alestiidae	<i>Alestes macrophthalmus</i> Günther, 1867	Amacro
	<i>Brycinus schoutedeni</i> Boulenger, 1912	Ascho
	<i>Brycinus taeniurus</i> Günther, 1867	
	<i>Brycinus tholloni</i> Pellegrin, 1901	Athol
	<i>Brycinus intermedius</i> (Boulenger, 1903)	
	<i>Brycinus kingsleyae</i> (Günther, 1896)	Bkings
	<i>Brycinus longipinnis</i> (Günther, 1864)	Blong
	<i>Brycinus macrolepidotus</i> Valenciennes, 1850	Bopis
	<i>Brycinus opisthotaenia</i> (Boulenger, 1903)	
	<i>Brycinus</i> ssp. (7 species)	
	<i>Bryconaethiops macrops</i> Boulenger, 1920	Bmacr
	<i>Bryconaethiops microstoma</i> Günther, 1873	Bmicr
	<i>Bryconaethiops</i> sp. (1 species)	
	<i>Nannopetersius lamberti</i> Poll, 1967	Nlamb
	<i>Phenacogrammus ansorgii</i> (Boulenger, 1910)	Panso
	<i>Phenacogrammus gabonensis</i> (Poll, 1967)	
	<i>Phenacogrammus major</i> (Boulenger, 1903)	
	<i>Phenacogrammus</i> sp. (1 species)	
Distichodontidae	<i>Distichodus hypostomatus</i> Pellegrin, 1900	Dhypo
	<i>Distichodus notospilus</i> Günther, 1867	Dnoto
	<i>Hemistichodus vaillanti</i> Pellegrin, 1900	
	<i>Nannaethiops unitaeniatus</i> Günther, 1872	
	<i>Nannocharax fasciatus</i> Günther, 1867	
	<i>Nannocharax parvus</i> Pellegrin, 1906	
	<i>Nannocharax</i> sp. (1 species)	
	<i>Neolebias kerguennae</i> Daget, 1980	
	<i>Neolebias trewavasae</i> Poll & Gosse, 1963	Ntrew
	<i>Neolebias unifasciatus</i> Steindachner, 1894	
	<i>Xenocharax spilurus</i> Günther, 1867	Xspilu
	<i>Hepsetus odoe</i> (Bloch, 1794)	Hodoe
Hepsitidae		
Clupeiformes		
Clupeidae	<i>Odaxothrissa ansorgii</i> Boulenger, 1910	
	<i>Pellonula leonensis</i> Boulenger, 1916	
	<i>Pellonula vorax</i> Günther, 1868	
Cyprinodontiformes		
Aplocheilidae	<i>Aphyosemion cameronense</i> (Boulenger, 1903)	Acame
	<i>Aphyosemion joergenscheeli</i> Huber & Radda, 1977	
	<i>Aphyosemion ocellatum</i> Huber & Radda, 1977	
	<i>Aphyosemion</i> ssp. (4 species)	
	<i>Epiplatys neumanni</i> Berkenkamp, 1993	Eneum
	<i>Aphyosemion batesii</i> (Boulenger, 1911)	Fbate
Poeciliidae	<i>Plataplochilus cabinda</i> (Boulenger, 1911)	Pcabi
	<i>Plataplochilus terveri</i> (Huber, 1981)	
Cypriniformes		
Cyprinidae	<i>Barbus aloyi</i> Roman, 1970	
	<i>Labeobarbus batesii</i> Boulenger, 1903	
	<i>Barbus brazzaei</i> Pellegrin, 1901	Bbraz
	<i>Barbus brichardi</i> Poll & Lambert, 1959	
	<i>Barbus camptacanthus</i> (Bleeker, 1863)	Bcamp
	<i>Barbus caudovittatus</i> Boulenger, 1902	Bcaudo
	<i>Labeobarbus compiniei</i> (Sauvage, 1879)	Bcomp
	<i>Barbus diamouanganai</i> Teugels & Mamonekene, 1992	Bdiam
	<i>Barbus guirali</i> Thominot, 1886	Bguira
	<i>Barbus holotaenia</i> Boulenger, 1904	Bholo
	<i>Barbus jae</i> Boulenger, 1903	
	<i>Labeobarbus malacanthus</i> Pappenheim, 1911	Bmala
	<i>Barbus martorelli</i> Roman, 1970	
	<i>Barbus micronema</i> Boulenger, 1904	
	<i>Barbus prionacanthus</i> Mahnert & Géry, 1982	Bprio
	<i>Barbus progenys</i> Boulenger, 1903	Bprog
	<i>Labeobarbus rubrostigma</i> Poll & Lambert, 1964	
	<i>Barbus trispilomimus</i> Boulenger, 1907	Btrisp

Order and family	Species	Species code†
	<i>Barbus</i> ssp. (18 species)	
	<i>Labeo annectens</i> Boulenger, 1903	Lanne
	<i>Labeo batesii</i> Boulenger, 1911	Lbate
	<i>Labeo</i> ssp. (8 species)	
	<i>Opsaridium ubangiense</i> (Pellegrin, 1901)	Ouban
	<i>Raiamas batesii</i> (?) (Boulenger, 1914)	
	<i>Raiamas buchholzi</i> (Peters, 1876)	Rbuch
	<i>Raiamas</i> sp. (1 species)	
	<i>Varicorhinus sandersi</i> Boulenger, 1912	Vsande
	<i>Varicorhinus werneri</i> Holly, 1929	
	<i>Varicorhinus</i> sp. (1 species)	
Gonorynchiformes		
Kneriidae	<i>Parakneria</i> sp. (1 species)	
Osteoglossiformes		
Mormyridae	<i>Boulengeromyrus knoepffleri</i> Taverne & Géry, 1968	
	<i>Brienomyrus brachyistius</i> (Gill, 1862)	Bbrac
	<i>Paramormyrops hopkinsi</i> Taverne & Thys van den Audenaerde, 1985	
	<i>Paramormyrops kingsleyae kingsleyae</i> (Günther, 1896)	Bking
	<i>Paramormyrops sphekodes</i> (Sauvage, 1879)	Bsphe
	<i>Brienomyrus</i> sp. (5 species)	
	<i>Ivindomyrus opdenboschi</i> Taverne & Géry, 1975	
	<i>Marcusenius</i> sp. (4 species)	
	<i>Marcusenius moorii</i> (Günther, 1867)	Mmoor
	<i>Marcusenius ntemensis</i> (Pellegrin, 1927)	
	<i>Mormyrops zanclostris</i> (Günther, 1867)	Mzanc
	<i>Paramormyrops gabonensis</i> Taverne, Thys van den Audenaerde & Heymer, 1977	Pgabo
	<i>Petrocephalus microphthalmus</i> Pellegrin, 1908	
	<i>Petrocephalus simus</i> Sauvage, 1879	Psimu
	<i>Petrocephalus</i> sp. (2 species)	
	<i>Ivindomirus marchei</i> (Sauvage, 1879)	Pmarc
	<i>Stomatorhinus walkeri</i> (Günther, 1867)	
	<i>Xenomystus nigri</i> (Günther, 1868)	
Notopteridae		
Perciformes		
Anabantidae	<i>Ctenopoma kingsleyae</i> Günther, 1896	Ckings
	<i>Ctenopoma maculatum</i> Thominot, 1886	
	<i>Ctenopoma</i> ssp. (2 species)	
	<i>Microctenopoma nanum</i> (Günther, 1896)	Mnanu
Channidae	<i>Parachanna</i> sp. (1 species)	
Cichlidae	<i>Benitochromis batesii</i> (Boulenger, 1901)	
	<i>Chilochromis duponti</i> Boulenger, 1902	Cdupo
	<i>Chromidotilapia kingsleyae</i> Boulenger, 1898	Cking
	<i>Chromidotilapia</i> ssp. (7 species)	
	<i>Hemichromis fasciatus</i> Peters, 1857	Hfasc
	<i>Divandu albimarginatus</i> Lamboj & Snoeks, 2000	Dalbi
	<i>Oreochromis niloticus niloticus</i> (Linnaeus, 1758)	
	<i>Oreochromis schwebischii</i> (Sauvage, 1884)	
	<i>Oreochromis</i> ssp. (3 species)	
	<i>Parananochromis caudifasciatus</i> (Boulenger, 1913)	
	<i>Parananochromis gabonicus</i> (Trewavas, 1975)	Pgabn
	<i>Parananochromis longirostris</i> (Boulenger, 1903)	Plong
	<i>Pelvicachromis subocellatus</i> (Günther, 1872)	Psubo
	<i>Pelvicachromis</i> ssp. (4 species)	
	<i>Sarotherodon galilaeus</i>	
	<i>Sarotherodon melanotheron</i>	
	<i>Sarotherodon</i> sp. (1 species)	
	<i>Thysochromis ansorgii</i> (Boulenger, 1901)	
	<i>Tilapia cabrae</i> Boulenger, 1899	Tcabre
	<i>Tilapia guineensis</i> (Günther, 1862)	Tguin
	<i>Tilapia rendalli</i> (Boulenger, 1897)	
	<i>Tilapia tholloni</i> (Sauvage, 1884)	Tthol
	<i>Tilapia</i> ssp. (5 species)	
Haemulidae	<i>Pomadasys jubelini</i> (Cuvier, 1830)	
	<i>Pomadasys perotai</i> (Cuvier, 1830)	
Lutjanidae	<i>Lutjanus goreensis</i> (Valenciennes, 1830)	
Monodactylidae	<i>Monodactylus sebae</i> (Cuvier, 1829)	

Appendix 1. Continued

Order and family	Species	Species code†
Mugilidae	<i>Liza falcipinnis</i> (Valenciennes, 1836)	
Polynemidae	<i>Polydactylus quadrifilis</i> (Cuvier, 1829)	
Sciaenidae	<i>Pseudotolithus elongatus</i> (Bowdich, 1825)	
Siluriformes		
Amphiliidae	<i>Paramphilius baudoni</i> Pellegrin, 1928	Abaudo
	<i>Amphilius brevis</i> Boulenger, 1902	
	<i>Amphilius longirostris</i> (Boulenger, 1901)	
	<i>Amphilius pulcher</i> Pellegrin, 1929	Apulc
	<i>Doumea typica</i> Sauvage, 1879	Dtypi
	<i>Phractura brevicauda</i> Boulenger, 1911	Pbrev
	<i>Phractura intermedia</i> Boulenger, 1911	
	<i>Phractura longicauda</i> Boulenger, 1903	
	<i>Phractura</i> sp. (1 species)	
Claroteidae	<i>Anaspidoglanis macrostoma</i> (Pellegrin, 1909)	Amacr
	<i>Anaspidoglanis</i> ssp. (2 species)	
	<i>Chrysichthys auratus auratus</i> (Geoffroy Saint-Hilaire, 1809)	
	<i>Chrysichthys nigrodigitatus</i> (Lacepède, 1803)	Cnigr
	<i>Chrysichthys ogoensis</i> (Pellegrin, 1900)	Cogoo
	<i>Chrysichthys thysi</i> Risch, 1985	
	<i>Chrysichthys</i> ssp. (4 species)	
	<i>Parauchenoglanis balayi</i> (Sauvage, 1879)	Pbala
	<i>Parauchenoglanis guttatus</i> (Lönnberg, 1895)	Pgutt
	<i>Parauchenoglanis pantherinus</i> (Pellegrin, 1929)	Ppant
	<i>Parauchenoglanis</i> ssp. (4 species)	
Clariidae	<i>Clarias camerunensis</i> Lönnberg, 1895	Ccame
	<i>Clarias gariepinus</i> (Burchell, 1822)	Cgari
	<i>Clarias jaensis</i> Boulenger, 1909	Cjaen
	<i>Clarias longior</i> Boulenger, 1907	
	<i>Clarias pachynema</i> Boulenger, 1903	Cpach
	<i>Clarias platycephalus</i> Boulenger, 1902	Cplat
	<i>Clarias submarginatus</i> Peters, 1882	
	<i>Clarias</i> sp. (1 species)	
	<i>Gymnallabes typus</i> Günther, 1867	
Malapteruridae	<i>Malapterurus electricus</i> (Gmelin, 1789)	Melec
Mochokidae	<i>Atopochilus savognani</i> Sauvage, 1879	Asavo
	<i>Atopochilus</i> sp. (2 species)	
	<i>Synodontis albolineatus</i> Pellegrin, 1924	
	<i>Synodontis atherinoides</i> Poll & Roberts, 1968	
	<i>Synodontis batesii</i> Boulenger, 1907	Sbate
	<i>Synodontis tessmanni</i> Pappenheim, 1911	
	<i>Synodontis</i> ssp. (4 species)	
Schilbeidae	<i>Parailia occidentalis</i> (Pellegrin, 1901)	
	<i>Parailia</i> sp. (1 species)	
	<i>Parutropius debauwi</i> (Boulenger, 1900)	Pdeba
	<i>Schilbe grenfelli</i> (Boulenger, 1900)	Sgren
	<i>Schilbe multitaeniatus</i> (Pellegrin, 1913)	Smult
	<i>Schilbe</i> ssp. (2 species)	
Synbranchiformes		
Mastacembelidae	<i>Mastacembelus marcheii</i> (Sauvage, 1879)	
	<i>Mastacembelus niger</i> Sauvage, 1879	Mnige

†Species code used in the statistic analysis.

Appendix

Appendix 2. Mean values of environmental variables for the 52 sampled sites.

Site code	River basin	Latitude	Longitude	pH	CON	SAD	DIS	ELE	STW	DEP	FIM	RIB	STG
ST01	Komo	00°42.675'N	10°21.381'E	6.90	19.1	25.0	20.0	530	7	1.5	1	1	1
ST02	Noya	00°38.294'N	10°19.112'E	6.73	28.0	4.3	5.0	540	1	0.4	0	0	1
ST03	Komo	01°00.239'N	10°45.547'E	6.79	15.5	3.0	3.7	636	1	1.5	1	1	1
ST04	Komo	01°00.100'N	10°45.834'E	6.4	11.0	2.2	3.5	629	3	0.3	0	1	0
ST05	Ogowe	00°59.521'N	10°55.756'E	7.02	23.9	0.7	1.0	452	1	0.3	0	2	0
ST06	Ogowe	00°58.830'N	10°57.168'E	7.02	25.7	5.5	3.0	458	25	2.0	1	2	2
ST07	Ogowe	00°57.249'N	10°59.137'E	6.37	27.1	1.6	1.0	510	1	0.3	0	2	1
ST08	Ogowe	00°48.949'N	11°39.024'E	6.58	21.9	12.2	7.6	480	46	5.0	1	2	2
ST09	Ogowe	00°49.050'N	11°37.199'E	6.26	16.3	1.2	0.9	490	1	0.2	0	2	1
ST10	Ogowe	00°50.666'N	11°22.582'E	6.45	14.8	1183.0	75.0	524	44	5.0	1	2	2
ST11	Woleu	01°28.187'N	11°27.711'E	5.52	19.5	935.6	56.5	674	50	3.5	1	3	1
ST12	Woleu	01°23.920'N	11°24.491'E	6.22	10.2	82.0	13.6	680	5	0.5	1	3	1
ST13	Woleu	01°32.974'N	11°26.394'E	5.88	11.5	3.7	3.1	676	1	0.3	0	3	0
ST14	Ntem	02°07.250'N	11°44.549'E	6.50	22.6	1415.0	83.7	564	42	10.0	1	4	1
ST15	Ntem	02°17.843'N	11°33.053'E	7.29	21.7	11400.0	145.0	576	100	10.0	1	4	2
ST16	Ntem	02°05.888'N	E12°11.530	5.73	17.1	1897.0	69.6	566	20	2.0	1	4	1
ST17	Ogowe	00°35.897'N	11°29.749'E	7.18	18.5	2003.0	109.0	332	20	2.0	1	2	3
ST18	Ogowe	01°03.244'S	10°59.346'E	7.53	29.1	4900.0	110.0	300	103	2.0	1	2	2
ST19	Ogowe	0°58.288'S	10°54.716'E	7.22	35.6	5.0	3.0	460	1.5	0.3	0	2	3
ST20	Ogowe	2°02.484'S	11°07.946'E	8.20	200.0	294.0	28.0	450	10	0.8	1	2	1
ST21	Ogowe	2°24.390'S	11°21.904'E	8.41	282.0	770.0	50.0	340	24	1.0	1	2	1
ST22	Nyanga	2°45.870'S	11°08.612'E	7.14	26.1	185.0	23.0	100	20	1.0	1	5	1
ST23	Nyanga	2°39.248'S	11°11.153'E	6.91	26.0	50.0	8.0	200	2	0.3	0	5	1
ST24	Ogowe	2°12.542'S	11°24.739'E	7.85	25.6	6800.0	170.0	114	63	2.1	1	2	0
ST25	Ogowe	1°57.213'S	11°46.240'E	6.77	16.4	1.5	1.0	604	1	0.2	0	2	1
ST26	Ogowe	1°58.771'S	11°55.483'E	7.00	17.3	780.0	55.0	670	33	2.0	1	2	0
ST27	Ogowe	1°54.388'S	11°56.561'E	6.47	15.2	4.0	2.0	695	1	0.2	0	2	1
ST28	Nyanga	2°17.063'S	12°13.180'E	7.25	16.7	192.0	43.0	636	20	2.0	1	5	2
ST29	Ogowe	1°23.914'S	12°09.325'E	7.43	45.3	733.0	64.0	469	29	2.0	1	2	2
ST30	Ogowe	1°12.943'S	12°26.735'E	7.53	58.3	1642.0	90.0	312	50	2.0	1	2	2
ST31	Ogowe	0°59.663'S	12°11.625'E	7.77	73.6	443.0	50.0	331	15	1.0	1	2	1
ST32	Ogowe	1°00.518'S	12°14.935'E	7.56	65.2	65.0	14.0	365	2.5	0.35	0	2	1
ST33	Ogowe	1°36.676'S	11°35.909'E	7.43	32.0	512.0	48.0	500	23	1.5	1	2	0
ST34	Ogowe	S1°38.406	E11°31.866	6.66	15.3	9.0	3.0	535	1.5	0.2	0	2	1
ST35	Ogowe	1°50.026'S	11°15.043'E	7.63	36.0	210.0	40.0	136	34	2.0	1	2	2
ST36	Nyanga	3°02.123'S	10°52.622'E	8.36	251.0	368.0	50.0	83	7	1.0	1	5	2
ST37	Nyanga	2°47.340'S	10°43.716'E	8.00	116.0	6000.0	85.0	36	100	2.0	1	5	0
ST38	Nyanga	3°22.743'S	11°34.217'E	8.44	268.0	850.0	60.0	124	7	1.5	1	5	2
ST39	Nyanga	S2°47.374	10°46.639'E	8.13	338.0	43.0	13.0	65	1.5	0.3	0	5	0
ST40	Nyanga	2°43.719'S	10°36.621'E	8.05	95.8	14.0	8.0	130	10	0.4	0	5	1
ST41	Ogowe	00°02.536'S	11°00.166'E	8.26	91.0	461.0	40.0	79	2	0.3	0	2	3
ST42	Ogowe	00°06.361'S	11°35.528'E	5.50	46.0	105000.0	445.0	120	100	2.0	1	2	2
ST43	Ogowe	00°31.269'N	12°49.383'E	6.96	49.0	19930.0	195.0	472	250	5.0	1	2	0
ST44	Ogowe	00°56.579'N	13°44.795'E	5.19	45.0	4.2	2.0	522	3	0.3	0	2	1
ST45	Ogowe	00°31.152'N	12°47.961'E	6.86	25.0	7.1	3.3	536	2	0.6	0	2	1
ST46	Ogowe	00°28.800'N	12°25.873'E	7.09	30.0	5.6	2.0	493	1.5	0.2	0	2	1
ST47	Nyanga	02°47.000'S	10°43.000'E	8.00	116.0	22000.0	350.0	36	100	2.0	1	5	0
ST48	Nyanga	02°47.000'S	10°46.000'E	8.13	338.0	43.0	13.0	82	1.5	0.3	0	5	0
ST49	Ogowe	01°21.000'S	12°11.000'E	5.10	30.0	10.0	7.0	577	3	0.6	0	2	0
ST50	Ogowe	01°33.000'S	14°13.000'E	5.20	17.0	676.0	57.0	471	8	1.0	1	2	0
ST51	Ogowe	01°41.000'S	13°39.000'E	7.14	35.0	1238.0	86.0	351	21	1.5	1	2	2
ST52	Ogowe	00°38.000'S	12°25.000'E	8.20	340.0	15.0	6.0	325	3	0.3	0	2	1

Appendix 3A. Presence-absence of the 78 most common species as a function of sites position along the longitudinal gradient. See Appendices 1 and 2 for sites and species code.

	Site code																										
Species code	ST05	ST09	ST25	ST07	ST04	ST03	ST13	ST27	ST44	ST02	ST19	ST06	ST46	ST45	ST34	ST49	ST08	ST40	ST52	ST01	ST39	ST48	ST23	ST32	ST12	ST22	
Fbate	1	1					1			1																	
Abaudo	1			1						1	1																
Acame	1	1		1	1	1				1										1							
Mnige	1			1	1		1														1						
Ntrew		1			1	1	1						1														
Mnanu	1	1		1	1	1	1						1						1		1		1				
Cjaen	1				1					1			1	1													
Cplat	1																		1								
Bcamp	1				1	1	1	1			1		1	1	1				1	1			1			1	
Ccame	1				1						1		1						1			1	1				
Pbala	1	1		1	1	1	1		1					1								1			1		
Amacr	1	1				1	1					1		1		1									1		
Ppant	1																				1			1			
Pgabn	1	1				1																					
Plong	1	1			1				1					1													
Pgabo		1		1		1														1					1		
Cpach	1		1	1			1	1						1	1					1				1	1		
Bbraz	1				1																						
Bholo	1													1				1	1		1	1		1			
Dalbi	1																		1			1					
Eneum	1					1			1				1	1													
Hodoe		1					1										1	1			1	1		1	1		
Apulc			1										1		1												
Bking			1					1	1				1	1	1	1							1	1			
Pbrev			1					1					1						1			1	1	1			
Asavo						1						1														1	
Bcomp						1						1														1	
Dnoto							1																		1		
Bprio								1				1	1				1							1	1	1	
Melec									1					1													
Hfasc									1					1			1	1	1		1	1		1	1		
Bcaudo											1							1					1				
Ouban											1		1	1			1	1	1					1	1		
Ascho													1											1			
Bmala													1														
Bprog													1														
Dhypo																	1									1	
Dtypi												1						1		1						1	
Pgutt														1					1					1			
Psimu														1						1							
Rbuch														1				1						1			
Sbate														1													
Bkings														1													
Bguira														1				1	1				1				

Fish assemblages structure and function

	Site code																									
Species code	ST05	ST09	ST25	ST07	ST04	ST03	ST13	ST27	ST44	ST02	ST19	ST06	ST46	ST45	ST34	ST49	ST08	ST40	ST52	ST01	ST39	ST48	ST23	ST32	ST12	ST22
<i>Cgari</i>													1					1								
<i>Mmoor</i>													1													
<i>Bsphe</i>													1													
<i>Mzanc</i>													1													
<i>Psubo</i>																		1								1
<i>Cdupo</i>																		1								
<i>Athol</i>																		1								
<i>Cking</i>																		1	1			1	1			
<i>Blong</i>																			1			1				
<i>Pcabi</i>																			1			1	1			
<i>Ckings</i>																					1	1				
<i>Btrisp</i>																					1	1				
<i>Xspilu</i>																					1	1				
<i>Tguin</i>																						1				
<i>Bdiam</i>																						1				
<i>Vsande</i>																							1			1
<i>Lanne</i>																								1		
<i>Pdeba</i>																										
<i>Bmicr</i>																										
<i>Panso</i>																										
<i>Tcabre</i>																										
<i>Lbate</i>																										
<i>Nlamb</i>																										
<i>Cnigr</i>																										
<i>Bmacr</i>																										
<i>Tthol</i>																										
<i>Sgren</i>																										
<i>Cogoo</i>																										
<i>Bbrac</i>																										
<i>Bopis</i>																										
<i>Pmarc</i>																										
<i>Amacro</i>																										
<i>Smult</i>																										
SAD (km²)	0.7	1.2	1.5	1.6	2.2	3.0	3.7	4.0	4.2	4.3	5.0	5.5	5.6	7.1	9.0	10.0	12.2	14.0	15.0	25.0	43.0	43.0	50.0	65.0	82.0	185.0

Appendix 3B. Presence-absence of the 78 most common species as a function of sites position along the longitudinal gradient. See Appendices 1 and 2 for sites and species code.

Species code	Site code																									
	ST28	ST35	ST20	ST36	ST31	ST41	ST33	ST50	ST29	ST21	ST26	ST38	ST11	ST10	ST51	ST14	ST30	ST16	ST17	ST18	ST37	ST24	ST15	ST43	ST47	ST42
Fbate																										
Abaudo																										
Acame																										
Mnige																										
Ntrew																										
Mnanu																										
Cjaen																										
Cplat	1																									
Bcamp	1										1															
Ccame	1										1															
Pbala			1							1				1		1										
Amacr													1	1	1								1			
Ppant				1																			1			
Pgabn																							1			
Plong		1													1									1		
Pgabo																1			1							
Cpach									1		1															
Bbraz																				1						
Bholo		1	1	1	1					1							1					1	1		1	1
Dalbi			1							1			1		1	1						1	1			
Eneum																										
Hodoe			1	1	1					1		1		1	1	1				1	1	1				
Apulc																										
Bking	1	1		1	1			1	1		1	1			1					1	1			1		1
Pbrev																				1						
Asavo		1			1				1			1		1									1	1		
Bcomp		1		1	1	1						1			1		1					1				1
Dnoto			1	1	1					1		1	1			1	1				1	1	1	1	1	1
Bprio	1						1		1		1			1	1					1				1		
Melec			1			1																				
Hfasc			1	1	1	1		1	1	1		1			1		1	1	1	1	1	1		1	1	
Bcaudo		1					1				1				1											
Ouban		1			1										1		1			1						1
Ascho		1	1	1	1								1		1	1	1		1	1		1				1
Bmala							1								1								1			
Bprog			1		1		1										1									
Dhypo		1			1		1					1					1			1	1	1	1	1	1	
Dtypi	1			1					1		1	1			1											
Pgutt		1							1			1														
Psimu		1	1															1		1	1	1	1	1	1	1
Rbuch		1	1	1	1	1				1							1			1	1	1	1	1	1	1
Sbate			1	1						1			1										1			
Bkings			1	1	1							1	1				1			1	1	1		1	1	1

Fish assemblages structure and function

	Site code																									
Species code	ST28	ST35	ST20	ST36	ST31	ST41	ST33	ST50	ST29	ST21	ST26	ST38	ST11	ST10	ST51	ST14	ST30	ST16	ST17	ST18	ST37	ST24	ST15	ST43	ST47	ST42
Bguira			1		1					1		1				1	1		1	1	1		1	1	1	
Cgari			1	1																					1	
Mmoor		1	1	1	1							1					1	1	1	1	1	1	1	1	1	1
Bsphe					1	1																				1
Mzanc																	1									1
Psubo																				1						
Cdupo		1	1							1		1								1		1				
Athol										1		1									1					
Cking		1													1							1			1	
Blong		1	1	1		1											1			1	1	1		1	1	1
Pcabi																					1					
Ckings										1		1								1						
Btrisp																									1	
Xspilu			1							1											1	1	1	1	1	1
Tguin			1					1	1									1								
Bdiam												1		1	1						1					
Vsande																				1						
Lanne												1								1		1		1	1	
Pdeba		1	1														1		1	1	1	1			1	
Bmicr		1	1													1	1		1	1		1	1			
Panso		1	1	1								1										1				
Tcabre			1					1		1					1											
Lbate			1				1			1									1					1	1	
Nlamb			1														1					1				
Cnigr				1													1			1	1	1		1	1	
Bmacr					1												1									1
Tthol								1	1						1						1			1		
Sgren												1								1	1				1	
Cogoo												1					1						1	1		
Bbrac												1									1			1	1	1
Bopis													1			1	1	1	1			1	1	1		1
Pmarc																			1		1	1		1	1	1
Amacro																				1	1			1	1	
Smult																							1	1		
SAD (km²)	192.0	210.0	294.0	368.0	443.0	461.0	512.0	676.0	733.0	770.0	780.0	850.0	935.6	1183.0	1238.0	1415.0	1642.0	1897.0	2003.0	4900.0	6000.0	6800.0	11400.0	19930.0	22000.0	105000.0

SAD, surface area of the drainage.

Article 3

**Test for convergence of temperate and tropical stream fish
assemblages**

Carla Ibañez, Jérôme Belliard, Robert M. Hughes, Pascal Irz, André Kamdem-Toham &
Thierry Oberdorff

En préparation

Test for convergence of temperate and tropical stream fish assemblages

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ABSTRACT

Making the hypothesis of convergence relates to the deterministic view that community (or assemblage) structure can be predicted from the environment, which is thus expected to drive evolution in a predictable direction. Here we present results from a comparative study of freshwater fish assemblages from headwater streams in four zoogeographic regions around the world (i.e. zoogeographic regions belonging to European, North American, African and South American continents), with the general objective of testing whether these assemblages display convergent structures under similar environmental conditions (i.e. assemblage position in the stream longitudinal continuum). We tested this hypothesis by comparing ecomorphological characteristics and trophic ecology of our stream fish assemblages. Independently of phylogenetic and historical constraints, fish assemblage richness and trophic structure of the four zoogeographic regions were found to be convergent along streams longitudinal continuum to a substantial degree. For the four regions, assemblage richness tended to increase along the streams longitudinal gradient and the percentage of invertivorous species tended to significantly decrease along the gradient with a parallel significant increase of the percentage of omnivorous species, supporting theoretical predictions of the river continuum concept. However, the herbivores/detritivores and piscivores guilds were virtually absent of the sites sampled in our European and North American streams while present in African and South American streams. This divergence can be linked to differences in trophic energy (resource supply) availability between temperate and tropical systems.

Key words: intercontinental convergence, fish assemblages, streams, longitudinal continuum, species richness, trophic guilds.

INTRODUCTION

The hypothesis of community convergence is that under similar environmental conditions, the structure of phylogenetically unrelated communities should be similar (i.e. The same causes should produce the same effects; Orians & Paine 1983, Schluter 1986). Hence, making the hypothesis of convergence relates to the deterministic view that community structure can be predicted (at least partly) from the environment, which 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 these patterns (Lawton 1999, Ben-Moshe *et al.* 2001). Previous investigations that looked for community-level convergence found mixed results going from total absence of convergence (Price *et al.* 2000, Verdu *et al.* 2002, Stephens & Wiens 2004) to occurrence of partially convergent communities (Schluter 1986, Winemiller 1991, Losos *et al.* 1998, Ben-Moshe *et al.* 2001, Lamouroux *et al.* 2002, Melville *et al.* 2006, Irz *et al.* 2007). In fact, examples of community convergence seem mostly restricted to island biotas, whereas for continental communities, lack of convergence seems the norm (Melville *et al.* 2006).

The degree of community convergence obviously depends on historical contingencies (Ricklefs & Schluter 1993, Melville *et al.* 2006) but should be also strongly influenced by the degree of constraints exercised by the environment on the communities. Concerning the latter point (i.e. degree of environmental constraints) rivers or streams offer environmental conditions harsh enough to potentially operate a strong selective pressure towards aquatic community properties. For example, at the inter-river 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) but also to biogeographical history (Oberdorff *et al.* 1997, Tedesco *et al.* 2005). At the intra-basin scale (i.e. among sites within streams or rivers of various

continents), fish or macroinvertebrate assemblage structures seem to also display consistent patterns (e.g. patterns in species richness, trophic guilds or other functional traits) along streams or rivers longitudinal continuum (Schlosser 1982, Oberdorff *et al.* 1993, Poff 1997, Usseglio-Poletera *et al.* 2000, Finn & Leroy Poff 2005, Hoeinghaus *et al.* 2007, Ibañez *et al.* 2007a). These patterns are usually attributed to changes in physical conditions of streams or rivers from upstream to downstream areas creating strong constraints on assemblages structure linked to food availability (the river continuum concept, RCC; Vannote *et al.* 1980) and/or to habitat spatial heterogeneity (the river habitat template, Townsend & Hildrew 1994).

For example, Lamouroux *et al.* (2002) found that some morphological traits of fish assemblages on two continents (Europe and North America) were similarly related to stream environmental conditions such as hydraulics and geomorphology.

Factors such as stream width, water depth, current velocity, substrate diversity and associated composite variables like stream order, distance from sources or surface area of the drainage have also been found to influence the characteristics of fish assemblages (see Matthews 1998 and Tejerina-Garro *et al.* 2005 for reviews).

At this spatial scale, comparative studies are now needed to ascertain the extent to which patterns in assemblage structure already observed along longitudinal gradient are representative of streams or rivers as a whole, based on the premise that under a particular set of selective forces (i.e. habitat constraints) specific assemblage traits will be selected. Here we present results from a comparative study of freshwater fish assemblages from headwater streams in four continents (i.e. Europe, North America, Africa and South America) with the general objective of testing whether these assemblages display convergent structures. To do so, we analyzed the fish assemblage at the local scale (site scale) and asked whether the longitudinal position of sites was a primary factor organizing assemblage structure among these streams. By assemblage structure, we mean here the number of species, the total density

of individuals and the percentage (both in term of richness and density) of each trophic guild in the assemblage.

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

Furthermore, we performed a comparative morphological study to visualize the relative degree of ecomorphological resemblance between species from three of our four different regional faunas (i.e. Europe, North America and South America).

MATERIAL AND METHODS

Physical and biological data used in this study were collected in 48 sites of several headwater streams from different regions of Africa (AF; i.e. 10 sites in Gabonian streams), South America (SA; i.e. 15 sites in Bolivian streams), North America (NA; i.e. 8 sites in Middle Appalachian streams) and Europe (EU; i.e. 15 sites in French streams). Data for Africa were extracted from Ibañez *et al.* (2007a), data for South America from Tedesco *et al.* (2007) and Ibañez *et al.* (2007b), data for Europe from the French *Office National de l'Eau et des Milieux Aquatiques* (ONEMA) database, and data for North America from the Environmental Monitoring and Assessment Program (EMAP, U.S. EPA) records. A detailed description of the different methodologies employed in the four regions (including sampling and habitat description methods) is given in Ibañez *et al.* (2007a, b), Oberdorff *et al.* (2001), Reynolds *et al.* (2003) and Tedesco *et al.* (2007).

Environmental factors

Two geomorphological variables were used to describe local environmental conditions: Mean stream width (*STW*, m) and mean stream depth (*DEP*, m). Two variables were further used to describe the site spatial position within the upstream downstream gradient: Distance from sources (*DIS*, km) and surface area of the drainage basin upstream of the site (*SAD*, km²) (Table 1).

As testing convergence assumes that the same environments are present in the different zoogeographic regions studied, the 48 sites were chosen (as far as possible) to belong to morphologically similar headwater streams, to be similar in altitude, and to display a similar longitudinal gradient in habitat characteristics (Table 1).

Estimating local fish species richness and density

In France, USA and Bolivia, fishes were collected using electro-fishing during the dry season (Table 2). In Bolivia two fishing removals were performed for each site after having blocked the upstream and downstream edges of the sampled area by closing nets. This was nevertheless not the case for France and USA where sites were sampled using a one pass open sampling technique. Consequently, in all subsequent analyses, we used, concerning Bolivia, only results of the first pass to homogenize the sampling effort in these three regions. Concerning Africa, fish were also collected during the dry season but using the ichthyotoxin (rotenone) sampling method (as water conductivity was too low to employ electro-fishing). Although this last sampling technique is not fully comparable to electro-fishing, it usually gives comparable estimates of assemblage species richness (Glowacki & Penczak 2005). We thus combined these data with those obtained for the three other regions when analyzing the species richness and the percentage of each trophic guild (in term of richness) present in the assemblage (Tables 1 and 3).

Defining fish trophic guilds

Species trophic traits of the four continents were collected from the literature and coded similarly. Based on its principal adult food, each species was assigned into one of the four trophic groups: invertivores (INV), omnivores (OMN), herbivores/detritivores (HERB) and piscivores (PIS) as indicated by the literature (Oberdorff *et al.* 2002, Ibañez *et al.* 2007a,b, Tedesco *et al.* 2007, Goldstein & Simon 1999), supplemented with information provided in *Fishbase*: <http://www.fishbase.org> (Table 3).

Defining morphological traits

We recorded nine morphological traits, based on earlier functional interpretations, and providing information on different aspects of the species niche that are relevant for co-existence in the local assemblage by differentiation in local habitat use (Tables 4 and 5). Two of the measured morphological traits were converted in % of standard length in order to minimize the influence of body size. For French species we used data compiled in Pont *et al.* (1992) and Lanoiselée (2004), supplemented with information provided in *Fishbase*: <http://www.fishbase.org>. For North American species we used data from Lee *et al.* (1980) and our own measurements made on several species belonging to the ichthyological collection of the Muséum National d'Histoire Naturelle, Paris, France (see appendix 1 for details). For Bolivian species the morphological variables were measured on individuals captured in the upper Rio Chipiriri river catchment of the Bolivian Amazon (Ibañez *et al.* 2007b, Tedesco *et al.* 2007). As most of the data concerning African species were missing, African species were not included in the analysis.

Statistical analyses

Species richness, species density (number of individuals/m²), species body size and all environmental variables were log transformed prior to analysis. Arcsine square root transformations were conducted on all ecological variables that were percentages (i.e. trophic guilds and morphological variables). Normality of all variables was ensured prior to analyses.

Site-scale convergence was first analyzed by testing the respective effects of physical habitat and zoogeographic regions on fish assemblage structure, where a comparable effect of physical habitat within regions indicating convergence (Schluter 1986, Oberdorff *et al.* 1997, Lamouroux *et al.* 2002). We used the first principal component of a PCA performed on the four environmental variables (log-transformed) as a proxy for environment (PC1) providing a rough characterization of longitudinal changes in habitat characteristics (only PC1 was retained as being the only axis having an eigenvalue ≥ 1). We then tested for assemblage-level convergence across continents by using generalized linear models (GLM), examining how PC1 and zoogeographic regions (coded as a categorical variable; SA=1, AF=2, NA=3, EU=4) influenced assemblage structure (i.e. the number of species, the total density of individuals and the percentage of each trophic guild in the assemblage). Following Oberdorff *et al.* 1997 and Lamouroux *et al.* (2002) convergence was indicated by (i) a significant effect of the habitat variable (PC1) on the dependent biological variable, and (ii) the lack of a significant interaction between PC1 and zoogeographic regions (i.e. slopes of the relationships between the biological variables and PC1 not statistically different across zoogeographic regions). A supplementary significant effect of zoogeographic regions in the full model highlights the potential influence of contemporary environments (e.g. climate/productivity), historical contingencies and/or phylogenetic conservatism on the relationships.

We assessed the degree of overall ecomorphological resemblance between fish species from the different regional faunas by carrying out a principal components analysis (PCA) to

visualize species morphological characters from the different regional fish assemblages. Only fish assemblages from Europe, North America and South America were included in the analysis as morphological data concerning African fishes were not presently available. Owing to the peculiar characteristics of the species *Anguilla anguilla* (Europe), *Synbranchus marmoratus* and *Gymnotus carapo* (South America), and their potential effect on the PCA (concentration of the species in the intersection of the axes), these three species were excluded from this analysis.

All statistical analyses were performed using SYSTAT® 12.

RESULTS

Each of the four zoogeographic regions was dominated by different families (Table 2) and a pairwise comparison of the percentage of common families between these regions generally shows low values: 0% for SA vs. EU or NA, 2.9% for AF vs. SA, 4.4% for AF vs. EU or NA and 29% for NA vs. EU.

Species morphology across zoogeographic regions

The first axis (PC1) of the PCA accounts for 36.3% of the ecomorphological variation and the second axis (PC2), accounts for a further 17.7% (Table 6). High PC1 scores were significantly associated to flatness index (FI), relative body depth (RBD), relative peduncle length (RPL), ratio of peduncle height on peduncle width (RPHW), ratio of the pectoral fin length on pectoral fin width (RPELW) and standard length (SL). PC2 was significantly related to morphological variables such as relative peduncle length (RPL) and ratio of caudal fin height on caudal fin width (RCHW) (Table 6). Figure 1 and Table 7 summarize results from the PCA. Tropical fish assemblages (South America) exhibit a wider spectrum of body shapes compared to other regions (North America and Europe) even if a general ecomorphological resemblance can be observed between the three regional assemblages (i.e.

all assemblages overlapped strongly in the morphospace, Figure 1). Following the first two PCA components, four main groups of species can be distinguished. The first one (upper right part of Figure 1; I) is constituted by small species with large pectoral and caudal fins (e.g. *Pygocentrus nattereri* (South America), *Etheostoma olmstedi* (North America) *Pungitius pungitius* (Europe)). The second one (upper left part of Figure 1; II) is constituted by species displaying a long caudal peduncle and a mouth orientation most often inferior or sub-terminal (e. g. *Barbatula barbatula* (Europe), *Rhinichthys cataractae* (North America), *Rineloricaria lanceolata* (South America)). The third one (lower left part of Figure 1; III) is constituted by large species (e.g. *Prochilodus nigricans* (South America), *Leuciscus cephalus* (Europe), *Salmo trutta* (North America)). Finally the fourth one (lower right part of Figure 1; IV) is constituted by species displaying a high flatness index, a high body depth and exhibiting a terminal or supra-terminal mouth (e.g. *Astyanax abramis* (South America), *Lepomis auritus* (North America)).

Assemblage structure along streams longitudinal gradient in four zoogeographic regions

Site species richness increases along the longitudinal gradient (PC1) and this increase was significantly convergent across the four zoogeographic regions (Table 8a). 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 zoogeographic regions, $P > 0.05$), species richness was overall significantly different between regions (zoogeographic effect strongly significant, $P < 0.001$), except between Africa and South America (Least Square Means difference = -0.078, $P > 0.05$ after Bonferroni adjustment) and between North America and Europe (LSM difference = 0.127, $P > 0.05$ after Bonferroni adjustment) (Table 8a). 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 longitudinal gradient (PC1) confirms convergent patterns for invertivores and omnivores (in term of percentage of richness) in the four regions (Table 8a) with a significant overall effect of zoogeographic regions (zoogeographic effect strongly significant, $P < 0.001$) except between North America and Europe (Least Square Mean pairwise differences = 0.09, $P > 0.05$ and = -0.09, $P > 0.05$ for invertivores and omnivores respectively, after Bonferroni adjustment). The percentage of invertivores decreased along the longitudinal gradient while the percentage of omnivores increased, invertivores being more represented in North American and European streams while omnivores dominated the assemblage in South American and African ones (Figure 2a). However there was no convergent pattern for herbivores/detritivores or piscivores among the four regions (Table 8a), but a significant overall effect of zoogeographic regions (zoogeographic effect strongly significant, $P < 0.001$) except between North America and Europe (Least Square Mean pairwise differences = 0.001, $P > 0.05$ and 0.001, $P > 0.05$ for herbivores/detritivores and piscivores respectively, after Bonferroni adjustment) where these trophic guilds are, in fact, virtually absent from the assemblages (Figure 2a).

The same analysis performed on assemblage trophic guilds, but using this time, species densities instead of species richness (only SA, NA and EU were analyzed), gives qualitatively similar results concerning the percentages of each assemblage trophic guild (Table 8b and Figure 2b). In return, no significant convergent pattern was found concerning the variation of total fish density along the longitudinal gradient even if the general tendency is a slight decrease of density along the gradient for the three regions. Total densities were statistically similar between EU and SA (Least Square Mean pairwise differences = -0.155, $P > 0.05$), but significantly lower for NA compared to EU (Least Square Mean pairwise

differences=-0.604, $P<0.0001$) and SA (Least Square Mean pairwise differences=-0.759, $P<0.0001$).

DISCUSSION

Phylogeny

Similarities in assemblage structure across zoogeographic regions 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 common families between the four regions varied from 0 for SA vs. EU or NA to 29% for NA vs. EU. Then, even if the studied faunas cannot be considered totally independent (particularly NA and EU) we can be confident that phylogenetic constraint will not be a strong factor affecting our results.

Morphological comparison

As pictured in Figure 1 and Table 7, we observed broad resemblance in species ecomorphology between the three zoogeographic regions analyzed. Indeed, all assemblages greatly overlapped in our PCA multivariate space. The divergences noticed were observed for very few species, specific to each of the three zoogeographic regions, but mainly from the South American one. For this latter region, the fish assemblages presented a higher degree of morphological specialization (i.e. a greater morphological variance) compared to the temperate ones. These results are similar to the ones found by Strauss (1987) and Winemiller (1992) who analyzed ecomorphological characteristics of freshwater fish assemblages from different regions around the world and who found that, despite a greater morphological diversification in tropical than in temperate stream fish assemblages, they were overall fundamentally similar.

Comparison of fish assemblage richness and structure across zoogeographic regions

Changes in local assemblage richness have been previously noted along the longitudinal gradient of streams worldwide, species richness usually increasing along this gradient. This increase is often attributed to a downstream increase in habitat size, habitat diversity, or both (see Terejina Garro 2005 for a review). Some authors have further used different ecological attributes of species (i.e. reproductive, trophic or morphological traits) to explain assemblage structure along the longitudinal gradient of streams or rivers (Angermeier & Karr 1983; Oberdorff *et al.* 1993, 2002; M  rigoux *et al.* 1998; Goldstein & Meador 2004; Iba  ez *et al.* 2007a. For example, Oberdorff *et al.* (1993, 2002) and Iba  ez *et al.* (2007a) working respectively on temperate and tropical streams, have shown longitudinal trends in fish trophic groups (i.e. a transition from invertivorous to omnivorous and piscivorous guilds from upstream to downstream areas). Our study confirms such trends and goes a step further by formally revealing convergent longitudinal patterns in fish assemblage richness and trophic structure between streams of four continents. Specifically, assemblage richness tended to increase along the streams longitudinal gradient and the percentage of invertivores tended to significantly decrease along the gradient with a parallel significant increase of the percentage of omnivores. In other words, common environmental constraints seem to influence food availability within streams, which leads to trophic constraints on assemblages and ultimately to trophic guilds proportionality. However, we found no convergent pattern for herbivorous/detritivorous and piscivorous guilds among stream longitudinal gradient of temperate and tropical streams. In fact, herbivores/detritivores and piscivores were absent of the sites sampled in European and North American streams and did not display any particular tendency along the longitudinal continuum of African and South American streams. This last result could relate to the fact that a general convergent pattern can be modified by abiotic

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. One version of the energy hypothesis (Wright 1983) proposes that limits to diversity (in term of number of species and functional guilds) are set by the amount of energy flowing through the food web (e.g. herbivore diversity is limited by primary production, and so on up the food chain). Following this hypothesis and every thing else being equal, an increase in energy availability should thus lead to a significant increase of specialist and top predator species (Abrams 1995, Srivastava & Lawton 1998). Temperature and solar energy being higher in the tropics than in temperate areas, we can expect a higher trophic energy input in tropicals streams compared to temperate ones. Previous studies analysing fish assemblage structure in tropical streams seem to support this hypothesis (Ibañez *et al.* 2007b, Tedesco *et al.* 2007). This could explain, independently of any other environmental constraint, the presence of herbivorous/detritivorous and piscivorous guilds in the African and South American sites studied as well as their absence in the European and North American ones.

Our observations of species trophic traits along the streams longitudinal gradient were also consistent with the predictions provided by the theoretical framework of the river continuum concept (RCC) (Vannote *et al.* 1980) which suggests a longitudinal progression in fish trophic guilds that begins upstream with generalized invertivores and ends downstream with omnivores, detritivores, herbivores and piscivores (Schlosser 1987, Oberdorff *et al.* 1993, 2002). The data analyzed also show that after factoring out the longitudinal gradient effect, tropical streams are still more species rich than their European or North American counterparts. Part of the reason for this observed trend, independent of contemporary climate, may lies in Pleistocene events where massive extinctions 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 related, at least partly, to regional richness (Hugueny & 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. A potential explanation for this result might relate to the strong insularity of the streams studied (headwater streams) preventing most of immigration processes from downstream areas (Taylor & Warren 2001).

Whatever the zoogeographic region considered, we found no significant patterns in sites total fish density along streams longitudinal continuum. However, this result should be taken with great caution and difficult to discuss further, since the one-pass electrofishing sampling technique usually poorly estimates the total abundance of species (contrary to species relative abundances) within a site (Angermeier & Smogor 1995, Pusey *et al.* 1998).

We also noticed that the representation of the different trophic guilds was not proportional among assemblages in our different zoogeographic regions. Invertivores (both in term of percentage of richness and percentage of density) were more represented along the longitudinal gradient of temperate streams while omnivores, herbivores/detritivores and piscivores were more represented along the longitudinal gradient of tropical streams. This result is in agreement with the one obtained by Winemiller (1992) and potentially confirms the possible effect of higher trophic energy input (resources available) and subsequent potential longer food webs (based on the general supposition that productive systems support more feeding links; but see Vander Zanden & Fetzer 2007) in tropical (higher trophic energy input) compared to temperate streams (lower trophic energy input).

In a more applied context, a vast literature has been dedicated to the development of regionally adapted biological indicators for the assessment of streams and rivers integrity on different continents (see Hughes and Oberdorff 1999, Karr and Chu 2000 for review). These biological indicators usually follow the methodology of the index of biotic integrity (IBI) first formulated by Karr (1981) for use in Midwestern USA streams, and which 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 allows the comparison of assemblages extracted from different species pools, which certainly contributes to explain the development of this type of index outside its original area. However, the application of IBIs worldwide implies an independent evolution of species with similar ecological characteristics (ecological guilds) in similar environments in different regions. By formally identifying, to a substantial degree, convergent patterns in stream assemblage richness and structure in comparable environments of different zoogeographic regions, our study provides support for the use of such indicators worldwide.

REFERENCES

- Angermeier, P. L. and R. A. Smogor. 1995. Estimating number of species and relative abundances in stream-fish communities: effects of sampling effort and discontinuous spatial distributions. *Canadian Journal of Fisheries and Aquatic Sciences* **52**: 936-949.
- Abrams, P. A. 1995. Monotonic or unimodal diversity-productivity gradients: what does competition theory predict? *Ecology* **76**: 2019-2027.
- Angermeier, P. L. and J. R. Karr. 1983. Fish communities along environmental gradients in a system of tropical streams. *Environmental Biology of Fishes* **9**: 117-135.

- Ben-Moshe, A., T. Dayan, and D. Simberloff. 2001. Convergence in morphological patterns and community organization between Old and New World rodent guilds. *American Naturalist* **158**:484-495.
- Gatz A. J. 1979. Ecological morphology of freshwater stream fishes. *Tulane Studies in Zoology and Botany* **21**: 91-124.
- Glowacki L. and T. Penczak 2005. Species richness estimators applied to fish in a small tropical river sampled by conventional methods and rotenone. *Aquatic Living Resources* **18**:159-168.
- Goldstein, R. M., and T. P. Simon. 1999. Toward a united definition of guild structure for feeding ecology of North American freshwater fishes. Pages 123-202 *in* T. P. Simon, editor. *Assessing the sustainability and biological integrity of water resource quality using fish communities*. CRC Press, Boca Raton, Florida.
- Goldstein, R. M., and M. R. Meador. 2004. Comparisons of fish species traits from small streams to large rivers. *Transactions of the American Fisheries Society* **133**:971-983.
- Griffiths, D. 1997. Local and regional species richness in north American lacustrine fish. *Journal of Animal Ecology* **66**: 49-56.
- Guégan, J. F., S. Lek and T. Oberdorff. 1998. Energy availability and habitat heterogeneity predict global riverine fish diversity. *Nature* **391**:382-384.
- Hawkins, B. A., R. Field, H. V. Cornell, D. J. Currie, J. F. Guégan, D. M. Kaufman, J. T. Kerr, G. G. Mittelbach, T. Oberdorff, E. E. Porter and J. R. G. Turner. 2003. Energy, water, and broad-scale geographic patterns of species richness. *Ecology* **84**: 3105-3117.
- Hoeinghaus, D. J., K. O. Winemiller and J. S. Birnbaum. 2007. Local and regional determinants of stream fish assemblage structure: inferences based on taxonomic vs. functional groups. *Journal of Biogeography* **34**: 324-338.

- Hughes, R. M., and T. Oberdorff. 1999. Applications of IBI concepts and metrics to waters outside the United States and Canada. Pages 79-93 in T. P. Simon, editor. Assessing the sustainability and biological integrity of water resource quality using fish communities. CRC Press, Boca Raton, Florida.
- Hugueny, B., and D. Paugy. 1995. Unsaturated fish communities in African rivers. *American Naturalist* **146**:162-169.
- Hugueny, B. and M. Pouilly. 1999. Morphological correlates of diet in an assemblage of West African freshwater fishes. *Journal of Fish Biology* **54**: 1310-1325.
- Ibañez, C., T. Oberdorff, G. Teugels, V. Momononekene, S. Lavoué, Y. Fermon, D. Paugy and A. Kamdem Toham. 2007a. Fish assemblages structure and function along environmental gradients in rivers of Gabon (Africa). *Ecology of freshwater fish* **16**: 315-334.
- Ibañez, C., P. A. Tedesco, R. Bigorne, B. Hugueny, M. Pouilly, C. Zepita, J. P. Zubieta and T. Oberdorff. 2007b. Dietary-morphological relationships in fish assemblages of small forested streams of the Bolivian Amazon. *Aquatic Living Resources* **20**: 131-142.
- Irz, P., C. Argillier and T. Oberdorff. 2004. Native and introduced fish species richness in French lakes: local and regional influences. *Global Ecology and Biogeography* **13**: 335-344.
- Irz P., F. Michonneau, T. Oberdorff, T. R. Whittier, N. Lamouroux, D. Mouillot and C. Argillier. 2007. Fish community comparisons along environmental gradients in lakes of France and Northeast USA. *Global Ecology and Biogeography* **16**:350-366.
- Karr, J. R. 1981. Assessment of biotic integrity using fish communities. *Fisheries* **6**:21-27.
- Karr, J. R., and E. W. Chu. 2000. Sustaining living rivers. *Hydrobiologia* **422**:1-14.

- Lamouroux, N., N. L. Poff, and P. L. Angermeier. 2002. Intercontinental convergence of stream fish community traits along geomorphic and hydraulic gradients. *Ecology* **83**:1792-1807.
- Lanoiselée, C. 2004. Diversité fonctionnelle des communautés de poissons de plans d'eau. Mémoire de DEA "Écologie des systèmes continentaux". Université Paul Sabatier, Toulouse, France.
- Lawton, J. H. 1999. Are there general laws in ecology? *Oikos* **84**:177-192.
- Losos, J. B., T. R. Jackman, A. Larson, K. de Queiroz, and L. Rodriguez-Schettino. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. *Science* **279**:2115-2118.
- Mahon, R. 1984. Divergent structure in fish taxocenes of north temperate streams. *Canadian Journal of Fisheries and Aquatic Sciences* **41**:330-350.
- Matthews, W. J. 1998. Patterns in freshwater fish ecology, 2nd edition. Chapman & Hall, New York.
- Melville J., L. J. Harmon and J. B. Losos. 2006. Intercontinental community convergence of ecology and morphology in desert lizards. *Proceedings of the Royal Society (B)* **273**: 557-563.
- Mérigoux, S., D. Ponton, and B. de Mérona. 1998. Fish richness and species-habitat relationships in two coastal streams of French Guiana, South America. *Environmental Biology of Fishes* **51**: 25-39.
- Oberdorff, T., E. Guilbert and, J. C. Lucchetta. 1993. Patterns of fish species richness in the Seine River basin, France. *Hydrobiologia* **259**: 157-167.
- Oberdorff T., J. F. Guégan and B. Hugueny B. 1995. Global scale patterns in freshwater fish species diversity. *Ecography* **18**: 345-352.

- Oberdorff, T., B. Hugueny, and J.-F. Guégan. 1997. Is there an influence of historical events on contemporary fish species richness in rivers? Comparisons between Western Europe and North America. *Journal of Biogeography* **24**:461-467.
- Oberdorff, T., B. Hugueny, A. Compin, and D. Belkessam. 1998. Non-interactive fish communities in the coastal streams of North-western France. *Journal of Animal Ecology* **67**:472-484.
- Oberdorff T., D. Pont, B. Hugueny and D. Chessel. 2001. A probabilistic model characterizing riverine fish communities of French rivers: a framework for environmental assessment. *Freshwater Biology* **46**: 399-415.
- Oberdorff T., D. Pont, B. Hugueny and J. P. Porcher. 2002. Development and validation of a fish-based index (FBI) for the assessment of rivers "health" in France. *Freshwater Biology* **47**:1720-1735.
- Orians, G. H., and R. T. Paine. 1983. Convergent evolution at the community level. Pages 431–458 in D. J. Futuyma and M. Slatkin, editors. *Coevolution*. Sinauer, Sunderland.
- Piet, G. 1998. Ecomorphology of a size-structured tropical freshwater fish community. *Environmental Biology of Fishes* **51**: 67-86.
- Poff, N. L. 1997. Landscape filters and species traits: Towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* **16**:391-409.
- Pont, D., B. de Mérona and P. Boët. 1992. Signification des échelles spatio-temporelles dans la variabilité des peuplements piscicoles des grands cours d'eau. Rapport - Programme Interdisciplinaire de recherche sur l'Environnement "Facteurs de l'environnement, utilisation de l'espace et structuration spatio-temporelle des peuplements piscicoles". 133pp.

- Price, T., I. J. Lovette, E. Bermingham, H. L. Gibbs, and A. D. Richman. 2000. The imprint of history on communities of North American and Asian warblers. *American Naturalist* **156**:354-367.
- Pusey, B. J., M. J. Kennard, J. M. Arthur, and A. H. Arthington. 1998. Quantitative sampling of stream fish assemblages: single vs multiple-pass electrofishing. *Australian Journal of Ecology* **23**: 365-374.
- Reynolds, L., A. T. Herlihy, P. R. Kaufmann, S. V. Gregory, and R. M. Hughes. 2003. Electrofishing effort requirements for assessing species richness and biotic integrity in Western Oregon streams. *North American Journal of Fisheries Management* **23**: 450-461.
- Ricklefs, R. E., and D. Schluter. 1993. Species diversity: Regional and historical influences. Pages 350-363 in R. E. Ricklefs and D. Schluter, editors. *Species diversity in ecological communities*. The University of Chicago Press, Chicago.
- Schlosser, I. J. 1982. Fish community structure and function along two habitat gradients in a headwater stream. *Ecological Monographs* **52**:395-414.
- Schlosser, I. J. 1987. A conceptual framework for fish communities in small warmwater streams. Pages 17-24 in W. J. Matthews and D. C. Heins, editors. *Community and evolutionary ecology in North American stream fishes*. University of Oklahoma Press, Norman.
- Schluter, D. 1986. Tests for similarity and convergence of finch communities. *Ecology* **67**:1073-1085.
- Srivastava, D. S., and J. H. Lawton. 1998. Why more productive sites have more species: an experimental test of theory using tree-hole communities. *American Naturalist* **152**: 510-529.

- Stephens, P. R., and J. J. Wiens. 2004. Convergence, divergence, and homogenization in the ecological structure of Emydid turtle communities: the effect of phylogeny and dispersal. *American Naturalist* **164**:244-254.
- Strauss, R. E. 1987. The importance of phylogenetic constraints in comparisons of morphological structure among fish assemblages. In *Community and evolutionary ecology of North American stream fishes* (eds. W. J. Matthews and D. C. Heins). University of Oklahoma Press, Norman, USA, pp. 136-143.
- Taylor, C. M. and M. L. Warren Jr. 2001. Dynamics in species composition of stream fish assemblages: environmental variability and nested subsets. *Ecology* **82**: 2320-2330.
- Tedesco P., T. Oberdorff, C. A. Lasso, M. Zapata and B. Hugueny. 2005. Evidence of history in explaining diversity patterns in tropical riverine fish. *Journal of Biogeography* **32**: 1899-1907.
- Tedesco P., C. Ibañez, R. Bigorne, R. Camacho, E. Goitia, B. Hugueny, M. Maldonado, N. Moya, M. Rivero, S. Tomanova, J. P. Zubieta and T. Oberdorff. 2007. Local scale species-energy relationships in tropical riverine fish assemblages of some forested streams of the Bolivian Amazon. *CR Biologies* **330**: 255-264.
- Tejerina Garro F. L., M. Maldonado, C. Ibañez, D. Pont, N. Roset & T. Oberdorff. 2005. Distinguishing the respective effects of natural and anthropogenic environmental changes on riverine fish assemblages: a framework for ecological assessment of rivers. *Brazilian Archives of Biology and Technology* **48**: 91-108.
- Usseglio-Polatera, P., M. Bournaud, P. Richoux and H. Tachet. 2000. Biological and ecological traits of benthic freshwater macroinvertebrates: relationships and definition of groups with similar traits. *Freshwater Biology* **43**: 175-2005.
- Vander Zanden, M. J., and W. W. Fetzer. 2007. Global patterns of aquatic food chain length. *Oikos* **8**:1378-1388.

- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**: 130-137.
- Verdu, M., J. A. Barron-Sevilla, A. Valiente-Banuet, N. Flores-Hernandez, and P. Garcia-Fayos. 2002. Mexical plant phenology: is it similar to Mediterranean communities? *Botanical Journal of the Linnean Society* **138**:297-303.
- Watson, D. J. and E. K. Balon. 1984. Ecomorphological analysis of fish taxocenes in rainforest stream of northern Borneo. *Journal of Fish Biology* **25**: 371-384.
- Winemiller, K. O. 1991. Ecomorphological diversification in lowland freshwater fish assemblages from 5 biotic regions. *Ecological Monographs* **61**:343-365.
- Winemiller, K. O. 1992. Ecomorphology of freshwater fishes. *National Geographic Research & Exploration* **8**:308-327.
- Wright D. H. 1983. Species-energy theory: an extension of species-area theory. *Oikos* **41**: 496-506.

FIGURE & TABLE LEGENDS

Fig. 1. Plot of the first two CP axes resulting from analysis of log-transformed morphological variables. Points from each region are enclosed by polygons. See Table 2 for species code and Table 4 for morphological variables code.

Fig. 2. Relationships between each assemblage trait analyzed and stream longitudinal gradient described by PC1 (see methods). Relationships are provided for sites of Europe (France, $n = 15$), North American (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 species density data (data were available only for Europe, North America and South America).

Table 1. Mean values of environmental variables for the 48 sampled sites (see text for variable codes). Also given are sites species richness, sites total density of individuals, sites number of individuals and sites regional species richness (species richness of the whole river basin).

Table 2. Total species list for the four zoogeographic regions.

Table 3. Presence-absence of species and their trophic traits in each of the 48 sites analyzed.

Table 4. Description of species traits and the functions they describe.

Table 5. Mean values of the nine morphological attributes. See Table 4 for variable codes. All values are log-transformed except MP (categorical variable, see Table 4).

Table 6. Results of the principal components analysis visualizing species morphological characters from the different regional fish assemblages. Only fish assemblages from Europe, North American and South America were included.

Table 7. Some examples of species (and associated morphological traits) characterizing the four groups defined by the first two PCA components.

Table 8. Results of covariance models tested in sites of France, USA, Gabon and Bolivia. Models predict the value of each dependent variable from the position of sites along the longitudinal gradient (represented by PC1, used as a covariate) and zoogeographic regions (used as a categorical variable). “PC1 effect” indicates whether the effect of PC1 is significant, “ZR effect” indicates whether the effect of zoogeographic regions is significant, and “PC1xZR effect” indicates whether the slopes of the relationships between the dependent variables and PC1 are significantly different (or not) across zoogeographic regions. Values in bold are statistically significant. (a) using species richness data and (b) using species densities (in this latter case only streams from France, USA and Bolivia are analyzed).

Table 1

Continent	Country	Code	DIS (Km)	SAD (Km ²)	DEPTH (m)	WIDTH (m)	Elevation (m)	Area sampled (m ²)	Local species richness	Number of individuals	Regional species richness
South america	Bolivia	SA1	2	1.5	0.39	6.04	250	241.78	21	220	>65
South america	Bolivia	SA2	10	10.5	0.29	6.93	250	270.08	21	279	>65
South america	Bolivia	SA3	8	12	0.27	7.27	250	232.67	17	260	>65
South america	Bolivia	SA4	6	8	0.15	9.40	250	516.06	22	269	>65
South america	Bolivia	SA5	4	4.5	0.34	8.97	250	289.23	18	178	>65
South america	Bolivia	SA6	11	19	0.36	9.70	250	273.54	17	155	>65
South america	Bolivia	SA7	7.5	8	0.42	7.25	250	163.85	14	359	>65
South america	Bolivia	SA8	9	13	0.33	8.94	250	281.47	21	170	>65
South america	Bolivia	SA9	4	6	0.29	6.73	250	309.58	17	418	>65
South america	Bolivia	SA10	4	7	0.14	3.75	250	99.38	11	309	>65
South america	Bolivia	SA11	2	5	0.26	6.83	250	336.13	20	448	>65
South america	Bolivia	SA12	2	3.5	0.36	7.38	250	169.69	19	618	>65
South america	Bolivia	SA13	4.5	7.5	0.26	6.69	250	300.23	16	492	>65
South america	Bolivia	SA14	2	0.8	0.43	4.64	250	125.28	12	83	>65
South america	Bolivia	SA15	4	3.5	0.16	3.94	250	110.32	17	148	>65
Europe	France	EU1	6	21	0.25	3.72	225	438.96	6	544	51
Europe	France	EU2	4	11	0.23	2.41	150	313.3	2	132	23
Europe	France	EU3	12	41	0.23	4.85	175	776	6	328	51
Europe	France	EU4	13	70	0.44	5.21	174	651.25	7	713	11
Europe	France	EU5	17	115	0.43	6.45	215	1006.2	5	1137	14
Europe	France	EU6	18	110	0.52	4.43	123	655.64	8	257	51
Europe	France	EU7	7	13	0.34	4.45	150	600.75	4	272	51
Europe	France	EU8	11	37	0.22	4.73	120	562.87	5	626	23
Europe	France	EU9	6	26	0.21	2.52	190	335.16	5	299	11
Europe	France	EU10	16	86	0.41	6.82	75	791.12	8	204	11
Europe	France	EU11	9	29	0.28	4.23	50	520.29	5	358	17
Europe	France	EU12	17	89	0.33	7.35	45	529.2	7	298	18
Europe	France	EU13	5	7	0.15	2.81	245	362.49	4	412	16
Europe	France	EU14	5	10	0.32	3.35	60	402	3	618	11
Europe	France	EU15	15	75	0.15	4.99	55	673.65	6	1281	16
North america	United States	NA1	5	10.7	0.22	4.37	428	655.50	4	198	92
North america	United States	NA2	2	2.9	0.17	4.05	462	607.50	2	30	92
North america	United States	NA3	12.3	48.5	0.26	8.54	213	1280.25	11	359	92
North america	United States	NA4	13.8	41.7	0.12	4.36	365	653.25	10	252	61
North america	United States	NA5	8.1	34.7	0.33	8.00	308	1200.45	5	315	61
North america	United States	NA6	22.5	46.2	0.43	9.65	316	1448.10	10	106	61
North america	United States	NA7	10.05	24.5	0.2	5.9	410	885.59	11	430	65
North america	United States	NA8	0.88	1.8	0.19	3.45	482	516.96	4	71	50
Africa	Gabon	AF1	1	1.6	0.3	1	510		8		76
Africa	Gabon	AF2	0.9	1.2	0.2	1	490		16		76
Africa	Gabon	AF3	3	5	0.3	1.5	460		5		76
Africa	Gabon	AF4	2	4	0.2	1	695		10		76
Africa	Gabon	AF5	14	65	0.35	2.5	365		16		76
Africa	Gabon	AF6	3	9	0.2	1.5	535		6		76
Africa	Gabon	AF7	2	4	0.3	3	522		6		76
Africa	Gabon	AF8	3	7.1	0.6	2	536		27		76
Africa	Gabon	AF9	2	5.6	0.2	1.5	493		15		76
Africa	Gabon	AF10	6	15	0.3	3	325		17		76
Standard deviation			5.4	29.77	0.1	2.51	150				

Table 2

Africa - Gabon			South America - Bolivia		
Order and family	genera and species		Order and family	genera and species	Code
Characiformes			Beloniformes		
Alestiidae	<i>Alestes schoutedeni</i>	Boulenger, 1912	Belontiidae	<i>Potamorhaphis eigenmanni</i>	Miranda-Ribeiro, 1915 SAPOE
	<i>Brycinus kingsleyae</i>	(Günther, 1896)	Characiformes		
	<i>Brycinus longipinnis</i>	(Günther, 1864)	Anostomidae	<i>Leporinus striatus</i>	Kner, 1858 SALES
Citharinidae	<i>Nealebias trewavasae</i>	Poll & Gosse, 1963	Characidae	<i>Acestrorhynchus</i> sp.	SAACE
	<i>Nannocharax fasciatus</i>	Günther, 1867		<i>Astyanax</i> sp.	SAAST
	<i>Nannocharax parvus</i>	Pellegrin, 1906		<i>Astyanax abramis</i>	(Jenyns, 1842) SAASA
	<i>Nannocharax</i> sp.			<i>Astyanax lineatus</i>	(Perugia, 1891) SAASL
Hepsetidae	<i>Hepsetus odoe</i>	(Bloch, 1794)		<i>Characidium bolivianum</i>	Pearson, 1924 SACHB
Cyprinodontiformes				<i>Gephyrocharax chaparae</i>	Fowler, 1940 SAGEC
Apocheilidae	<i>Aphyosemion cameronense</i>	(Boulenger, 1903)		<i>Hemigrammus cf. belottii</i>	(Steindachner, 1882) SAHEB
	<i>Aphyosemion joergenscheeli</i>	Huber & Radda, 1977		<i>Hemigrammus cf. lunatus</i>	Durbin, 1918 SAHEL
	<i>Aphyosemion ocellatum</i>	Huber & Radda, 1977		<i>Hemibrycon</i> sp.	SAHEM
	<i>Aphyosemion</i> ssp.			<i>Moenkhausia oligalepis</i>	(Günther, 1864) SAMOO
	<i>Epiplatys neumanni</i>	Berkenkamp, 1993		<i>Phenacogaster pectinatus</i>	(Cope, 1870) SAPH
	<i>Fundulopanchax batesii</i>	(Boulenger, 1911)		<i>Serrapinnus</i> sp.	SASER
Poeciliidae	<i>Platiplocheilus terveri</i>	(Huber, 1981)		<i>Tytocharax cf. madeirae</i>	Fowler, 1913 SATYM
Cypriniformes			Curimatidae		
Cyprinidae	<i>Barbus brazzai</i>	Pellegrin, 1901		<i>Steindachnerina dobula</i>	(Günther, 1868) STSTD
	<i>Barbus campocanthus</i>	(Bleeker, 1863)		<i>Steindachnerina guentheri</i>	(Eigenmann & Eigenmann, 1889) SASTG
	<i>Barbus caudovittatus</i>	Boulenger, 1902		<i>Cyphocharax spilurops</i>	(Eigenmann & Eigenmann, 1889) SACYS
	<i>Barbus guirali</i>	Thomson, 1886	Erythrinidae	<i>Hoplias malabaricus</i>	(Bloch, 1794) SAHOM
	<i>Barbus holotaenia</i>	Boulenger, 1904	Gasteropelecidae	<i>Carnegiella myersi</i>	Fernandez-Yepez, 1950 SACAM
	<i>Barbus jae</i>	Boulenger, 1903	Lebiasinidae	<i>Pyrrhulina vittata</i>	Regan, 1912 SAPYV
	<i>Barbus prionacanthus</i>	Mahmet & Géry, 1982	Parodontidae	<i>Parodon cf. buckleyi</i>	Boulenger, 1887 SAPAB
	<i>Barbus</i> ssp.		Prochilodontidae	<i>Prochilodus nigricans</i>	Spix & Agassiz, 1829 SAPRN
	<i>Labeo annectens</i>	Boulenger, 1903	Gymnotiformes		
	<i>Opsaridium ubangense</i>	(Pellegrin, 1901)	Gymnotidae	<i>Gymnotus carapo</i>	Linnaeus, 1758 SAGYC
	<i>Raiamas buchholzi</i>	(Peters, 1876)	Perciformes		
Osteoglossiformes			Cichlidae	<i>Apistogramma</i> sp.	SAAPI
Mormyridae	<i>Brienomyrus hopkinsi</i>	Taverne & Thys van den Audenaerde, 1985		<i>Cichlasoma boliviense</i>	Kullander, 1983 SACIB
	<i>Brienomyrus kingsleyae kingsleyae</i>	(Günther, 1896)		<i>Crenicichla cf. semicincta</i>	Steindachner, 1892 SACRS
	<i>Brienomyrus sphecodes</i>	(Savauge, 1879)		<i>Mikrogeophagus altispinosus</i>	(Haseman, 1911) SAMIA
	<i>Marcusenius moorii</i>	(Günther, 1867)		<i>Sotonoperca jurupari</i>	(Heckel, 1840) SASAJ
	<i>Mastacembelus</i> ssp.		Siluriformes		
	<i>Oxymormyrus sanctirostris</i>	(Günther, 1867)	Callichthyidae	<i>Corydoras</i> spp.	SACOR
	<i>Paramormyrops gabonensis</i>	Taverne, Thys van den Audenaerde & Heymer, 1977		<i>Callichthys callichthys</i>	(Linnaeus, 1758) SACAC
	<i>Petrocephalus simus</i>	Savauge, 1879	Heptapteridae	<i>Imparfinis cf. stictonotus</i>	(Fowler, 1940) SAIMS
Perciformes				<i>Pimelodella</i> sp.	SAPIM
Anabantidae	<i>Microctenopoma nanum</i>	(Günther, 1896)		<i>Rhamdia quelen</i>	(Quoy & Gaimard, 1824) SARHQ
Channidae	<i>Parachanna</i> sp.		Loricariidae	<i>Ancistrus</i> sp.	SAANC
Cichlidae	<i>Chromidotilapia kingsleyae</i>	Boulenger, 1898		<i>Hypostomus gr. cochliodon</i>	Kner, 1854 SAHYC
	<i>Hemichromis fasciatus</i>	Peters, 1857		<i>Rineloricaria lanceolata</i>	(Günther, 1868) SARIL
	<i>Divandu albimarginatus</i>	Lamboy & Snocks, 2000	Pseudopimelodidae	<i>Microglanis</i> sp.	SAMIC
	<i>Parananochromis gabonicus</i>	(Trewavas, 1975)	Trichomycteridae	<i>Ituglanis cf. amazonicus</i>	(Steindachner, 1882) SAITA
	<i>Parananochromis longirostris</i>	(Boulenger, 1903)	Synbranchiformes		
	<i>Pelvicachromis</i> ssp.		Synbranchidae	<i>Synbranchus marmoratus</i>	Bloch, 1795 SASYM
Siluriformes					
Amphiliidae	<i>Amphilius baudoni</i>	Pellegrin, 1928			
	<i>Amphilius brevis</i>	Boulenger, 1902			
	<i>Amphilius longirostris</i>	(Boulenger, 1901)			
	<i>Amphilius pulcher</i>	Pellegrin, 1929			
	<i>Phractura brevicauda</i>	Boulenger, 1911			
Bagridae	<i>Anaspidoglanis macrostoma</i>	(Pellegrin, 1909)			
	<i>Anaspidoglanis</i> ssp.				
	<i>Parauchenoglanis balayi</i>	(Savauge, 1879)			
	<i>Parauchenoglanis loennbergi</i>	Fowler, 1958			
	<i>Parauchenoglanis pantherinus</i>	(Pellegrin, 1929)			
	<i>Parauchenoglanis</i> ssp.				
Clariidae	<i>Clarias camerunensis</i>	Lönnberg, 1895			
	<i>Clarias goriepinus</i>	(Burchell, 1822)			
	<i>Clarias jaensis</i>	Boulenger, 1909			
	<i>Clarias longior</i>	Boulenger, 1907			
	<i>Clarias pachynema</i>	Boulenger, 1903			
	<i>Clarias platycephalus</i>	Boulenger, 1902			
Malapteruridae	<i>Malapterurus electricus</i>	(Gmelin, 1789)			
Mochokidae	<i>Synodontis albolineatus</i>	Pellegrin, 1924			
	<i>Synodontis batesii</i>	Boulenger, 1907			
Synbranchiformes					
Mastacembelidae	<i>Mastacembelus niger</i>	Savauge, 1879			

Table 2 (continuation)

North America - USA			Europe - France				
Order and family	genera and species		Code	Order and family	genera and species		Code
Cypriniformes				Anguilliformes			
Cyprinidae	<i>Camptostoma anomalum</i>	(Rafinesque, 1820)		Anguillidae	<i>Anguilla anguilla</i>	(Linnaeus, 1758)	EUANA
	<i>Clinostomus funduloides</i>	Girard, 1856	NACAA	Cypriniformes			
	<i>Exoglossum maxillingua</i>	(Lesueur, 1817)	NACLF	Cyprinidae	<i>Alburnoides bipunctatus</i>	(Bloch, 1782)	EUALB
	<i>Margariscus margarita</i>	(Cope, 1867)	NAEXM		<i>Gobio gobio</i>	(Linnaeus, 1758)	EUGOG
	<i>Rhinichthys atratulus</i>	(Hermann, 1804)	NAMAM		<i>Phoxinus phoxinus</i>	(Linnaeus, 1758)	EUPHP
	<i>Rhinichthys cataractae</i>	(Valenciennes, 1842)	NARHA		<i>Leuciscus cephalus</i>	(Linnaeus, 1758)	EULEC
	<i>Semotilus atromaculatus</i>	(Mitchill, 1818)	NARHC		<i>Rutilus rutilus</i>	(Linnaeus, 1758)	EURUT
	<i>Semotilus corporalis</i>	(Mitchill, 1817)	NASEA		Gasterosteiformes		
Catostomidae	<i>Catostomus commersonii</i>	(Lacepède, 1803)	NASEC	Gasterosteidae	<i>Gasterosteus aculeatus</i>	Linnaeus, 1758	EUGAA
	<i>Hypentelium nigricans</i>	(Lesueur, 1817)	NACAC		<i>Pungitius pungitius</i>	(Linnaeus, 1758)	EUPUP
			NAHYN	Perciformes			
Perciformes				Percidae			
Percidae	<i>Etheostoma flabellare</i>	Rafinesque, 1819		Percidae	<i>Perca fluviatilis</i>	Linnaeus, 1758	EUPEF
	<i>Etheostoma olmstedii</i>	Storer, 1842	NAETF		Salmoniformes		
Centrarchidae	<i>Lepomis auritus</i>	(Linnaeus, 1758)	NAETO	Salmonidae	<i>Salmo trutta</i>	Linnaeus, 1758	EUSAT
	<i>Lepomis gibbosus</i>	(Linnaeus, 1758)	NALEA		<i>Thymallus thymallus</i>	(Linnaeus, 1758)	EUTHT
	<i>Lepomis macrochirus</i>	Rafinesque, 1819	NALEG	Scorpaeniformes			
	<i>Lepomis megalotis</i>	Rafinesque, 1820	NALEM	Balitoridae	<i>Barbatula barbatula</i>	(Linnaeus, 1758)	EUBAB
Salmoniformes					Cottidae	<i>Cottus gobio</i>	Linnaeus, 1758
Salmonidae	<i>Salvelinus fontinalis</i>	(Mitchill, 1814)	NALEE				
	<i>Salmo trutta</i>	Linnaeus, 1758	NASAF				
Scorpaeniformes							
Cottidae	<i>Cottus bairdii</i>	Girard, 1850	NASAT				
	<i>Cottus cognatus</i>	Richardson, 1836	NACOB				
	<i>Cottus girardi</i>	Robins, 1961	NACOC				
Siluriformes							
Ictaluridae	<i>Noturus insignis</i>	(Richardson, 1836)	NANOI				

Table 3

Africa - Gabon												South America - Bolivia															North America - U.S.A.														
Species	AF1	AF2	AF3	AF4	AF5	AF6	AF7	AF8	AF9	AF10	TG	Species	SA1	SA2	SA3	SA4	SA5	SA6	SA7	SA8	SA9	SA10	SA11	SA12	SA13	SA14	SA15	TG	Species	NA1	NA2	NA3	NA4	NA5	NA6	NA7	NA8	TG			
<i>Alectes schultzei</i>											OMN	<i>Acestrotrichorus</i> sp.																PIS	<i>Campostoma ananadum</i>									OMN			
<i>Amphilius bairdii</i>											INV	<i>Ancistrus</i> spp.																IHER	<i>Catostomus commersonii</i>									OMN			
<i>Amphilius brevis</i>											INV	<i>Apistogramma</i> sp.																INV	<i>Clinostomus funduloides</i>									INV			
<i>Amphilius longirostris</i>											INV	<i>Astyanax abramis</i>																OMN	<i>Cottus bairdii</i>									INV			
<i>Amphilius pulcher</i>											INV	<i>Astyanax lineatus</i>																OMN	<i>Cottus cognatus</i>									INV			
<i>Anaspidoglanis macrystoma</i>											INV	<i>Astyanacinus</i> sp.																OMN	<i>Cottus girardi</i>									INV			
<i>Anaspidoglanis</i> ssp.											INV	<i>Callichthys callichthys</i>																INV	<i>Etheostoma flabellare</i>									INV			
<i>Aphyosemion camerunense</i>											INV	<i>Carnegiella myersi</i>																INV	<i>Etheostoma alvaresti</i>									INV			
<i>Aphyosemion joergense</i>											INV	<i>Characidium bolivianum</i>																INV	<i>Exocoelotomus maxilligius</i>									INV			
<i>Aphyosemion ocellatum</i>											INV	<i>Cichlasoma boliviense</i>																OMN	<i>Hypentelium nigricans</i>									OMN			
<i>Aphyosemion</i> ssp.											INV	<i>Corydoras</i> spp.																OMN	<i>Lepomis auratus</i>									INV			
<i>Barbus brazei</i>											INV	<i>Crenichthys cf. semicinctus</i>																OMN	<i>Lepomis gibbosus</i>									INV			
<i>Barbus camptocanthus</i>											INV	<i>Cyphocharax spilargyris</i>																IHER	<i>Lepomis macrochirus</i>									INV			
<i>Barbus caudovittatus</i>											INV	<i>Gephyrocharax chaparai</i>																INV	<i>Lepomis megalotis</i>									INV			
<i>Barbus guirali</i>											INV	<i>Gymnotus carapo</i>																PIS	<i>Margariscus margarita</i>									INV			
<i>Barbus holotaenia</i>											INV	<i>Hemigrammus cf. helatit</i>																OMN	<i>Noturus insignis</i>									INV			
<i>Barbus jae</i>											INV	<i>Hemigrammus cf. lunatus</i>																INV	<i>Rhinichthys atratulus</i>									INV			
<i>Barbus prionacanthus</i>											INV	<i>Hemibrycon</i> sp.																INV	<i>Rhinichthys cataractae</i>									INV			
<i>Barbus</i> ssp.											INV	<i>Hoplias malabaricus</i>																PIS	<i>Salvelinus fontinalis</i>									INV			
<i>Brienomyrus hopkinsi</i>											INV	<i>Hypostomus</i> gr. <i>cochlidodon</i>																IHER	<i>Salmo trutta</i>									INV			
<i>Brienomyrus kingleyae</i>											INV	<i>Imparfinis cf. stictionatus</i>																INV	<i>Semotilus atromaculatus</i>									INV			
<i>Brienomyrus sphickades</i>											INV	<i>Inglanis cf. amazonicus</i>																INV	<i>Semotilus corporalis</i>									INV			
<i>Brycinus kingleyae</i>											OMN	<i>Lepomis striatus</i>																OMN													
<i>Brycinus longipinnis</i>											OMN	<i>Mikrogeophagus altispinosus</i>																OMN													
<i>Chromidotilapia kingleyae</i>											OMN	<i>Microglanis</i> sp.																INV													
<i>Clarias camerunensis</i>											OMN	<i>Moenkhausia oligolepis</i>																INV													
<i>Clarias guirapinus</i>											OMN	<i>Parodon cf. buckleyi</i>																IHER													
<i>Clarias jacksoni</i>											OMN	<i>Phenacogaster pectinatus</i>																INV													
<i>Clarias longior</i>											OMN	<i>Pimelodella</i> spp.																INV													
<i>Clarias pachynema</i>											OMN	<i>Potamorhaphis eigenmanni</i>																INV													
<i>Clarias platycephalus</i>											OMN	<i>Pruchilodus nigricans</i>																IHER													
<i>Divandul albimarginatus</i>											OMN	<i>Pyrhulina vittata</i>																INV													
<i>Epiplatys nana</i>											INV	<i>Rhamdia quelen</i>																OMN													
<i>Fundulopanchax batesii</i>											INV	<i>Rineloricaria lanceolata</i>																HER													
<i>Hemichromis fasciatus</i>											PIS	<i>Satanoperca jurupari</i>																INV													
<i>Hepsetus odon</i>											PIS	<i>Serrapinnus</i> sp.																INV													
<i>Labeo annectens</i>											HER	<i>Steindachnerina dobula</i>																HER													
<i>Malapterurus electricus</i>											PIS	<i>Steindachnerina guentheri</i>																HER													
<i>Marcusenius moorii</i>											INV	<i>Synbranchius marmoratus</i>																PIS													
<i>Mastacembelus niger</i>											INV	<i>Tytochirus cf. maderiae</i>																INV													
<i>Mastacembelus</i> ssp.											INV																														
<i>Microcinipoma nana</i>											INV																														
<i>Mormyrops zanzibaricus</i>											INV																														
<i>Nannocharax fasciatus</i>											INV																														
<i>Nannocharax parvus</i>											INV																														
<i>Nannocharax</i> sp.											INV																														
<i>Neolebias trewavasae</i>											INV																														
<i>Opsaridium ubangense</i>											INV																														
<i>Parachanna</i> sp.											OMN																														
<i>Paramormyrops gabonensis</i>											INV																														
<i>Parananochromis gabonensis</i>											OMN																														
<i>Parananochromis longirostris</i>											OMN																														
<i>Parauchenoglanis balayi</i>											INV																														
<i>Parauchenoglanis guttatus</i>											INV																														
<i>Parauchenoglanis pantherinus</i>											INV																														
<i>Parauchenoglanis</i> ssp.																																									

Table 4

Description	Code	Function	Author
Standard length: Distance from the tip of the snout to the last vertebra	SL	No specific function, but could inform on physical habitat	Hugueny & Pouilly (1999), Gatz (1979), Piet (1998)
Relative body depth is the maximum body depth divided by the standard length	RBD	Hydrodynamics	Gatz (1979), Watson & Balon (1984)
Flatness index is the maximum body depth divided by the maximum body width	FI	Hydrodynamics	Gatz (1979), Watson & Balon (1984)
Relative peduncle length is the peduncle length divided by the standard length	RPL	Swimming speed and endurance	Gatz (1979), Mahon (1984)
Ratio of peduncle height on peduncle width	RPHW	Amplitude of swimming movements	Mahon (1984)
Ratio of caudal fin height on caudal fin width	RCHW	Swimming behavior: especially the amount of swimming	Gatz (1979), Watson & Balon (1984)
Ratio of the pectoral fin is estimated as a length to width ratio	RPELW	Ability to resist currents	Watson & Balon (1984)
Eye position is proportion of head depth measured at the middle of the eye which occurs below the middle of the eye	EP	Vertical habitat preferences	Watson & Balon (1984)
Orientation of the mouth: 1. supraternal, 2. terminal, 3. subterminal 4. inferior	MP	Method of food acquisition	Gatz (1979)

Table 5

Species	Code	SL	RBD	FI	RPL	RPHW	RCHW	RPELW	EP	MP
<i>Acestrorhynchus</i> sp.	SAACE	5.00	0.20	1.87	0.08	2.07	0.62	1.98	0.74	1
<i>Ancistrus</i> spp.	SAANC	4.42	0.20	0.69	0.29	2.25	0.90	2.06	0.83	4
<i>Apistogramma</i> sp.	SAAPI	3.44	0.34	2.03	0.14	4.22	2.17	2.52	0.74	2
<i>Astyanax abramis</i>	SAASA	4.30	0.37	2.73	0.10	3.40	0.92	2.25	0.78	2
<i>Astyanax lineatus</i>	SAASL	3.81	0.37	3.07	0.10	3.65	0.96	2.28	0.80	1
<i>Astyanacinus</i> sp.	SAAST	4.33	0.41	2.95	0.09	3.41	0.88	2.21	0.74	1
<i>Callichthys callichthys</i>	SACAC	4.28	0.24	0.99	0.06	3.34	0.98	1.29	0.83	2
<i>Carnegiella myersi</i>	SACAM	3.09	0.44	4.58	0.06	3.68	1.75	4.38	0.92	1
<i>Characidium bolivianum</i>	SACHB	3.97	0.22	1.69	0.16	2.72	1.19	2.17	0.83	2
<i>Cichlasoma boliviense</i>	SACIB	4.24	0.45	2.03	0.10	5.34	1.51	2.48	0.82	2
<i>Corydoras</i> spp.	SACOR	3.90	0.36	1.40	0.12	2.80	1.22	2.12	0.83	3
<i>Crenicichla cf. semicincta</i>	SACRS	4.55	0.21	1.50	0.12	3.24	1.49	1.78	0.83	2
<i>Cyphocharax spiluroopsis</i>	SACYS	4.26	0.37	2.27	0.11	2.67	0.99	2.29	0.73	1
<i>Gephyrocharax chaparae</i>	SAGEC	3.79	0.28	2.83	0.10	4.00	1.27	2.37	0.73	1
<i>Gymnotus carapo</i>	SAGYC	4.72	0.11	1.59	0.00	1.41	0.41	1.87	0.92	1
<i>Hemigrammus cf. belottii</i>	SAHEB	3.42	0.29	2.47	0.14	4.00	1.31	3.97	0.72	1
<i>Hemigrammus cf. lunatus</i>	SAHEL	3.20	0.33	2.91	0.10	2.98	1.32	3.35	0.68	1
<i>Hemibrycon</i> sp.	SAHEM	4.13	0.37	2.94	0.10	4.05	0.94	2.46	0.76	1
<i>Hoplias malabaricus</i>	SAHOM	4.88	0.20	1.31	0.12	3.29	1.07	2.76	0.87	1
<i>Hypostomus gr. cochliodon</i>	SAHYC	3.73	0.40	2.88	0.13	2.81	1.06	2.53	0.75	4
<i>Imparfinis cf. stictonotus</i>	SAIMS	3.59	0.17	1.21	0.18	4.22	1.97	2.50	0.82	2
<i>Ituglanis cf. amazonicus</i>	SAITA	3.86	0.13	1.33	0.17	5.57	0.84	1.40	1.68	2
<i>Leporinus striatus</i>	SALES	4.65	0.26	1.66	0.11	2.77	0.92	2.14	0.77	2
<i>Mikrogeophagus altispinosus</i>	SAMIA	4.07	0.44	2.28	0.14	3.27	1.20	2.42	0.74	2
<i>Microglanis</i> sp.	SAMIC	3.59	0.20	0.97	0.15	4.14	1.64	1.76	0.92	1
<i>Moenkhausia oligolepis</i>	SAMOO	3.93	0.43	2.92	0.08	3.59	0.90	2.71	0.75	1
<i>Parodon cf. buckleyi</i>	SAPAB	4.56	0.27	1.61	0.16	3.79	0.77	1.28	0.79	4
<i>Phenacogaster pectinatus</i>	SAPHP	3.57	0.35	3.35	0.07	4.40	1.37	3.40	0.72	1
<i>Pimelodella</i> spp.	SAPIM	4.48	0.18	1.36	0.19	2.75	1.80	1.88	0.92	2
<i>Potamorhaphis eigenmanni</i>	SAPOE	5.08	0.04	0.95	0.02	3.37	1.39	3.00	0.74	2
<i>Prochilodus nigricans</i>	SAPRN	5.11	0.33	2.08	0.13	3.02	0.67	2.24	0.61	2
<i>Pyrrhulina vittata</i>	SAPYV	3.34	0.26	1.92	0.16	3.17	1.60	3.07	0.73	1
<i>Rhamdia quelen</i>	SARHQ	4.78	0.19	1.19	0.19	3.57	1.08	1.76	0.89	2
<i>Rineloricaria lanceolata</i>	SARIL	4.40	0.09	0.69	0.52	0.42	1.27	2.01	0.83	4
<i>Satanoperca jurupari</i>	SASAJ	4.49	0.39	2.37	0.14	3.80	1.11	3.01	0.88	2
<i>Serrapinnus</i> sp.	SASER	3.33	0.35	2.92	0.10	3.91	0.87	1.49	0.75	2
<i>Steindachnerina dobula</i>	SASTD	4.56	0.31	1.95	0.13	2.88	0.91	2.12	0.75	3
<i>Steindachnerina guentheri</i>	SASTG	4.31	0.34	2.08	0.12	3.58	0.87	2.21	0.80	3
<i>Synbranchius marmoratus</i>	SASYM	5.32	0.00	1.20	0.00	0.00	0.00	0.00	0.89	1
<i>Tytocharax cf. madeirae</i>	SATYM	2.70	0.30	2.79	0.09	3.79	1.51	3.10	0.75	1
<i>Alburnoides bipunctatus</i>	EUALB	4.33	0.30	0.63	0.00	2.00	0.60	1.70	0.60	2
<i>Anguilla anguilla</i>	EUANA	6.34	0.10	1.14	0.18	2.50	21.80	1.10	0.70	1
<i>Barbatula barbatula</i>	EUBAB	3.83	0.35	1.28	0.38	2.53	2.34	3.23	0.36	4
<i>Cotus gobio</i>	EUCOG	3.92	0.23	1.15	0.15	2.50	1.67	1.88	0.84	2
<i>Gasterosteus aculeatus</i>	EUGAA	3.90	0.22	2.35	0.11	2.15	1.80	2.66	0.66	2
<i>Gobio gobio</i>	EUGOG	4.42	0.20	0.48	0.20	1.80	0.60	1.60	0.80	3
<i>Leuciscus cephalus</i>	EULEC	5.66	0.30	0.08	0.12	2.00	0.60	1.60	0.60	2
<i>Perca fluviatilis</i>	EUPEF	5.58	0.30	0.88	0.13	1.50	0.70	1.30	0.80	2
<i>Phoxinus phoxinus</i>	EUPHP	3.97	0.20	0.49	0.15	1.30	0.60	1.60	0.60	3
<i>Pungitius pungitius</i>	EUPUP	3.76	0.23	1.76	0.12	1.84	1.44	1.33	0.70	1
<i>Rutilus rutilus</i>	EURUT	4.66	0.30	0.47	0.18	1.90	0.60	1.70	0.60	2
<i>Salmo trutta</i>	EUSAT	5.26	0.20	0.50	0.19	2.60	0.50	1.50	0.70	2
<i>Thymallus thymallus</i>	EUTHT	5.34	0.19	1.63	0.17	2.61	0.77	2.09	0.66	3
<i>Camptostoma anomalum</i>	NACAA	4.07	0.21	1.57	0.24	3.65	0.92	2.50	0.57	3
<i>Catostomus commersonii</i>	NACAC	5.03	0.21	1.58	0.13	3.05	1.27	3.02	0.76	4
<i>Clinostomus funduloides</i>	NACLF	4.05	0.19	1.44	0.22	2.85	0.72	2.13	0.56	1
<i>Cottus bairdii</i>	NACOB	4.02	0.21	1.03	0.13	2.87	1.85	2.31	0.74	2
<i>Cottus cognatus</i>	NACOC	3.98	0.20	0.89	0.18	0.82	2.25	2.93	0.87	2
<i>Cottus girardi</i>	NACOG	5.43	0.18	0.80	0.06	3.11	1.14	0.86	0.81	2
<i>Etheostoma flabellare</i>	NAETF	3.70	0.18	1.42	0.21	4.01	1.21	2.03	0.77	3
<i>Etheostoma olmstedii</i>	NAETO	3.98	0.15	1.44	0.23	3.78	1.88	4.65	0.78	2
<i>Exoglossum maxillingua</i>	NAEXM	5.01	0.21	0.98	0.23	4.59	0.63	1.65	0.83	3
<i>Hypentelium nigricans</i>	NAHYN	5.66	0.15	1.06	0.15	2.08	0.74	1.31	0.77	4
<i>Lepomis auritus</i>	NALEA	4.34	0.44	2.87	0.21	4.48	1.05	3.54	0.74	1
<i>Lepomis gibbosus</i>	NALEE	4.65	0.40	2.47	0.21	3.72	1.07	2.72	0.70	1
<i>Lepomis macrochirus</i>	NALEG	4.35	0.49	3.04	0.22	4.49	1.05	2.44	0.67	1
<i>Lepomis megalotis</i>	NALEM	5.08	0.41	2.27	0.16	3.54	0.78	0.98	0.70	1
<i>Margariscus margarita</i>	NAMAM	4.96	0.17	1.22	0.21	3.81	0.74	1.68	0.56	3
<i>Noturus insignis</i>	NANOI	4.39	0.15	0.93	0.11	4.94	1.58	2.25	0.72	2
<i>Rhinichthys atratulus</i>	NARHA	3.83	0.17	1.44	0.23	3.82	1.52	2.67	0.60	2
<i>Rhinichthys cataractae</i>	NARHC	3.94	0.18	1.30	0.25	2.91	1.64	2.54	0.65	4
<i>Salvelinus fontinalis</i>	NASAF	4.55	0.18	1.93	0.15	4.09	1.37	3.01	0.70	1
<i>Salmo trutta</i>	NASAT	4.41	0.20	0.50	0.19	2.60	0.50	1.50	0.70	2
<i>Semotilus atromaculatus</i>	NASEA	4.99	0.20	1.42	0.21	3.35	0.97	1.97	0.67	1
<i>Semotilus corporalis</i>	NASEC	5.26	0.24	2.47	0.21	2.80	1.37	2.09	0.69	1

Table 6

Variable	PC1	PC2
Correlations of morphological variables with ordinations axes		
SL	-0.724	-0.356
RBD	0.537	-0.189
FI	0.887	-0.105
RPL	-0.260	0.692
RPHW	0.750	-0.320
RCHW	0.492	0.607
RPEHW	0.704	0.456
EP	0.298	-0.413
MP	-0.457	0.304
Summary statistics for ordination axes		
Eigenvalues	0.362	0.177

Table 7

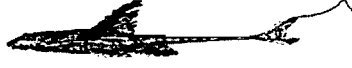
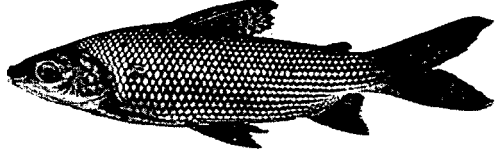
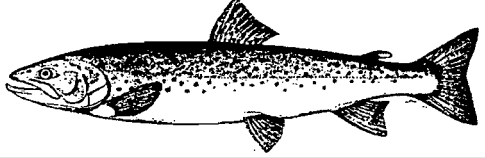
PCA quadrats	Morphological traits	Scientific name	Picture of the specimen
I	RCHW/ RPEHW	Percidae: <i>Etheostoma olmsiedi</i> (North America.)	
		Gasterosteidae: <i>Pungitius pungitius</i> (Europe)	
		Lebiasinidae: <i>Pyrrhulina vittata</i> (South America)	
II	MP / RPL	Balitoridae: <i>Barbatula barbatula</i> (Europe)	
		Cyprinidae: <i>Rhinichthys cataractae</i> (North America.)	
		Loricariidae: <i>Rineloricaria lanceolata</i> (South America)	
III	SL	Erythrinidae: <i>Prochilodus nigricans</i> (South America)	
		Cyprinidae: <i>Leuciscus cephalus</i> (Europe)	
		Salmonidae: <i>Salmo trutta</i> (North America)	
IV	FI / RBD RPHW / EP	Characidae: <i>Astyanax abramis</i> (South America)	
		Centrarchidae: <i>Lepomis auritus</i> (North America)	

Table 8

(a)

Assemblage traits	PC1 effect P value	ZR effect P value	PC1XZR effect P value	R ² full model
Local species richness (LSR)	0.000	0.000	0.340	0.764
Percentage of invertivores (%INV)	0.004	0.000	0.249	0.756
Percentage of omnivores (%OMN)	0.009	0.000	0.142	0.553
Percentage of herbivores/detritivores (%HERB)	0.325	0.000	0.742	0.818
Percentage of piscivores (%PIS)	0.410	0.000	0.243	0.481

(b)

Assemblage traits	PC1 effect P value	ZR effect P value	PC1XZR effect P value	R ² full model
Total density of individuals	0.175	0.000	0.343	0.462
Percentage of invertivores (%INV)	0.030	0.000	0.781	0.666
Percentage of omnivores (%OMN)	0.019	0.000	0.935	0.622
Percentage of herbivores/detritivores (%HERB)	0.748	0.000	0.919	0.656
Percentage of piscivores (%PIS)	0.121	0.001	0.272	0.475

Figure 1.

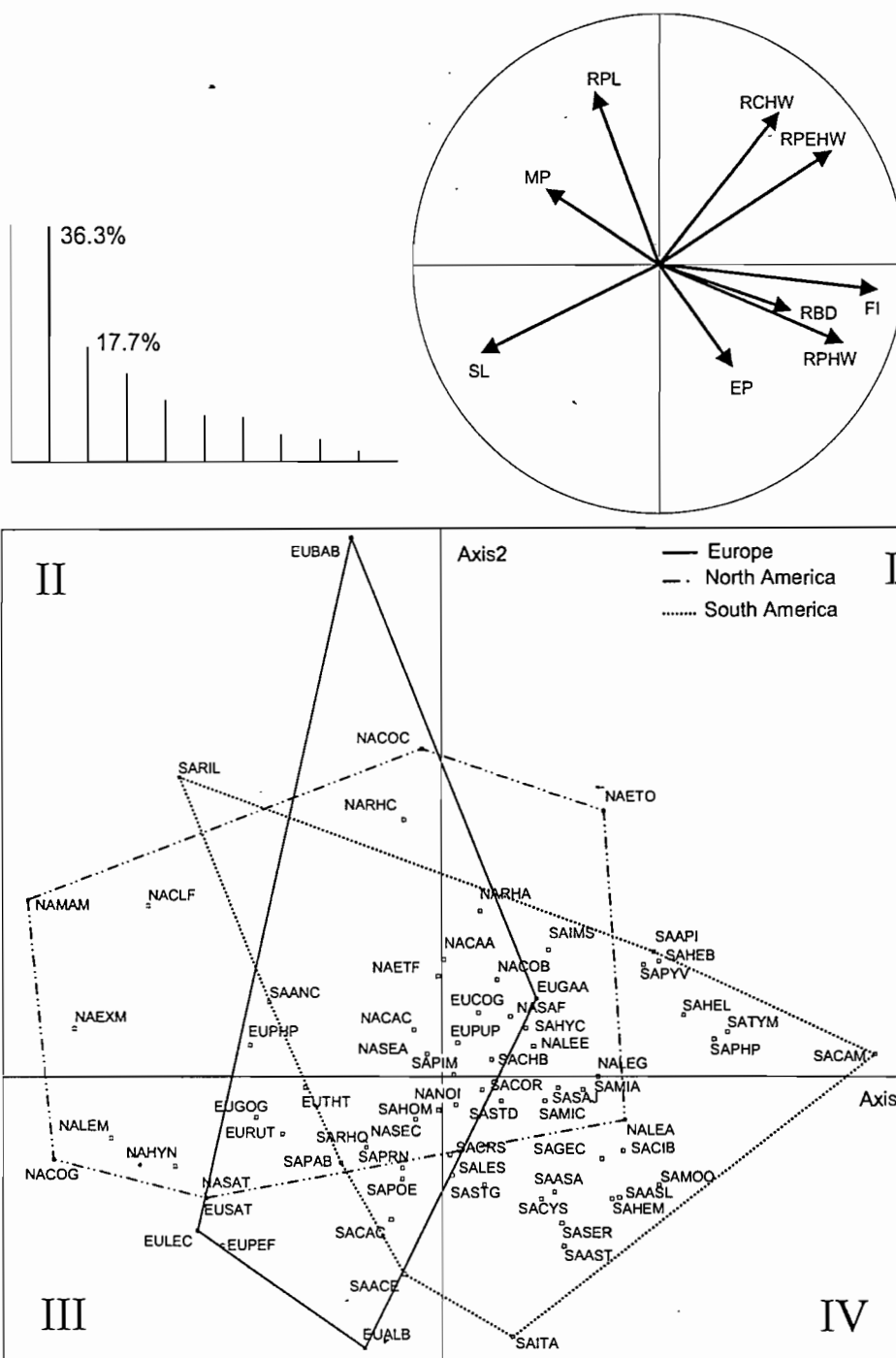


Figure 2 (a)

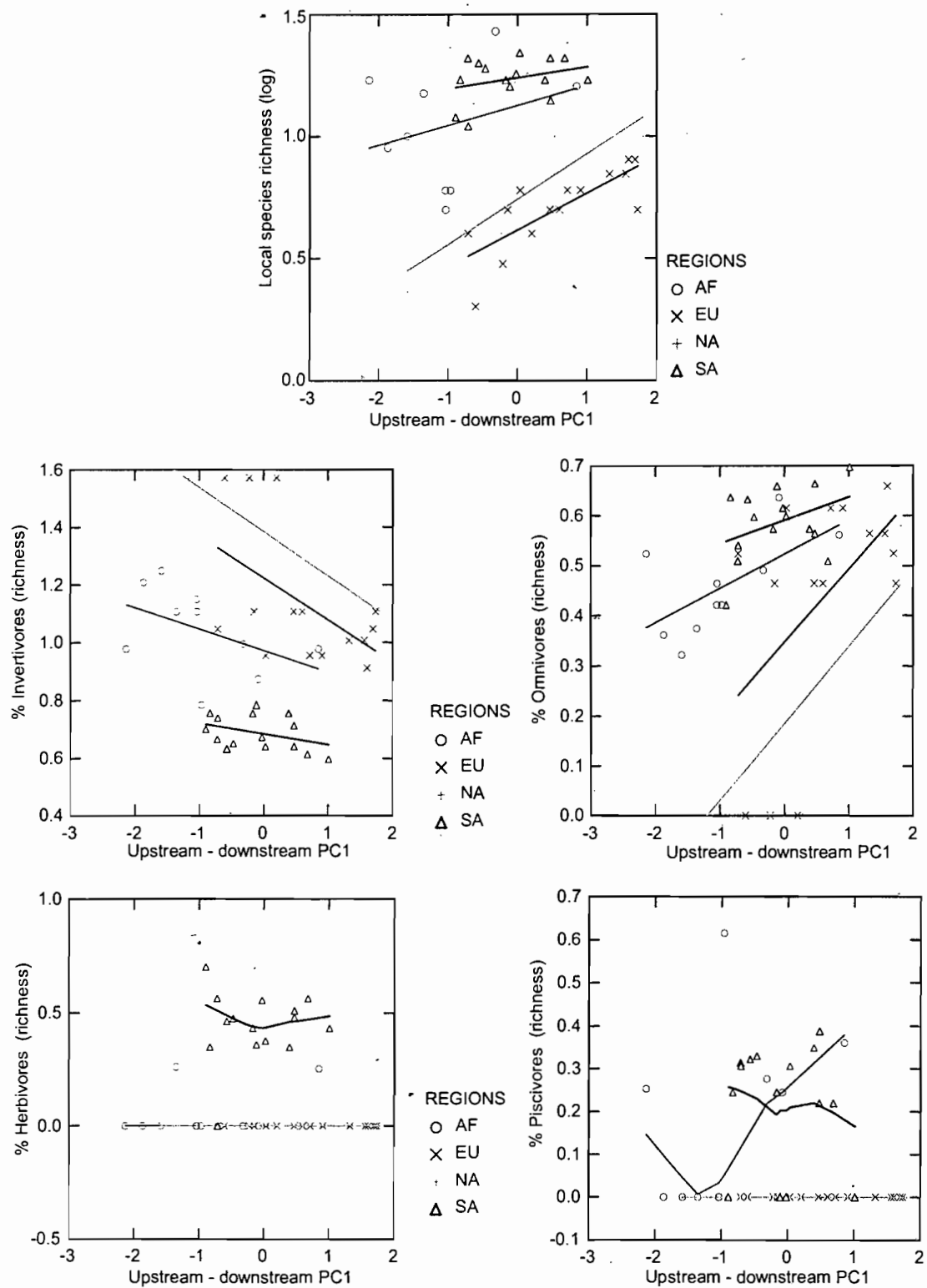
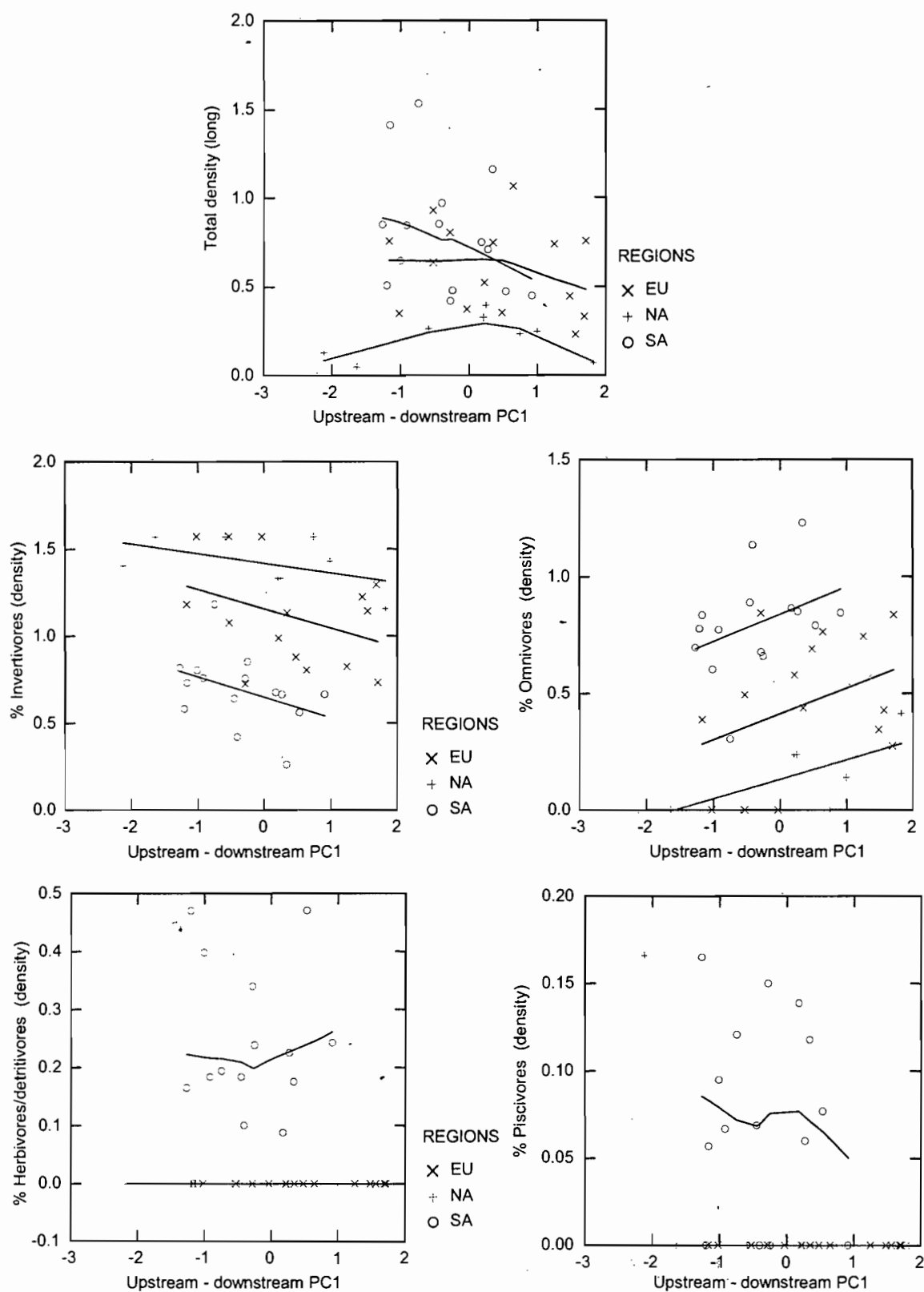


Figure 2 (b)



Appendix 1.

Zoogeographic regions U. S. A.	MNHN reference	Number of individuals
<i>Campostoma anomalum</i>	1987-0866	4
<i>Catostomus commersonii</i>	1889-0317	1
	0000-3833	1
	A-2477	1
	0000-3814	1
<i>Cottus bairdii</i>	1905-0529	2
<i>Cottus cognatus</i>	0-4675	1
<i>Etheostoma flabellare</i>	1985-0110	4
<i>Etheostoma olmstedii</i>	0-6781	2
<i>Hypentelium nigricans</i>	0-2865	1
<i>Lepomis gibbosus</i>	1889-0428	1
	0000-4674	2
<i>Lepomis macrochirus</i>	1987-0875	5
<i>Lepomis megalotis</i>	1987-0877	4
<i>Noturus insignis</i>	B-0164	1
	1889-0311	2
	0000-0340	2
<i>Rhinichthys atratulus</i>	1889-0392	1
	1889-0395	2
<i>Rhinichthys cataractae</i>	1905-0523	2
	A-2716	1
<i>Salvelinus fontinalis</i>	A-2437	1
<i>Semotilus atromaculatus</i>	1974-0016	4
<i>Semotilus corporalis</i>	A-1302	1
	B-0131	2
	A-2723	1
France		
<i>Cotus gobio</i>	1986-0913	2
<i>Gasterosteus aculeatus</i>	0000-6664	2
	0000-0681	1
<i>Pungitius pungitius</i>	1925-0170	2
	0000-7106	1
<i>Thymallus thymallus</i>	B-2480	2
	1898-1156	1

Article 4

**Local-scale species–energy relationships in fish assemblages of
some forested streams of the Bolivian Amazon**

Pablo A. Tedesco, Carla Ibañez, Nabor Moya, Rémy Bigorne, Jimena Camacho, Edgar
Goitia, Bernard Hugueny, Mabel Maldonado, Mirtha Rivero, Sylvie Tomanová, José P.
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Ecology / Écologie

Local-scale species–energy relationships in fish assemblages of some forested streams of the Bolivian Amazon

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Abstract

Productivity (trophic energy) is one of the most important factors promoting variation in species richness. A variety of species–energy relationships have been reported, including monotonically positive, monotonically negative, or unimodal (i.e. hump-shaped). The exact form of the relationship seems to depend, among other things, on the spatial scale involved. However, the mechanisms behind these patterns are still largely unresolved, although many hypotheses have been suggested. Here we report a case of local-scale positive species–energy relationship. Using 14 local fish assemblages in tropical forested headwater streams (Bolivia), and after controlling for major local abiotic factors usually acting on assemblage richness and structure, we show that rising energy availability through leaf litter decomposition rates allows trophically specialized species to maintain viable populations and thereby to increase assemblage species richness. By deriving predictions from three popular mechanistic explanations, i.e. the ‘increased population size’, the ‘consumer pressure’, and the ‘specialization’ hypotheses, our data provide only equivocal support for the latter. **To cite this article:** P.A. Tedesco et al., *C. R. Biologies* 330 (2007).

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Résumé

Relation énergie disponible/richeesse spécifique chez les peuplements de poissons de cours d'eau forestiers de l'Amazonie bolivienne. L'énergie disponible dans un écosystème a depuis toujours été considérée comme une contrainte fondamentale à la richesse spécifique animale et végétale qui lui est inféodée. Différentes relations entre richesse et énergie ont été rapportées jusqu'à maintenant, incluant des relations positives, négatives ou unimodales. La forme de la relation semble dépendre, entre autres, de

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l'échelle spatiale abordée. Cela étant, les mécanismes à l'origine de ces différentes relations sont encore mal connus, malgré le nombre important d'hypothèses émises sur le sujet. Nous rapportons ici un cas de relation positive entre énergie disponible et richesse spécifique à l'échelle locale. En utilisant 14 peuplements de poissons présents sur différents cours d'eau tropicaux de Bolivie, nous montrons que, toutes choses étant égales par ailleurs, une augmentation de l'énergie disponible (mesurée par le biais du taux de décomposition de la litière végétale) favorise le maintien des populations d'espèces spécialistes et génère in fine une augmentation de la richesse totale du peuplement. Par ailleurs, nous avons établi plusieurs prédictions spécifiques à trois importantes explications mécanistes de la relation énergie/richeesse (c'est-à-dire l'hypothèse d'une augmentation de la taille des populations, celle de la pression de prédation et celle de la spécialisation) afin de tenter de départager ces dernières. Les données analysées réfutent l'hypothèse d'une augmentation de la taille des populations et celle de la pression de prédation, et n'apportent qu'un support partiel à l'hypothèse de la spécialisation. *Pour citer cet article : P.A. Tedesco et al., C. R. Biologies 330 (2007).*

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Keywords: Energy availability; Species richness; Species–energy theory; Specialization hypothesis; Tropical riverine fish; Bolivia

Mots-clés : Énergie disponible ; Richesse spécifique ; Théorie énergie–espèce ; Hypothèse de la spécialisation ; Poissons ; Cours d'eau tropicaux ; Bolivie

1. Introduction

Energy availability, generally determined by the rate of energy supply for an assemblage or a community [1], has long been considered and still emerges as a fundamental constraint to plant and animal species richness [2–5]. The exact form of this relationship seems to depend on the organism group [6], the energy estimates [7], the history of the community assembly [8] and the spatial scale involved [6,9–13]. However, the mechanisms behind this pattern remain unclear [4,5,14–18], although many hypotheses have been suggested [6,15,19]. This is probably partly because few specific predictions of the hypotheses have been explicitly formulated (but see [4,5,17,20,21]).

Previous large-scale studies concerning riverine fishes suggest a positive linear species–energy relationship [22,23]. Considering that the pattern observed at the global scale could hold true at the local scale, we used a standardized sampling protocol to analyze patterns of tropical fish assemblage structure across a gradient of energy in light of the predictions derived from three popular hypotheses, as follows.

The 'increased population size' hypothesis [15–17, 20,24] postulates that the species richness of an assemblage is regulated in a two-step process. First, as the energy availability of a habitat increases, so does its ability to support more individuals of each taxon (i.e. taxon density). Second, as density increases, local extinction rates decrease, increasing, ultimately, species richness. The 'increased population size' hypothesis thus posits that taxon density is limited by habitat energy availability, and assemblage richness is limited by assemblage density [17,20]. It is possible to derive four testable predictions from this hypothesis. Everything else being equal, (a) species richness should increase with en-

ergy availability, (b) total abundance of the assemblage should increase with energy availability, (c) the average density per species should increase with energy availability, and (d) species richness should increase with total abundance. Prediction (d) is necessarily true when predictions (a) and (b) are true.

The 'consumer pressure' hypothesis [4,15,17,25,26] assumes that the number of trophic levels in a food web is limited by energy. If an increase in energy availability allows the appearance of a specialized predator (highest trophic level), this prevents competitors from reaching densities where they exclude other species [27]. Therefore, diversity increases with energy availability. We can derive three testable predictions from this hypothesis. We should expect (a) a positive relationship between species richness and energy availability, (b) a positive relationship between the density of top-level predator species and energy availability, and (c) a negative relationship between the average density per species in the assemblage and the density of top-level predator species.

Finally, the 'specialization' hypothesis [4,15,17,18, 21,28] assumes that more energy enables greater development of specialist strategies, either by reducing niche breadth or by generating greater resource diversity and/or habitat heterogeneity. Again in this case, more productive assemblages should have more species. This predicts (a) a positive relationship between species richness and energy availability, (b) a positive relationship between the number of specialist species and energy availability, and (c) a potentially negative relationship between the population size of generalist species and energy availability as a consequence of increasing competition with specialist species [17,21].

We tested these predictions analyzing the relationship between energy availability and fish species rich-

ness, density and biomass, in 14 comparable sites within five tropical forested headwater streams belonging to the same drainage basin.

2. Materials and methods

2.1. Choice of sites within the watershed

The study was conducted in five tropical, highly forested, headwater tributaries including 14 sites situated in the upper Rio Chipiriri catchment of the Bolivian Amazon (total area <100 km²). The five tributaries originated in the same region, were similar in size and environmental characteristics (i.e. physical and water quality characteristics), and were located between the coordinates 16°40'S, 65°25'W and 17°00'S, 65°15'W at a mean altitude of 270 m. At the basin scale, based on aerial photographs provided by the PRAEDAC (Alternative Development Strategy Program for the Chapare, Bolivia), the percentage of canopy cover along the five tributaries was identical and approximated 100 percent. At the local scale, the 14 sites had similar habitat characteristics, same regional species pool, and were all heavily shaded with a slight gradient of canopy cover (e.g., Fig. 1) (mean canopy cover 61% ±15.3 SD).

2.2. Estimating fish species richness, density and biomass

Electro-fishing was performed during the dry season from July to October. The 14 sample sites (around 40 m long reaches; mean channel width 3.9–9.7 m) encompassed complete sets of the characteristic stream form (e.g., pools and riffles). For each site, the upstream and downstream edges of the sampled area were blocked by



Fig. 1. Picture of one of the 14 sites, as an example of the canopy cover significance.

closing nets (1-mm mesh size). Two fishing removals were performed per site, applying a constant fishing effort. The two-pass method gave reliable estimates of fish abundance and richness: about 72 percent (±6.9 SD) of fish and 90 percent (±8 SD) of species were caught during the first pass, thus demonstrating the global efficiency of this method [29]. Fishes were fixed in formal 4% and brought to laboratory for identification to the species level, counting and weighing. Young-of-the-year fishes were never caught during the study and thus cannot influence our results. Density (individuals/m²) and biomass (g/m²) of each species were estimated using the Zippin method [30].

2.3. Fish trophic groups

The adult feeding habits of 44 of the 48 collected species were drawn from stomach contents analysis and from the literature (available on request) at the genus (19 species) or species levels (29 species). Species were then assigned into trophic groups as detritivorous, omnivorous, invertivorous, or piscivorous (see Appendix A). Species belonging to the detritivorous, invertivorous, and piscivorous trophic groups were considered as specialized species (i.e. species having specialized diets), whereas species belonging to the omnivorous trophic group were considered as generalist species. The piscivorous species were also considered as specialized predators for testing the 'consumer pressure' hypothesis. However, excluding them from the specialists in the analysis did not change the nature of the relationships between specialist species and productivity.

2.4. Estimating energy availability and other environmental variables

We estimated energy availability within each site by measuring the leaf litter decomposition rate generated by small detritivorous invertebrates, bacteria and fungi (0.073 g/day on average), hypothesizing a constant leaf input between the five tributaries (as, at the basin scale, the percentage of canopy cover along the five tributaries was assumed identical, see above). Allochthonous organic matter such as leaves, entering the system throughout the year, is the major energy source for these tropical forested streams [31–34] like for most small forested streams [35–39], far exceeding autochthonous primary production, which is light-limited [39,40]. Since terrestrial litter inputs drive microbial [39–41] and stream invertebrate [36,37,42] communities, and since litter breakdown results primarily from

the activity by those communities (e.g., [31,33,34,43]), our measure of basal productivity (i.e. leaf litter decomposition rate) is thus likely to be the most appropriate measure of energy supply for higher trophic levels in these detritus-based systems [31,37,38].

To measure the leaf litter decomposition rate, we used the litter-bag technique [44]. Recently senesced leaves of *Eschweilera coriacea* (a common riparian tree species throughout the study area) were collected during late September from a single tree. Approximately 10 g of leaves, previously dried to constant mass at 65 °C, were weighed and placed into doubled 1-mm plastic mesh litter bags (15 × 20 cm standardized bags). Three replicate bags per site were placed on the stream bottom, weighed, and secured. Following deployment, the litter bags were retrieved after 45 days (about 30% of leaf mass loss). The leaves were rinsed individually with water to remove adhering fine particulate matter and dried to constant mass at 65 °C. Since the decay rate was measured on a single time interval, the productivity rate per site was estimated by the mean leaf weight loss among the replicates, rather than applying the commonly used negative exponential model [43,44].

To not confound the potential effect of factors other than energy on assemblage richness and structure, we estimated several local environmental variables using standard methods. These variables included, for each sampled site: total surface area sampled (mean value 291.10 m² ± 97.51 SD), mean flow velocity (mean value 0.25 m/s ± 0.22 SD), mean depth (mean value 0.27 m ± 0.084 SD), mean width (mean value 7.70 m ± 1.53 SD), percent of canopy cover (mean canopy cover 61% ± 15.3 SD), water conductance (mean value 322 µS/cm ± 53.92 SD), pH (mean value 7.76 ± 0.37 SD), and substratum type [45] later converted into a diversity index (Shannon–Weiner index; mean value 1.416 ± 0.24 SD). Depth, width, flow velocity and substratum type were measured by cross-stream transects at 3–5 m intervals (depending on the stream size), with sampling points spaced 1-m apart (only for depth, flow velocity and substratum type) [45]. Shading by overhanging vegetation (i.e. percentage of canopy cover) was visually assessed in evenly spaced cross-channel transects. These environmental variables are strong descriptors of physical and hydrological conditions at the local scale and can be considered as important abiotic determinants of richness and structure of local fish assemblages (see [46] for a review).

2.5. Estimating secondary productivity

The energy flux reaching our fish assemblages should reflect the production of detritivorous invertebrates,

in turn depending on the availability and decomposition rate of terrestrial litter, and eventually on aquatic primary production. In our sites, aquatic primary production was negligible (for our sites, mean chlorophyll *a* concentration for phytoplankton = 2.86 µg/l ± 0.94 SD and mean chlorophyll *a* for periphyton = 1.56 µg/cm² ± 0.86 SD) and availability of terrestrial litter was assumed constant (i.e. at the basin scale, the percentage of canopy cover along the five tributaries approximated 100%). Then, to ascertain that our measure of energy availability (leaf litter degradation rate) was not speculative, we sampled macroinvertebrates assemblages to verify that secondary production (i.e. detritivorous invertebrates) was also driven by allochthonous organic matter degradation. Five samples of the benthos were taken (at each site) using a Surber sampler (0.09 m² sampled area, 250 µm mesh size). All five replicates were taken in a single riffle with similar depth, flow and substrate. Samples were fixed in a 4% formalin solution. Further, macroinvertebrates were sorted and identified to genus, counted and assigned to functional feeding groups following Tomanová et al. [47], who detailed food resources consumed by invertebrates found in comparable Bolivian streams. Analyses of feeding groups were done according to their relative abundance in each assemblage and were restricted to shredders and scrapers (i.e. the two functional guilds directly related to leaf litter degradation). Shredders play a major role in energy and nutrient transfer in streams by participating actively in the fragmentation and decomposition of leaves, and usually prefer conditioned leaves (i.e. leaves partially degraded by microbial communities) [31,32, 48,49]. We can thus suppose that an increase in leaf litter degradation rate will influence positively the shredders guild. Scrapers usually feed directly on the fungi, algae and bacteria colonizing leaf matter and should thus also increase with leaf litter degradation rate. We used the proportional representation of these two guilds instead of absolute abundance to correlate with energy availability in order to minimize potential effects of fish predation on macroinvertebrates [50].

2.6. Data analysis

Stepwise multiple regression models (both forward and backward procedures) were used to test the dependence of fish species richness, density and biomass (for the entire assemblage and for the different trophic groups) on energy availability (i.e. leaf decomposition rate) and other potential factors. We computed stepwise models rather than entire models because there was some co-linearity among our environmental vari-

ables (see Appendix B). The square of the variable energy availability was added to the models to test for curvilinearity. When we found a significant quadratic effect for this variable, we then determined whether it was significantly unimodal (hump-shaped or U-shaped) using a statistical test developed by Mitchell-Olds and Shaw [51] (MOS's test, see [11] for its use in the context of species–energy relationships). This test determines whether the curvilinear relationship reaches a maximum or minimum within the observed range of energy availability [11]. All continuous variables were kept untransformed as they were all near normally distributed.

Spatial autocorrelation may be present in this local-scale stream system potentially leading to cases of pseudoreplication between sites. Two approaches were applied to avoid this bias: by first adding a categorical variable to the above regression models with a unique value for each tributary; and next by testing for spatial autocorrelation using Moran's *I* coefficients [52]. For that purpose, we constructed a distance class matrix where a value of 1 corresponds to sites separated by less than 5 km, a value of 2 corresponding to sites separated by a distance between 5 to 25 km, and a value of 3 corresponding to sites separated by more than 25 km. For each distance class, standardized Moran's *I* coefficients were computed for values of total species richness and leaf decomposition rates. A Bonferonni-corrected significance level (0.05/3) was used to assess the probability of observing at least one significant autocorrelation coefficient.

3. Results

Concerning invertebrates assemblages, both percents of shredders and scrappers were positively and significantly related to our measure of available energy (% shredders $R^2 = 0.296$, $P = 0.044$; % scrappers $R^2 = 0.320$, $P = 0.035$) (Fig. 2).

Concerning fish assemblages, results of the regression models are summarized in Table 1. Here, in the absence of spatial autocorrelation between sites (see Appendix C; non-significant Moran's *I* coefficients for

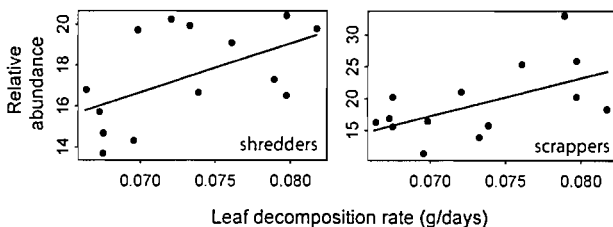


Fig. 2. Relative abundance of shredders and scrappers (invertebrate guilds) as a function of leaf decomposition rate.

Table 1
Results of stepwise multiple regression models of fish species richness, density and biomass (for the entire assemblage and for the different trophic groups) against energy availability (i.e. leaf decomposition rates) and other independent variables

	TSR	PSR	SSR	GSR	TD	PD	SD	GD	TB	PB	SB	GB
R^2	0.72***	0.00	0.74***	0.42	0.59**	0.65**	0.43**	0.59**	0.44*	0.67**	0.00	0.47*
Intercept	-390.70*	ns	-14.15*	-201.55*	163.53**	18.41**	1.17***	-3668.00**	2314.21*	538.82***	ns	1532.48**
Leaf decomposition rate (day^{-1})	10722.17*	ns	290.08*	5618.72*	-4357.19**	-487.01**	ns	24512.93**	-62220.97*	-14705.90***	ns	-41089.07**
(Leaf decomposition rate (day^{-1})) ²	-68963.93*	ns	ns	-37317.23*	29234.28**	3227.14**	ns	ns	419926.41*	100322.35***	ns	276557.55*
Surface area sampled (m^2)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Flow velocity (m/s)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Mean depth (m)	ns	ns	ns	ns	ns	ns	-0.016***	ns	ns	ns	ns	ns
Mean width (m)	ns	ns	0.87*	ns	ns	ns	ns	ns	ns	ns	ns	ns
Substratum diversity	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Canopy cover (%)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Tributary	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

R^2 values are given for each model. Table entries are regression coefficients. * $P < 0.05$ ** $P < 0.01$ *** $P < 0.001$. ns = not significant. – = variable not entered in model. TSR = total species richness; PSR = predator species richness; SSR = specialist species richness; GSR = generalist species richness; TD = total density; PD = predator density; SD = specialist density; GD = generalist density; TB = total biomass; PB = predator biomass; SB = specialist biomass; GB = generalist biomass.

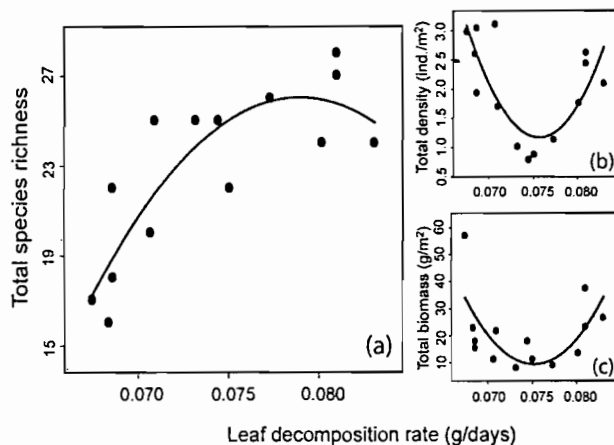


Fig. 3. Total fish species richness (a), total density (b) and total biomass (c) as a function of leaf decomposition rate. Species richness presents a significant ($P = 0.001$) quadratic pattern, whereas significant U-shaped patterns (see methods) are presented for total density ($P = 0.007$) and total biomass ($P = 0.041$).

species richness and energy availability, $P > 0.05/3$ following Bonferroni-corrected significance level), of a tributary effect and of other potential effects (Table 1), total species richness increases with energy (Fig. 3a). Even if a statistically significant level off can be noted for the higher energy sites (quadratic regression $R^2 = 0.720$, $P = 0.001$), there was no evidence of a unimodal relationship ($P > 0.05$ for the MOS's test).

When we examined the relationship between total density or total biomass and energy, and in the absence of other potential effects, we found a statistically significant U-shaped relationship for both (Fig. 3b; $R^2 = 0.594$, $P = 0.007$, and $P < 0.05$ for the MOS's test and Fig. 3c; $R^2 = 0.441$, $P = 0.041$ and $P < 0.05$ for the MOS's test). A similar pattern was observed when replacing in the model the total density by the average density per species in the assemblage ($R^2 = 0.758$, $P = 0.0004$ and $P < 0.05$ for the MOS's test). When separating the assemblages into trophic groups, we found a significant U-shaped relationship between

predator density or biomass and energy (Fig. 4a; $R^2 = 0.654$, $P = 0.003$ and $P < 0.05$ for the MOS's test and Fig. 4b; $R^2 = 0.673$, $P = 0.002$ and $P < 0.05$ for the MOS's test) and a positive relationship between predator density and the average density per species (Fig. 4c; $R^2 = 0.338$, $P = 0.029$). Concerning specialist and generalist species, we observed a positive relationship between specialist species richness and energy (Fig. 5a; $R^2 = 0.513$, $P = 0.004$), but no relationship between generalist diversity and energy was found (Fig. 5a). Furthermore, we found no relationship between specialist density or biomass and energy (Fig. 5b and c) and a U-shaped relationship between generalist density or biomass and energy (Fig. 5d; $R^2 = 0.594$, $P = 0.007$ and $P < 0.05$ for the MOS's test and Fig. 5e; $R^2 = 0.473$, $P = 0.029$ and $P < 0.05$ for MOS's test). Finally, the relationship between total species diversity and energy was almost exclusively driven by specialist species richness (total species richness vs. specialist species richness; $R^2 = 0.940$, $P < 0.001$) and the U-shaped relationship between total density and energy was mostly driven by generalist density (total density vs. generalist density; $R^2 = 0.875$, $P < 0.001$).

4. Discussion

In our study sites, the leaf litter decomposition rate was positively related to secondary production (i.e. percentage of detritivorous invertebrates in each assemblage). As the percentage of canopy cover along the five tributaries was considered identical at the basin scale (see Section 2) and as sites primary productivity was marginal, our measure of leaf degradation is a relevant measure of energy supply for fish assemblages in these systems.

Fish species richness in this local-scale study increased with energy availability. This result is consistent with the prediction shared by the three presently tested mechanisms and provides no means for discrim-

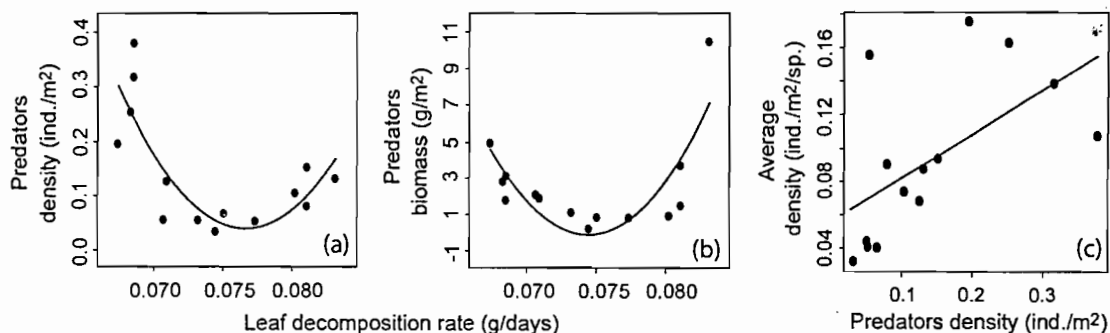


Fig. 4. Predators density and biomass as a function of leaf decomposition rate (a and b) and average density per species as a function of predators density (c). Linear and quadratic regressions are presented when significant ($P < 0.05$; see methods).

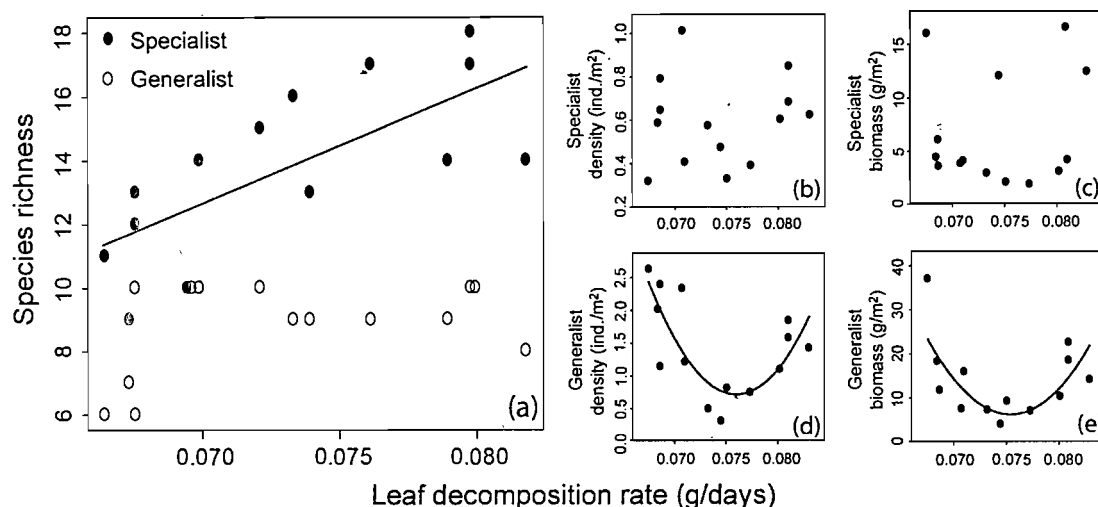


Fig. 5. Fish species richness for specialist and generalists as a function of leaf decomposition rate (a). Density and biomass as a function of leaf decomposition rate: (b) and (c) for specialists; (d) and (e) for generalists. Linear and quadratic regressions are presented when significant ($P < 0.05$; see methods). For specialist species richness, the significant effect of stream width has not been factored out in order to visually compare richness values between specialist and generalist species.

inating between them. However, the U-shaped relationships between (1) the total density (and total biomass) of the assemblage and energy and (2) the average density per species and energy are both inconsistent with predictions (b) and (c) of the 'increased population size' mechanism. Therefore, this last mechanism cannot be the direct cause of the noticed positive species–energy relationship.

Furthermore, the U-shaped relationship between predator density (or biomass) and productivity, and the absence of a negative relationship between predator density (as a measure of consumer pressure) and the average density per species are inconsistent with the predictions (a) and (b) associated with the 'consumer pressure' hypothesis, and thus refute this hypothesis.

In contrast, the positive linear relationship between specialist richness and energy availability was consistent with prediction (b) of the 'specialization' hypothesis. Nevertheless, the U-shaped relationship between the population size of generalist species and energy availability is inconsistent with prediction (c) of this hypothesis. Therefore, if prediction (c) is correct, the 'specialization' hypothesis receives only equivocal support from our findings.

A problem arises in explaining the U-shaped relationship between total density and energy availability (Fig. 3b). Our interpretation assumes that the degree of interspecific competition between members of the community depends on both species richness and productivity gradients (levels) (Fig. 6). At low productivities, fish communities are species-poor and generalist

species exhibit high densities. As resource availability rises (i.e. productivity), more specialists enter the communities, generating competitive interaction with generalists, which are usually inferior competitors on all except a few rare resource types [15,26,53]. This could explain the decreasing part of the U-shaped relationship (i.e. a phenomenon termed density overcompensation [54,55]) found between total density and productivity as this relationship is almost exclusively driven by generalist species. At intermediate productivities, community species richness levels off (Fig. 6). Beyond that level, the quasi-absence of new competitors entering the community allows, together with rising productivity, reduced competition, resulting in an increase in the average density per species and consequently in total density (Fig. 6; a phenomenon termed negative density compensation [54,55]).

To summarize, the species trophic status (i.e. their degree of trophic specialization), combined with the resource availability within a site, seems to determine the degree of competitive exclusion between species and, ultimately, total species richness and total abundance.

There is a popular view that spatial scale dictates the form of the richness–energy relationship [6,9–13, 56]. It has been noticed that the relationship generally follows a 'hump-shaped' (unimodal) trajectory at the local scale, and that at larger spatial scales, the relationship becomes most often monotonically positive [6,11]. However, the basic underlying conditions that could produce unimodal or monotonic patterns are still largely unresolved [15], even if some recent stud-

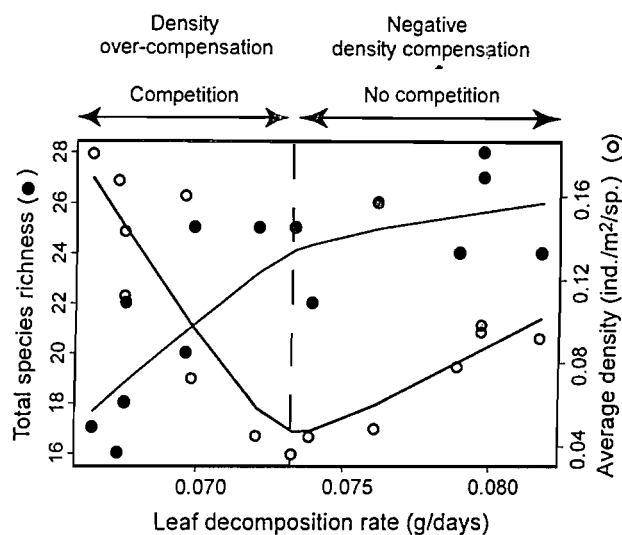


Fig. 6. Fish species richness and average density per species as a function of the leaf decomposition rate. Smoothed curves are given for both variables. A dotted line indicates the intermediate productivity level separating the degree of interspecific competition resulting in density overcompensation or negative density compensation.

ies [11,57] have hypothesized that scale dependence in richness–energy relationship could result from the way in which species turnover changes with energy availability. The positive relationship observed here between local fish species richness and energy availability, together with a previous similar relationship (richness monotonically increases with energy) obtained at the global scale [22,23] would tend to show that the shape of the relationship is invariant with spatial scale for this organism group. This remains to be tested in future studies.

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Appendix A. Fish species list and trophic regimes

FAMILY Species	Trophic regime
CHARACIDAE	
<i>Acestrorhynchus</i> sp.	Piscivorous
<i>Astyanacinus</i> sp.	
<i>Astyanax abramis</i>	Omnivorous
<i>Astyanax bimaculatus</i>	Omnivorous
<i>Astyanax lineatus</i>	Omnivorous
<i>Gephyrocharax</i> sp.	Invertivorous
<i>Hemigrammus</i> cf. <i>lunatus</i>	Omnivorous
<i>Hemigrammus</i> sp.	Omnivorous
<i>Hemibrycon</i> sp.	Invertivorous
<i>Knodus</i> sp.	Omnivorous
<i>Moenkhausia oligolepis</i>	Omnivorous
<i>Phenacogaster</i> cf. <i>pectinatus</i>	Omnivorous
<i>Tytocharax madeirae</i>	Invertivorous
<i>Characidae</i> sp.1	
<i>Characidae</i> sp.2	
<i>Characidae</i> sp.3	
GASTROPELECIDAE	
<i>Thoracocharax</i> sp.	Invertivorous
ERYTHRINIDAE	
<i>Hoplias malabaricus</i>	Piscivorous
CHARACIDIIDAE	
<i>Characidium bolivianum</i>	Invertivorous
<i>Characidium</i> sp.	Invertivorous
LEBIASINIDAE	
<i>Pyrhulina vittata</i>	Invertivorous
PARODONTIDAE	
<i>Parodon</i> sp.	Detritivorous
PROCHILODONTIDAE	
<i>Prochilodus nigricans</i>	Detritivorous
CURIMATIDAE	
<i>Steindachnerina dobula</i>	Detritivorous
<i>Steindachnerina guentheri</i>	Detritivorous
ANASTOMIDAE	
<i>Leporinus striatus</i>	Omnivorous
GYMNOTIDAE	
<i>Gymnotus carapo</i>	Invertivorous
HEPTAPTERIDAE	
<i>Imparfinis</i>	Invertivorous
<i>Khamdia quelem</i>	Omnivorous
PIMELODIDAE	
<i>Pimelodella</i> sp.1	Omnivorous
<i>Pimelodella</i> sp.2	Omnivorous
PSEUDOPIMELODIDAE	
<i>Batrochoglanis raninus</i>	Piscivorous
TRICHOMYCTERIDAE	
<i>Trichomycterus</i> sp.	Invertivorous
CALLICHTHYIDAE	
<i>Callichthys callichthys</i>	Omnivorous
<i>Corydoras</i> sp.	Omnivorous
LORICARIIDAE	
<i>Ancistrus</i> cf. <i>hoplogeny</i>	Detritivorous
<i>Ancistrus</i> sp.1	Detritivorous
<i>Ancistrus</i> sp.2	Detritivorous
<i>Farlowella</i> sp.	Detritivorous

FAMILY Species	Trophic regime
<i>Rinelricaria lanceolata</i>	Detritivorous
<i>Rinelricaria</i> sp.	Detritivorous
BELONIDAE	
<i>Potamorhaphis</i> sp.	Invertivorous
SYNBRANCHIDAE	
<i>Synbranchus</i> sp.	Piscivorous
CICHLIDAE	
<i>Apistograma</i> sp.	Invertivorous
<i>Cichlasoma boliviense</i>	Omnivorous
<i>Crenicichla semicincta</i>	Piscivorous
<i>Mikrogeophagus altispinosus</i>	Omnivorous
<i>Satanoperca</i> sp.	Invertivorous

Appendix B. Correlation matrix among environmental variables

	Total surface	Width	Depth	Flow velocity	Substratum diversity
Width	0.637	—	—	—	—
Depth	−0.465	0.112	—	—	—
Flow velocity	0.109	0.374	−0.307	—	—
Substratum diversity	0.387	0.303	0.020	0.085	—
Canopy cover	0.040	−0.144	−0.659	0.662	−0.162

Appendix C. Standardized Moran's *I* values for each distance class and associated *p*-values (in brackets) for the decomposition rate and total species richness

Distance class (km)	Leaf decomposition rate	Total species richness
1. <5	2.17 (0.03)	−0.05 (> 0.1)
2. 6–25	−0.12 (> 0.1)	0.15 (> 0.1)
3. >26	−1.67 (0.1)	−0.07 (> 0.1)

References

- [1] R. Kassen, A. Buckling, G. Bell, P.B. Rainey, Diversity peaks at intermediate productivity in a laboratory microcosm, *Nature* 406 (2000) 508–512.
- [2] K.J. Gaston, Global patterns in biodiversity, *Nature* 405 (2000) 220–227.
- [3] B.A. Hawkins, R. Field, H.V. Cornell, D.J. Currie, J.-F. Guégan, D.M. Kaufman, J.T. Kerr, G.G. Mittelbach, T. Oberdorff, E.M. O'Brien, E.E. Porter, J.R.G. Turner, Energy, water and broad-scale geographic patterns of species richness, *Ecology* 84 (2003) 3105–3117.
- [4] K.L. Evans, P.H. Warren, K.J. Gaston, Species–energy relationships at the macroecological scale: a review of the mechanisms, *Biol. Rev.* 79 (2005) 1–25.
- [5] D.J. Currie, G.G. Mittelbach, H.V. Cornell, R. Field, J.-F. Guégan, B.A. Hawkins, D.M. Kaufman, J.T. Kerr, T. Oberdorff, E.M. O'Brien, J.R.G. Turner, Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness, *Ecol. Lett.* 7 (2004) 1121–1134.
- [6] R.B. Waide, M.R. Willig, C.F. Steiner, G.G. Mittelbach, L. Gough, S.I. Dodson, G.P. Juday, R. Parmenter, The relationship between productivity and species richness, *Annu. Rev. Ecol. Syst.* 30 (1999) 257–300.
- [7] E. Groner, A. Novoplansky, Reconsidering diversity–productivity relationships: directness of productivity estimates matters, *Ecol. Lett.* 6 (2003) 695–699.
- [8] T. Fukami, P.J. Morin, Productivity–biodiversity relationships depend on the history of community assembly, *Nature* 424 (2003) 423–426.
- [9] K.L. Gross, M.R. Willig, L. Gough, R. Inouye, S.B. Cox, Patterns of species density and productivity at different spatial scales in herbaceous plant communities, *Oikos* 89 (2003) 417–427.
- [10] G.G. Mittelbach, C.F. Steiner, S.M. Scheiner, K.L. Gross, H.L. Reynolds, R.B. Waide, M.R. Willig, S.I. Dodson, L. Gough, What is the observed relationship between species richness and productivity?, *Ecology* 82 (2001) 2381–2396.
- [11] J.M. Chase, M.A. Leibold, Spatial scale dictates the productivity–biodiversity relationship, *Nature* 416 (2002) 427–430.
- [12] J.M. Chase, W.A. Ryberg, Connectivity, scale-dependence, and the productivity–diversity relationship, *Ecol. Lett.* 7 (2004) 676–683.
- [13] J.S. Weitz, D.H. Rothman, Scale-dependence of resource–biodiversity relationships, *J. Theor. Biol.* 225 (2003) 205–214.
- [14] J.M. Adams, Species diversity and productivity of trees, *Plants Today* 2 (1989) 183–187.
- [15] P.A. Abrams, Monotonic or unimodal diversity–productivity gradients: what does competition theory predict? *Ecology* 76 (1995) 2019–2027.
- [16] M.L. Rosenzweig, Z. Abramsky, How are diversity and productivity related?, in: R.E. Ricklefs, D. Schluter (Eds.), *Species Diversity in Ecological Communities*, The University of Chicago Press, Chicago, 1993, pp. 52–65.
- [17] D.S. Srivastava, J.H. Lawton, Why more productive sites have more species: an experimental test of theory using tree-hole communities, *Am. Nat.* 152 (1998) 510–529.
- [18] A.H. Hurlbert, Species–energy relationships and habitat complexity in bird communities, *Ecol. Lett.* 7 (2004) 714–720.
- [19] M.R. Willig, D.M. Kaufman, R.D. Stevens, Latitudinal gradients of biodiversity: Pattern, process, scale and synthesis, *Annu. Rev. Ecol. Syst.* 34 (2003) 273–309.
- [20] M. Kaspari, S. O'Donnell, J.R. Kercher, Energy, density and constraints to species richness: Ant assemblages along a productivity gradient, *Am. Nat.* 155 (2000) 280–293.
- [21] A. Bonn, D. Storch, K.J. Gaston, Structure of the species–energy relationship, *P. Roy. Soc. Lond. B* 271 (2004) 1685–1691.
- [22] T. Oberdorff, J.-F. Guégan, B. Hugué, Global scale patterns of fish species richness in rivers, *Ecography* 18 (1995) 345–352.
- [23] J.-F. Guégan, S. Lek, T. Oberdorff, Energy availability and habitat heterogeneity predict global riverine fish diversity, *Nature* 391 (1998) 382–384.
- [24] D.H. Wright, Species–energy theory: an extension of the species–area theory, *Oikos* 41 (1983) 496–506.
- [25] D. Tilman, S. Pacala, The maintenance of species richness in plant communities, in: R.E. Ricklefs, D. Schluter (Eds.), *Species Diversity in Ecological Communities*, The University of Chicago Press, Chicago, 1993, pp. 13–25.
- [26] J. Moen, S.L. Collins, Trophic interactions and plant species richness along a productivity gradient, *Oikos* 76 (1996) 603–607.
- [27] J.H. Knouft, Regional analysis of body size and population density in stream fish assemblages: testing predictions of the ener-

- getic equivalence rule, *Can. J. Fish. Aquat. Sci.* 59 (2002) 1350–1360.
- [28] T.W. Schoener, Alternatives to Lotka–Volterra competition: models of intermediate complexity, *Theor. Popul. Biol.* 10 (1976) 309–333.
- [29] F. Cattaneo, B. Hugueny, N. Lamouroux, Synchrony in brown trout, *Salmo trutta*, population dynamics: a ‘Moran effect’ on early-life stages, *Oikos* 100 (2003) 43–54.
- [30] C. Zippin, The removal method of population estimation, *J. Wildlife Manage.* 22 (1958) 82–90.
- [31] R.G. Pearson, N.M. Connolly, Nutrient enhancement, food quality and community dynamics in a tropical rainforest stream, *Freshwater Biol.* 43 (2000) 31–42.
- [32] M.A.S. Graça, C. Cressa, M.O. Gessner, M.J. Feio, K.A. Calles, C. Barrios, Food quality, feeding preferences, survival and growth of shredders from temperate and tropical streams, *Freshw. Biol.* 46 (2001) 947–957.
- [33] C. Mathuriau, E. Chauvet, Breakdown of leaf litter in a neotropical stream, *J. N. Am. Benthol. Soc.* 21 (2002) 384–396.
- [34] M.S. Wright, A.P. Covich, The effect of macroinvertebrate exclusion on leaf breakdown rates in a tropical headwater stream, *Biotropica* 37 (2005) 403–408.
- [35] R.L. Vannote, G. Wayne Minshall, K.W. Cummins, J.R. Sedell, C.E. Cushing, The river continuum concept, *Can. J. Fish. Aquat. Sci.* 37 (1980) 130–137.
- [36] J.B. Wallace, S.L. Eggert, J.L. Meyer, J.R. Webster, Effects of resource limitation on a detrital-based ecosystem, *Ecology* 69 (1999) 409–442.
- [37] J.B. Wallace, S.L. Eggert, J.L. Meyer, J.R. Webster, Multiple trophic levels of a forest stream linked to terrestrial litter inputs, *Science* 277 (1997) 102–104.
- [38] R.M. Thompson, C.R. Townsend, Energy availability, spatial heterogeneity and ecosystem size predict food-web structure in streams, *Oikos* 108 (2005) 137–148.
- [39] R.O. Hall, J.B. Wallace, S.L. Eggert, Organic matter flow in stream food webs with reduced detrital resource base, *Ecology* 81 (2000) 3445–3463.
- [40] J.R. Webster, J.B. Wallace, E.F. Benfield, Streams and rivers of eastern United States, in: C.E. Cushing, K.W. Cummins, G.W. Minshall (Eds.), *River and Stream Ecosystems*, Elsevier Press, Amsterdam, 1995, pp. 117–187.
- [41] M.D. Carter, K. Suberkropp, Respiration and annual fungal production associated with decomposing leaf litter in two streams, *Freshwater Biol.* 49 (2004) 1112–1122.
- [42] G.A. Polis, W.B. Anderson, R.D. Holt, Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs, *Annu. Rev. Ecol. Syst.* 28 (1997).
- [43] R.C. Petersen, K.W. Cummins, Leaf processing in a woodland stream, *Freshwater Biol.* 4 (1974) 343–368.
- [44] A.J. Boulton, P.I. Boon, A review of methodology used to measure leaf litter decomposition in lotic environments: time to turn over an old leaf?, *Aust. J. Freshw. Res.* 42 (1991) 1–43.
- [45] O.T. Gorman, J.R. Karr, Habitat structure and stream fish communities, *Ecology* 59 (1978) 507–515.
- [46] F.L. Tejerina-Garro, M. Maldonado, C. Ibañez, D. Pont, N. Roset, T. Oberdorff, Effects of natural and anthropogenic environmental changes on riverine fish assemblages: a framework for ecological assessment of rivers, *Braz. Arch. Biol. Techn.* 48 (2005) 91–108.
- [47] S. Tomanová, E. Goitia, J. Helešic, Trophic levels and functional feeding groups of macroinvertebrates in neotropical streams, *Hydrobiologia* 556 (2006) 251–264.
- [48] M.A.S. Graça, L. Maltby, P. Calow, Importance of fungi in the diet of *Gammarus pulex* and *Asellus aquaticus*. I. Feeding strategies, *Oecologia* 93 (1993) 139–144.
- [49] J.R. Webster, E.F. Benfield, Vascular plant breakdown in freshwater ecosystems, *Annu. Rev. Ecol. Syst.* 17 (1986) 567–594.
- [50] L.R. Williams, C.M. Taylor, M.L. Warren, Influence of fish predation on assemblage structure of macroinvertebrates in an intermittent stream, *Trans. Am. Fish. Soc.* 132 (2003) 120–130.
- [51] T. Mitchell-Olds, R.G. Shaw, Regression analysis of natural selection: Statistical inference and biological interpretation, *Evolution* 41 (1987) 1149–1161.
- [52] R.R. Sokal, N.L. Olden, Spatial autocorrelation in biology. 1. Methodology, *Biol. J. Linn. Soc.* 10 (1978) 199–249.
- [53] K.F. Liem, Functional versatility, speciation, and niche overlap: are fishes different?, in: D.G. Meyers, J.R. Strickler (Eds.), *Trophic Interactions within Aquatic Ecosystems*, American Association for the Advancement of Science, Washington, DC, 1984, pp. 269–305.
- [54] R.H. MacArthur, J.M. Diamond, J.R. Karr, Density compensation in island faunas, *Ecology* 53 (1972) 330–342.
- [55] S.J. Wright, Density compensation in island avifaunas, *Oecologia* 45 (1980) 385–389.
- [56] D.H. Wright, D.J. Currie, B.A. Maurer, Energy supply and patterns of species richness on local and regional scales, in: R.E. Ricklefs, D. Schluter (Eds.), *Species Diversity in Ecological Communities*, The University of Chicago Press, Chicago, IL, USA, 1993, pp. 66–74.
- [57] R.J. Whittaker, K.J. Willis, R. Field, Scale and species richness: towards a general, hierarchical theory of species diversity, *J. Biogeogr.* 28 (2001) 453–470.

Article 5

**Effects of Natural and Anthropogenic Environmental
Changes on Riverine Fish Assemblages: a Framework for
Ecological Assessment of Rivers**

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Effects of Natural and Anthropogenic Environmental Changes on Riverine Fish Assemblages: a Framework for Ecological Assessment of Rivers

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ABSTRACT

Freshwater is a basic need for the mankind. Effective biological tools (ecologically based, efficient, rapid and consistently applicable to different ecological regions) are needed to measure the "health" of rivers. Adapting such tools over a broad geographic area requires a detailed understanding of both the patterns of organisms assemblage composition and distribution within and among water bodies under natural conditions, and the nature of the major environmental gradients that cause or explain these patterns. A comprehensive review of the available literature dealing with the identification of environmental factors structuring riverine fish assemblages under natural conditions permits to identify the most consistent ones.

Keywords: Biological indices, fish community, environmental parameters, habitat

INTRODUCTION

Rivers are among the most intensively human influenced ecosystems on the earth. They serve for transportation, water supply and power generation and also as source of food and sinks for waste products. As a result, in highly industrialized countries and in some developing countries, many rivers are now severely polluted. Most common impacts are channel and bank modifications (i.e., canalisation for navigation or agricultural purposes, bank protection), flow regulation and fragmentation (i.e. dams and weirs, reservoirs for

water supply, diversion for irrigation and industrial purposes), chemical pollution (e.g. heavy metals, pesticides, fertilizers), and organic pollution (e.g. domestic and cattle-raising waste water). All these alterations have led to an extensive ecological degradation of these rivers making them no longer sustainable in providing goods and services (e.g. decline in water quality and availability, intense flooding, changes in the distribution and structure of aquatic biota) (Poff et al., 1997) (Fig. 1). Recognition of these adverse effects on river systems has driven initiatives for river restoration. Nevertheless, until recently river restoration protocols were contingent upon defined uses,

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which were typically human-oriented (drinking water, fishing, swimming) or extremely ill-defined (aquatic life, fish passage).

This kind of policy proved successful to solve problems related to point source pollution, but was poorly adapted to integrate management of river

ecosystems. As a consequence, while the chemical water quality in running waters has been considerably improved, the biological and hydromorphological qualities have continued to deteriorate.

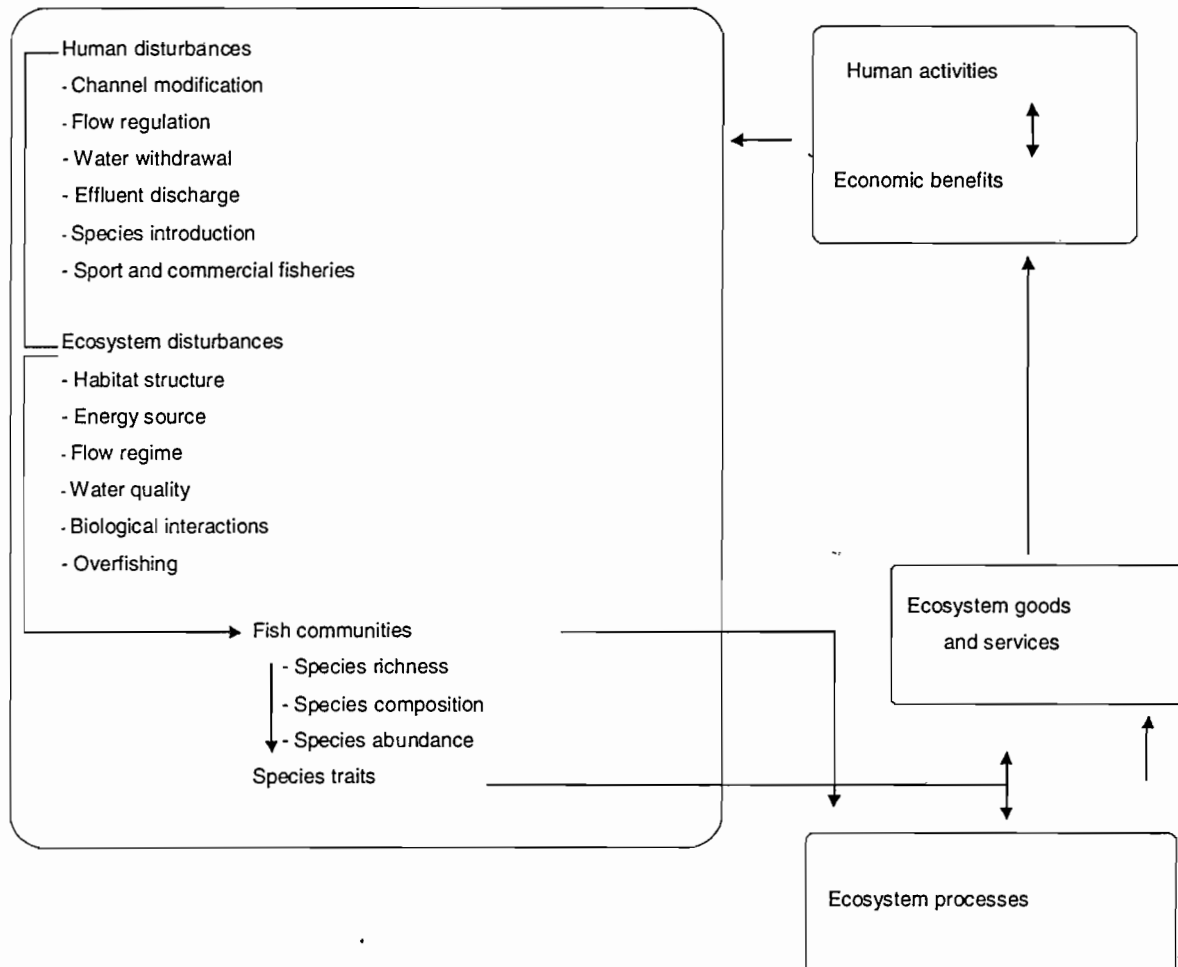


Figure 1 - Relationships between human activities and river ecosystem processes.

Developing countries, like those in South America, and highly industrialized countries, like those in Western Europe, have faced this situation differently. For example, water policy in Brazil continues to concentrate on water pollution even if major river environmental changes are observed due to deforestation, hydroelectric dams, waste water or gold mining (Pringle et al., 2000). In this case measures that attempt to anticipate or predict significant economic, social and ecological impacts rather than react to them, are increasingly necessary for avoiding extreme environmental

-degradation (Hocutt et al., 1994). The European Community has recently changed its water policy as emphasized by the new European Water Framework Directive (WFD), which requires the restoration and maintenance of "healthy" aquatic ecosystems by the assessment of their hydromorphological, chemical and biological characteristics. Thus, the goal is not only to preserve these ecosystems, but also to rehabilitate them in an attempt to restore their ecological structures, functions, and integrity. Consequently, in both highly industrialized and less developed

countries, it is necessary to develop practical and effective ecological tools based on biological assemblage for monitoring water resource quality (Hughes and Oberdorff, 1999).

These tools need to be ecologically based, efficient, rapid and consistently applicable to different ecological regions. Nevertheless, effectively adapting such tools over a broad geographic area requires a detailed understanding of both patterns of organisms assemblage composition and distribution within and among water bodies under natural conditions, and the nature of the major environmental gradients that cause, or at least explain, these patterns (Smogor and Angermeier, 1999). This will permit to obtain a response of aquatic biota to human stressors that can be discriminated from natural variation. For aquatic ecosystems, biological indicators can be chosen from many assemblages (i.e. phytoplankton, macrophytes, benthic invertebrate or fish), but fish are of particular interest because 1) they are present in most water bodies, 2) their taxonomy, ecological requirements and life histories are generally better known than those of other assemblages, 3) they occupy a variety of trophic levels and habitats, and 4) they have both economic and aesthetic values and thus help raise awareness of the value of conserving aquatic systems.

This paper proposes to illustrate the elaboration process of such biological tools. To address this issue we will first review the most important findings on the role of environmental factors in influencing local fish assemblages' structure in natural condition. We will limit to particular sets of factors that have been identified as significant in multiple studies and focus on both temperate and tropical fish fauna. We will also describe and evaluate (advantages and disadvantages) the fish-based methods integrating information on assemblage species richness, composition and abundance, and currently available for the assessment of the ecological quality of streams and rivers. Finally, we will give some guidelines for the elaboration of a biological tool based on fish assemblages for better assessment of rivers health across large regions for long time periods.

FACTORS STRUCTURING RIVERINE FISH ASSEMBLAGES IN TEMPERATE AND TROPICAL REGIONS

Although for many years intrinsic and extrinsic local processes (e.g. competition, predation, disturbance) were the focus of studies seeking to explain local fish assemblage structure (Schlosser, 1995), emphasis on the role of regional processes has increased as some studies have demonstrated their pervasive role in shaping local assemblages (Hughes et al., 1987; Whittier et al., 1988; Hugueny and Paugy, 1995; Hugueny et al., 1997; Belkessam et al., 1997; Angermeier and Winston, 1998; Oberdorff et al., 1998). Consequently, complete answers for the explanation of local fish assemblage richness and structure must address the relative importance of large-scale processes, which determine the species available to occur locally and small-scale processes, which should limit the number of species that actually occur locally (Angermeier and Winston, 1998). The important ecological question to be answered before defining biological tools based on fish assemblages to assess anthropogenic perturbations becomes what is the relative importance of local (biotic and abiotic) and regional factors in determining local assemblages structure and richness? The answer to this question it is crucial for establishing, and possibly regionalizing, suitable biological tools for evaluating the biotic integrity of rivers.

ROLE OF ABIOTIC FACTORS PROCESSES OCCURRING AT THE LOCAL LEVEL

Longitudinal changes in local assemblage richness and composition have usually been attributed to one of two processes: biotic zonation or continual addition of species downstream. Biotic zonation corresponds to discontinuities in river geomorphology or abiotic conditions promoting distinct assemblages along the longitudinal gradient (Huet, 1959; Schlosser, 1982; Balon et al., 1986; Rahel and Hubert, 1991; Oberdorff et al., 1993; Belliard et al., 1997). For example, species replacement may occur as a result of physiological specialization for temperature (Ferguson, 1958). However, additions of species are usually related to environmental gradients having smooth transitions of abiotic factors

contributing to nested patterns of assemblage composition along the longitudinal gradient (Sheldon, 1968, Rahel and Hubert, 1991).

Whatever be the process (i.e. biotic zonation or species addition) the local species richness usually increases along the upstream-downstream gradient. The few studies conducted in tropical streams and rivers reveal patterns that generally agree with patterns from temperate regions (e.g. Ibarra and Stewart 1989, Tito de Morais and Lauzanne, 1994; Mazzoni and Lobon-Cervia, 2000). This gradual accumulation of species is often attributed to a downstream increase in habitat size, habitat diversity, or both (e.g. measured as a function of stream width, volume, discharge, order, drainage basin area, depth, current velocity, substrate composition) (Sheldon, 1968; Bussing and Lopez, 1977; Sydenham, 1977; Gorman and Karr, 1978; Schlosser, 1982; Angermeier and Karr, 1983; Winemiller, 1983; Perez, 1984; Angermeier and Schlosser, 1989; Hugueny, 1990; Winemiller and Leslie, 1992; Paller, 1994; M rigoux et al., 1998; Tejerina-Garro, 2001) and in environmental stability (Horwitz, 1978; Matthews and Styron, 1981; Grossman et al., 1982; Schlosser, 1987; Poff and Ward, 1989; Schlosser and Ebel, 1989; Poff and Allan, 1995). Indeed, rivers are highly variable environments and are periodically subjected to extreme and often unpredictable fluctuations in their physical and chemical characteristics (e.g. flow, temperature, dissolved oxygen, pH, conductivity) and these fluctuations have been shown to affect the richness and structure of river fish assemblages (Horwitz, 1978; Grossman, 1982; Grossman et al., 1982, 1985, 1990, 1998; Schlosser, 1985; Merona, 1986; Schlosser and Ebel, 1989; Henderson and Walker, 1990; Poff and Allan, 1995; Landivar, 1995; Agostinho and Zalewski, 1995; Tito de Morais et al., 1995; Carrel and Rivier, 1996; Danehy et al., 1998; Lamouroux et al., 1999; Oberdorff et al., 2001b; Tejerina-Garro, 2001; Fialho 2002) by leading to local population extinctions, individual immigration and emigration in response to current conditions and through recruitment success (Freeman et al., 1988; Carrel and Rivier, 1996). Furthermore, the importance of intradrainage immigration in shaping assemblage richness and structure has been emphasized by Osborne and Wiley (1992). These authors observed that within a river basin, a higher local species richness occurred in sites belonging to tributary streams located lower in a

drainage network and connected to a main channel system than from similarly sized streams located in the headwaters of a drainage network. The potential mechanism responsible for this observed pattern was related to the immigration-extinction hypothesis (i.e. there should be a higher immigration rate in sites connected to the main channel which is assumed to be the colonization source).

These results suggest that extinction and colonization at the local scale are important processes in shaping fish assemblages and that environmental factors leading to temporal variability in populations size (e.g. discharge variability) are key components in explaining local fish assemblage structure and richness. However, the majority of the above studies mainly focused on species richness patterns without addressing explicitly the potential role of environmental factors on the functional aspect of these assemblages. Major exceptions are the studies of Rahel and Hubert (1991), Oberdorff *et al.* (1993), Belliard *et al.* (1997), M rigoux *et al.* (1998), Smogor and Angermeier (1999), Tejerina-Garro (2001) in lotic systems and Rodriguez and Lewis Jr. (1997) in lentic systems, which provided support for environmental factors effects on trophic and reproductive attributes of fish assemblages. Therefore, one can reasonably expect that functional attributes of fish assemblages would be related, as for species richness, to natural environmental gradients.

PROCESSES OCCURRING AT THE REGIONAL LEVEL

Patterns and processes observed in local fish assemblages are not only determined by local mechanisms acting within assemblages, but also result from processes operating at larger spatial scales (Hugueny and Paugy, 1995; Hugueny et al., 1997; Angermeier and Winston, 1998; Oberdorff et al., 1998, Jackson et al., 2001). The richness and structure of local fish assemblages has been linked to factors ranging from geomorphology and climate (Nelson et al., 1992; Hughes et al., 1987; Whittier et al., 1988; Matthews and Matthews, 2000; Tejerina-Garro, 2001), to richness of regional species pool (Hugueny and Paugy, 1995; Hugueny et al., 1997; Belkessam et al., 1997; Angermeier and Winston, 1998; Oberdorff et al., 1998; Gido and Brown, 1999). Concerning this

last relationship (local/regional richness) the emerging pattern is that few fish assemblages are truly saturated (Hugueny and Paugy 1995, Hugueny et al., 1997; Belkessam et al., 1997; Oberdorff et al., 1998). For example, Oberdorff *et al.* (1998) working on local fish assemblages of coastal streams of North-Western France found that these assemblages were unsaturated with species and with individuals and that inter-annual changes in populations were not strongly affected by densities of co-occurring species. Obviously in this study competition was not the main force driving these assemblages. Gido and Brown (1999) analysing colonization patterns by introduced freshwater fishes in 125 drainages across temperate North America, suggested that North American fish communities were not saturated in species, but instead, were capable of supporting higher levels of diversity if the pool of potential colonists and the rate of colonization from that pool was increased by species introduction. Then, studying local species assemblages in isolation cannot discover the determinants of local assemblage structure and richness, and the principal direction of control for local assemblage structure and richness is from regional to local (Cornell and Lawton, 1992; Lawton, 2000).

ROLE OF BIOTIC FACTORS COMPETITION AND PREDATION

An important question is to what extent predation and interspecific competition structure local riverine fish assemblages? The knowledge about it remains somewhat superficial even if some authors have suggested that these interactions may be strong enough to have pervasive effects (Werner, 1984, Jackson et al., 2001). However, there is little evidence that either predation or interspecific competition strongly affects local fish assemblages in rivers with the exception of few studies (Zaret and Rand, 1971; Schut et al., 1984; Wikramanayake and Moyle, 1989; Taylor, 1996; Resetarits, 1997, Jackson *et al.* 2001).

If we first consider interspecific competition, we can hypothesize that if this is really an important process, then it should set an upper limit to the number of species in an assemblage (another species could only be accommodated by the loss of a species). This hypothesis can be tested, for example, when introductions take place in a river.

Relative to this point, results of different studies previously detailed above show that local and regional fish communities are usually not saturated with species and are capable of supporting greater number of species if the pool of potential colonists and the rate of colonization from that pool was increased by species introduction (Belkessam et al., 1997; Angermeier and Winston, 1998; Oberdorff et al., 1998; Gido and Brown, 1999). These results strongly suggest that competition does not set the species saturation level in the assemblages studied and thus that competition is not a major force structuring these fish assemblages.

If we now consider predation, different studies have shown that this process can affect the choice of habitat by prey species within a river (Gorman, 1988; Schlosser and Angermeier, 1990). In tropical regions, mainly floodplain lakes, results suggest that predation is the mechanism responsible for fish structure in response to water transparency changes (Rodriguez and Lewis Jr., 1994, 1997). In other words, in some cases, fish assemblages' structure could be due to prey species' common avoidance of predators. Nevertheless, studies concerning competition or predation have noticed effects only on limited range of species combinations and thus are unable to provide real evidence that one of them is a major factor in organizing species assemblages.

SYNTHESIS

Table 1, even if obviously non-exhaustive, shows the significant relationships between local riverine fish assemblages and different environmental factors. Of the factors examined, we found the most consistent patterns of local assemblage structure and richness related to measures of river size (e.g. distance from sources, basin area, stream order, river width), elevation, river gradient, water velocity, depth, temperature, conductivity, habitat diversity, flow regimes, ecoregions and/or regional richness (i.e. pool of potential colonists). Relationships with competition and/or predation (biotic factors) were more equivocal. However, in this case it is necessary to point out the influence of the spatial scale used in each study considered in this paper. That is, small-scale studies usually indicate a greater importance of competition in structuring fish assemblages while large-scale

studies usually emphasize abiotic controls (Jackson et al., 2001).

Another possible explanation for the noticed weak effect of predation and competition in structuring local assemblages could come from the predominance of studies carried out in temperate zones (compared to tropical ones) where fish fauna (e.g. Europe, North America) is reduced in richness due to historical processes (Mahon, 1984; Oberdorff et al., 1997) and where few congeneric species co-exist. If we assume that congeneric species have similar ecological niches (closely related species) then they should be strong competitors and competitive exclusion or density adjustments should occur more often among congeneric species than in more distantly related ones. Then we can suppose that competition is more common in tropical zones compared to temperate ones (Ricklefs, 1993). Nevertheless, more studies are needed to quantify this effect and its possible impact on assemblage structure in tropical rivers. Thus, apparently development of accurate biological indicators will have to integrate the relevant environmental factors to obtain a response of fish assemblages to human

stressors that can be discriminated from natural variation.

FISH-BASED METHODS CURRENTLY AVAILABLE

There are relatively few ecological tools based on fish assemblages that uses structural and functional components of fish assemblages for assessment of river condition in temperate and tropical rivers. Two major approaches (tools) can be distinguished. Both use the "reference condition approach" (Bailey et al., 1998), which involves testing an ecosystem exposed to a potential stress against a reference condition that is unexposed to such a stress. Most common way is to select the reference sites that are "minimally disturbed" because pristine conditions no longer exist in most industrialized countries and coming back to prehistoric conditions first, will deny the place of humans in the landscape (Norris and Thoms, 1999) and second, will make restoration goals obsolete because obviously not attainable.

Table 1 - Results of empirical studies that describe the effect of environmental factors or phenomenon on local fish assemblage structure at different spatial scales.

Scale Factor	Effect	No effect
Local (site) <i>Altitude</i>	Beecher et al., 1988; Lauzanne et al., 1991*; Rahel and Hubert, 1991; Mastorillo et al., 1998; Angermeier and Winston, 1998; Oberdorff et al., 2001a	Maret et al., 1997; Waite and Carpenter, 2000
<i>River size</i> <i>Basin area</i> <i>Distance from sources</i> <i>River width</i> <i>Stream order</i>	Huet, 1959; Sheldon, 1968; Bussing and Lopez, 1977*; Sydenham, 1977*; Horwitz, 1978; Lauzanne and Loubens, 1988*; Angermeier and Karr, 1983*; Winemiller, 1983*; Mahon, 1984; Balon et al., 1986; Hugues and Gammon, 1987; Beecher et al., 1988; Matthews and Robinson, 1988; Paugy et al., 1988*; Ibarra and Stewart, 1989; Hugueny, 1990*; Lyons and Schneider, 1990*; Osborne and Wiley, 1992; Winemiller and Leslić, 1992*; Oberdorff et al., 1993; Lyons, 1996; Belliard et al., 1997; Maret et al., 1997; Mastorillo et al., 1998; Kamdem-Toham and Teugels, 1997*; Méricoux et al., 1998*; Angermeier and Winston, 1998; Matthews and Matthews, 2000; Tejerina Garro, 2001*	Mérona, 1981*
<i>River gradient</i>	Huet, 1959; Lyons, 1996; Maret et al., 1997; Mastorillo et al., 1998; Waite and Carpenter, 2000; Oberdorff et al., 2001*	
<i>Water velocity</i>	Hugueny, 1990*; Angermeier and Schlosser, 1989*; Lamouroux et al., 1999; Matthews and Matthews, 2000; Oberdorff et al., 2001*	

Cont. Table 1

Cont. Table 1

<i>Habitat diversity</i> §	Gorman and Karr, 1978*; Schlosser, 1982; Perez, 1984*; Angermeier and Schlosser, 1989*; Kamdem-Toham and Teugels, 1997*; Mérioux et al., 1998*; Tejerina-Garro, 2001*	Grossman et al., 1998
<i>Depth</i>	Sheldon, 1968; Evans and Noble, 1979; Schlosser, 1982; Gorman, 1988; Hugueny, 1990*; Winemiller and Leslie, 1992*; Taylor et al., 1993; Matthews and Matthews, 2000; Oberdorff et al., 2001a	
<i>Conductivity</i>	Taylor et al., 1993; Kamdem-Toham and Teugels, 1997*; Mérioux et al., 1998*; Tejerina-Garro, 2001*	
<i>Temperature</i>	Verneaux, 1977; Baltz et al., 1982; Schlosser, 1987; Rathert et al., 1999; Waite and Carpenter, 2000	
<i>Flow variability</i>	Horwitz, 1978; Meffe, 1984; Schlosser, 1985; Poff and Allan, 1995; Grossman et al., 1998; Oberdorff et al., 2001b	
<i>Competition and/or Predation</i>	Zaret and Rand, 1971*; Fausch and White, 1981; Baltz et al., 1982; Schut et al., 1984*; Gorman, 1988; Wikramanayake and Moyle, 1989*; Taylor, 1996; Resettarits, 1997	Schlosser, 1982; Oberdorff et al., 1998; Grossman et al., 1998; Gido and Brown, 1999; Oberdorff et al., 2001a
<i>Regional (basin) Ecoregion/Physiography Hydrological units</i>	Hughes et al., 1987; Hughes et al., 1998; Matthews and Robinson, 1988; Whittier et al., 1988; Nelson et al., 1992; Belliard et al., 1997; Oberdorff et al., 2001a	
<i>Basin richness</i>	Beecher et al., 1988; Hugueny and Paugy, 1995*; Belkessam et al., 1997; Hugueny et al., 1997*; Angermeier and Winston, 1998; Matthews and Robinson, 1988; Oberdorff et al., 1998	Matthews and Matthews, 2000

§ usually measured in three dimensions: depth, water velocity and substrate; * tropical studies

THE INDEX OF BIOTIC INTEGRITY (IBI)

The first approach to quantify the impact of human activities on the aquatic ecosystem is a multimetric index, the Index of Biotic Integrity (IBI), first formulated by Karr (1981) and latter refined by Karr *et al.* (1986) for use in Midwestern USA streams. The IBI is based on the hypothesis that there are predictable relationships between fish assemblage structure and the physical, chemical and biological condition of stream systems. The IBI employs a series of metrics based on assemblage structure that give reliable signals of river condition to calculate an index score at a site, which is then compared to the score expected at an unimpaired comparable site. Classes of metrics in the IBI include species richness, species

composition, trophic structure, total fish abundance, and individual fish condition (Table 2). Each metric reflects the quality of a different aspect of the fish assemblage that responds in a different manner to aquatic ecosystem stressors (Hughes and Noss, 1992). The combination of metrics reflects insights from individual, population, assemblage, ecosystem and zoogeographic perspectives.

The IBI methodology is outlined in Table 3. The primary underlying assumptions of the IBI concept are presented in Table 4. Since its introduction, the IBI has been modified for use in other regions and types of ecosystems throughout North America (Karr and Chu, 1999). It has also been modified for use outside North America (Hughes and Oberdorff, 1999) on six continents: Europe

(Oberdorff and Hughes, 1992; Oberdorff and Porcher, 1994; Berrebi dit Thomas et al., 1998; and Belliard et al., 1999 in France; Kestemont et al., 2000 and Belpaire et al., 2000 in Belgium; Kesminas and Virbickas, 2000 in Lithuania), Africa (Hugueny et al., 1996 in Guinea, Hocutt et al., 1994 on the Namibia-Angola border, Hay et al., 1996 in Namibia, Kamdem-Toham and Teugels, 1999 in Gabon), Asia (Ganasan and Hughes, 1998 in India), Australia (Harris, 1995), Central America (Lyons et al., 1995 in Mexico) and South America (Gutierrez, 1994 in Venezuela;

Araújo, 1998 in Brazil; Tejerina-Garro, 2001 in French Guiana). In South America, the index adaptations made by Gutierrez (1994) and Araújo (1998) have conserved the same metrics as used in temperate regions. However, a new approach was used in French Guiana (South America), which selected the metrics to be used based on an empirical study of the interaction fish fauna-habitat using taxonomical and functional descriptors (Tejerina-Garro, 2001).

Table 2 - IBI metrics for Midwestern USA streams (from Karr et al., 1986; Miller et al., 1988). ^aValue approximates (5), deviates somewhat (3), or deviates strongly (1) from the reference condition; ^bExpected value varies with stream size, region, and basin; ^cAdult diets typically include ≥ 25 % plant and ≥ 25 % animal material; ^dAdult diets usually composed largely of aquatic vertebrates or crayfish; ^eDisease, eroded fins, lesions, tumors, discoloration, excessive mucous, skeletal abnormalities, missing organs, and other external symptoms.

Category Metric	Scoring Criteria ^a		
	5	3	1
Species Richness			
1. Total number of fish species	b	b	b
2. Number of darter species	b	b	b
3. Number of sunfish species	b	b	b
4. Number of sucker species	b	b	b
Habitat guilds			
5. Number of intolerant species	b	b	b
6. % individuals as green sunfish	<5	5-20	>20
Trophic guilds			
7. % individuals as omnivores ^c	<20	20-45	>45
8. % individuals as insectivorous cyprinids	>45	20-45	<20
9. % individuals as piscivores ^d	>5	1-5	<1
Abundance			
10. Number of individuals	b	b	b
Reproduction and Condition			
11. % individuals as hybrids	0	>0-1	>1
12. % individuals with anomalies ^e	0-2	>2-5	>5

Even if these applications attest to the utility of the concept (Karr and Chu, 1999), it should be noticed anyway that none of these studies (except Belliard et al., 1999 and Tejerina-Garro, 2001) truly validated the methodology with independent datasets of both disturbed and reference sites.

Properly developed IBI's usually incorporate region-specific metrics and adjust metric criteria (usually only for taxonomic metrics) by river size (e.g. stream order or catchment's area) to isolate natural versus anthropogenic influences on local fish assemblage structure. Region-specific criteria

are set using broad regional land classification (e.g. ecoregions). The basis of this approach is the understanding that the character of a river (e.g. its water quality, flow regime, habitat structure, energy base) is in large part a function of the climate, topography, geology, soil, vegetation, and land use of its geographic region. Such an approach is efficient in grouping similar rivers (at least at some level of resolution), allowing the reduction of the natural regional variability.

THE FISH-BASED INDEX (FBI)

The second approach originates from a research program (1996-2000) initiated by the French Water Agencies and the Ministry of the Environment to develop a fish-based index that could be applicable nationwide (Oberdorff *et al.*, 2001a; Oberdorff *et al.*, 2002).

Such an index had to encompass the relative importance of potential regional and local processes influencing the distribution of riverine fish. Convinced that the IBI's concept was ecologically sound effective for assessment of the status, trends, and ecological integrity of a water body Oberdorff *et al.* (2001a, 2002) tried to improve the accuracy of such an index while maintaining its theoretical foundations. They did it by using the recent findings in aquatic ecology to distinguish, as far as possible, effects of anthropogenic disturbances from natural variation in assemblage structure and richness. The rationale for the development of the FBI is summarized in Table 5 and detailed in Oberdorff *et al.* (2002).

Three independent data sets were used: 1) two sets of reference sites, fairly evenly distributed across French rivers; 2) a third set of exposed (disturbed) sites. A variety of metrics based on occurrence and abundance data and reflecting different aspects of the fish assemblage structure and function were selected from available literature and for their potential to indicate degradation. For metrics based on species occurrences, logistic multiple regression procedures were applied, using the first data set of reference sites and defined by the main regional and local factors known to influence local fish assemblages (see Table 1) (i.e. drainage area, distance from sources, altitude, river gradient, water velocity, depth, temperature, and hydrological units), to elaborate the simplest possible response model that adequately explains the observed patterns of occurrence for each

species of a fish assemblage for a given site of any given river.

For a given occurrence metric, a theoretical assemblage for each site is obtained by summing the predicted probability of each species included in the considered metric. For metrics based on abundance data, stepwise multiple regression procedures were applied to elaborate the simplest possible response model that adequately explains the observed value of each metric (i.e. the sum of log-transformed density of individuals belonging to species considered in the metric) for a given site of any given river. All models retained a majority of environmental factors underlying their importance in structuring local fish assemblages as discussed earlier. After eliminating metrics for which residuals distribution values statistically differed from a normal distribution using the initial data set of reference sites, and after converting residual values of the *n* metric models into probabilities, models obtained for each metric were validated using the two independent data sets of reference and disturbed sites. These procedures allowed to select the most effective metrics in discriminating between reference and disturbed sites (Table 6). Overall, the FBI performed well in discriminating between reference and disturbed sites and in distributing sites along the gradient of perturbations (Fig. 2). It is thus a useful indicator of running-water ecosystems, which could be used to monitor change and provide a baseline for measuring the full biotic response to restoration of these rivers. Moreover, it can be applied in the different regions and river types of France using a consistent set of metrics despite the complex and heterogeneous geology and climate of that country.

The final index score was obtained by computing the combined probabilities corresponding to the remaining effective metrics. To avoid logical circularity, the optimal cut-off level for a local assemblage "impairment" was obtained by analysing distributions of index scores for the two independent data sets of reference and disturbed sites.

Table 3 - Principles of fish assemblage assessment with the IBI (Modified after Hughes and Oberdorff, 1999).

1. Select a relatively homogeneous region. A region may be an ecoregion, basin, or fish faunal region that is homogeneous with respect to a combination of environmental characteristics (e.g., climate, physiography, soil, vegetation) and potential fish species.
2. Determine the reference condition(s). References may be a set of minimally disturbed reference streams, a disturbance gradient, historical data, paleoecological information, and professional judgement.
3. List candidate metrics and assign species to trophic, tolerance, and habitat guilds. Regional fish texts usually provide this information, at least in developed countries.
4. Sample fish assemblages. This is best done (a) when they are least variable yet most limited by anthropogenic stressors and (b) in a manner yielding a representative collection of species and proportionate abundances, but that (c) is cost-effective.
5. Tabulate numbers of individuals collected by species at each reach.
6. Calculate values for each candidate IBI metric. Typically these are proportions or percents of individuals, or numbers of species in particular categories.
7. Develop scoring criteria. These are based on previously available information from step 2 or from fish data collected at minimally disturbed sites in step 4. Scoring criteria may be continuous (0-1 or 0-10) or based on classes (1, 3, 5 or 0, 5, 10). An IBI score represents comparisons between metric value at a sample site and those expected under reference conditions. Metric criteria are usually adjusted by river size.
8. Calculate metric scores and add these to obtain an IBI score.
9. Evaluate metric and index scores. Consider, differences between expected and obtained scores, compare variance results from repeated samples, assess responsiveness to environmental stressors. Modify or reject metrics that are highly variable or unresponsive, and recalculate if necessary.
10. Interpret IBI score as indicating an acceptable, marginally impaired, or highly impaired fish assemblage; or as excellent, good, fair, poor, very poor.

Table 4 - Assumed effects of environmental degradation on fish assemblages (from Fausch et al., 1990 and Hughes and Noss, 1992). ^aIn some waters; especially oligotrophic cold water systems, increased nutrients and temperatures often result in additional species and individuals.

Number of native species and of those in specialized taxa or guilds declines^a

Number of sensitive species declines

% of trophic and habitat specialists declines

Total number of individuals declines^a

% of large individuals and the number of size classes decrease

% of tolerant individuals increases

% of trophic and habitat generalists increases

% individuals with anomalies increases

Table 5 - General principles of fish assemblage assessment with the FBI (Oberdorff et al., 2002).

1. Determine the reference condition(s)
2. List candidate metrics and assign species to trophic, tolerance, and habitat guilds based on literature review
3. Model metrics in relation to regional and local environmental factors. The method is designed to predict a metric value at a particular reference site, independent of natural environmental factors. Eliminate metrics not adequately modelised
4. Validate the models using independent data sets of reference and disturbed sites in order to select the most effective metrics in discriminating between reference and disturbed sites (reject metrics that are highly variable or unresponsive)
5. Add metrics values to obtain an index score
6. Develop scoring criteria
7. Interpret index score as excellent, good, fair, poor, very poor

Table 6 - Fish assemblage metrics used to calculate the FBI for French rivers (after Oberdorff et al., 2002).

Category	Metrics
Taxonomic richness	1. Total number of species
Habitat composition	2. Number of reophilic species 3. Number of lithophilic species
Assemblage sensitivity	4. Tolerant species individuals
Trophic composition	5. Invertivorous species individuals 6. Omnivorous species individuals
Fish abundance	7. Total density of individuals

ADVANTAGES AND DISADVANTAGES OF BOTH INDEX

Both index have several advantages in common. They are broadly based ecological indexes that assess both assemblage structure and function at several trophic levels; they are flexible and widely adaptable and combine several types of metrics (e.g. taxonomic, reproductive, trophic and tolerance metrics) that individually provide different responses to perturbations. Consequently, they are responsive to general types of degradation, and should then be able to quantify the biological effects of human activities on aquatic ecosystems.

The main difference between the FBI and the IBI methodologies lies on the way metric (fish assemblage attributes) criteria are adjusted (i.e. the expected value of a metric for a given site

under conditions least affected by anthropogenic disturbance). As previously mentioned, the IBI approach consists in adjusting species richness-metric (e.g. total species richness, number of tolerant species, number of benthic species) criteria exclusively on the basis of empirical relations between river size (i.e. position of a given site along the upstream-downstream gradient) and taxa richness. Nevertheless, stratifying intra-regional criteria by using only a single factor like river size is clearly inadequate as previously discussed in this paper (see Table 1). Moreover, most of the time, abundance related metrics (i.e functional metrics such as total number of individuals, proportional abundance of omnivores, proportional abundance of lithophilic individuals) are not adjusted at all suggesting that these metrics are invariant across river sizes or

other environmental factors. Ignoring potential relations between environmental factors and these last metrics seems contrary to evidence that such relations exist (see Table 1). For example, the River Continuum concept (Vannote et al., 1980) explicitly predicts changes in fish trophic structure along a longitudinal gradient. This concept attempts to relate the gradient in physical factors that occurs along river systems, to change in assemblage structure and function. According to this concept, available food resources should change along this gradient and thus should be reflected by the trophic composition of the assemblages. These predictions have been confirmed for fish assemblages in French river by Oberdorff *et al.* (1993) (*i.e.* a decrease in invertivorous species and an increase in omnivorous species from upstream to downstream). Moreover, Oberdorff *et al.* (2002), provided empirical support that other functional

metrics varied with river size and other environmental factors. Oberdorff *et al.* (2002) used predictive models to assess the response of local assemblage attributes (metrics) to natural environmental gradients. The environmental variables selected correspond to five categories of environmental attributes of sites (*i.e.* river size (measured by a combination of drainage area and distances from sources), altitude, water velocity (measured by a combination of river width, river depth and river gradient) temperature, and hydrological units). All five attributes appeared critical in predicting metrics value for a given site. Although the predictor factors for each of the metric models were slightly different, all models included factors that incorporate information on each of these five attributes (Table 7).

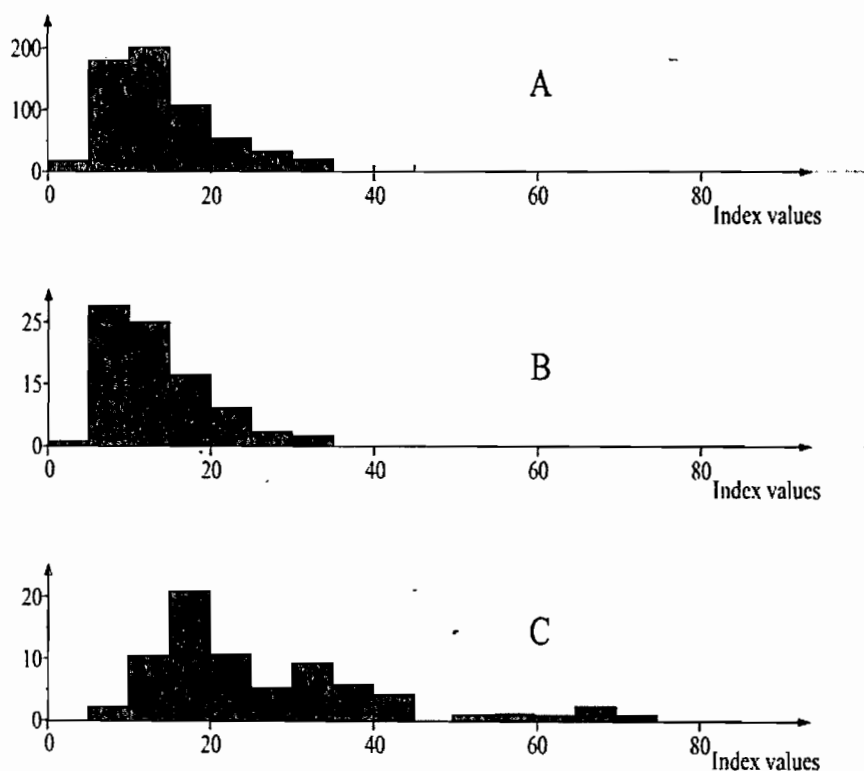


Figure 2 - Distribution of the index scores for the three independent data sets. (A) and (B) reference sites, (C) disturbed sites. From Oberdorff *et al.* (2002).

Thus, it is clear that to set appropriate metric criteria, one should compare how metrics vary with river size relative to how they differ across regions and/or drainages, and relevant local environmental gradients within each. This type of approach appears to be of importance for

elaboration of an accurate biological indicator. This strategy was adopted for the EC research programme (FAME, 2001-2004; <http://www.fame.boku.ac.at>) to develop a fish-based assessment method for the ecological status of European rivers.

Table 7 - Commonly used predictor factors for FBI models. *Total number of predictive models tested=38.

Scale Factor	Number of models*integrating factor as a predictor
Local	
Altitude	24
River size	36
Basin area	
Distance from sources	
Water velocity	27
River width	
River gradient	
Depth	
Temperature	33
Regional	
Hydrological units	26

CONCLUSIONS

The ability to protect biological resources relies on the ability to identify and predict the effects of human activities on biological systems. This depends first on the capacity in distinguishing between natural and human-induced variation in biological condition. To achieve this goal, it is important for researchers to continue to develop and improve multimetric fish-based indexes by accounting for the many possible sources of inter and intraregional variation in assemblages structure in natural conditions. A special attention should be given to analyse natural environmental effects on functional metrics, which has been until now too often neglected. Accounting for these natural variations will greatly enhance index's intended function, *i.e.*, to solely reflect anthropogenic disturbance effects (Smogor and Angermeier, 1999).

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RESUMO

A água dos rios constituem um recurso básico para a humanidade. Instrumentos biológicos eficazes (com fundamento ecológico, eficientes, rápidos e aplicáveis à regiões ecologicamente diferentes) são necessários para medir a "saúde" destes. Adaptar tais instrumentos a uma grande área geográfica requer uma compreensão detalhada dos padrões da composição da assembléia de organismos e da sua distribuição dentro e entre os corpos da água em condições naturais, e da natureza dos principais gradientes ambientais que causam ou explicam estes padrões. Uma revisão da literatura disponível pode ajudar a identificar os fatores ambientais mais consistentes que estruturam a assembléia de peixes de ambientes lóticos em condições naturais.

REFERENCES

- Agostinho, A. A. and Zalewski, M. (1995), The dependence of fish community structure and dynamics on floodplain and riparian ecotone zone in Parana River, Brazil. *Hydrobiologia*, **303**, 141-148.
- Angermeier, P. L. and Karr, J. R. (1983), Fish communities along environmental gradients in a system of tropical streams. *Environmental Biology of Fishes*, **9**, 117-135.

- Angermeier, P. L. and Schlosser, I. J. (1989), Species area relationships for stream fishes. *Ecology*, **70**, 1450-1462.
- Angermeier, P. L. and Winston, M. R. (1998), Local vs. Regional influences on local diversity in stream fish communities of Virginia. *Ecology*, **79**, 911-927.
- Araújo, E. G. (1998), Adaptação do índice de integridade biótica usando a comunidade de peixes para o rio Paraíba do Sul. *Rev. Brasil. Biol.*, **58**, 547-558.
- Bailey, R. C.; Kennedy, M. G.; Dervish, M. Z. and Taylor, R. M. (1998), Biological assessment of freshwater ecosystems using a reference approach: comparing predicted and actual benthic invertebrate communities in Yukon streams. *Freshwater Biology*, **39**, 765-774.
- Balon, E. K.; Crawford, S. S. and Lelek, A. (1986), Fish communities of the upper Danube River (Germany, Austria) prior to the new Rhein-Main-Donau connection. *Environmental Biology of Fishes*, **15**, 243-271.
- Baltz, D. M.; Moyle, P. B. and Knight, N. J. (1982), Competitive interactions between benthic stream fishes: riffle sculpin *Cottus gulosus*, and speckled dace, *Rhinichthys osculus*. *Canadian Journal of Fish and Aquatic Sciences*, **39**, 1502-1511.
- Beecher, H. A.; Dott, E. R. and Fernau, R. F. (1988), Fish species richness and stream order in Washington State streams. *Environmental Biology of Fishes*, **22**, 193-209.
- Belkessam, D.; Oberdorff, T. and Hugueny, B. (1997), Unsaturated fish assemblages in rivers of the North-Western France : potential consequences for species introductions *Bulletin Français de Pêche et Pisciculture*, **344/345**, 193-204.
- Belliard, J.; Berrebi dit Thomas, R. and Monnier, D. (1999), Fish communities and river alteration in the Seine Basin and nearby coastal streams. *Hydrobiologia*, **400**, 155-166.
- Belliard, J.; Boët, P. and Tales, E. (1997), Regional and longitudinal patterns of fish community structure in the Seine River basin, France. *Environmental Biology of Fishes*, **50**, 133-147.
- Belpaire, C.; Smolders, R.; Vanden Auweele, I.; Ercken, D.; Breine J., Van Thyne, G. and Ollevier, F. (2000), The index of biotic integrity characterizing fish populations and ecological quality of Flandrian water bodies. *Hydrobiologia*, **434**, 17-33.
- Berrebi dit Thomas, R.; Belliard J. and Boët P. (1998), Caractéristiques des peuplements piscicoles sensibles aux altérations du milieu dans les cours d'eau du bassin de la Seine. *Bulletin Français de Pêche et Pisciculture*, **348**, 47-64.
- Bussing, W. A. and Lopez, M. I. (1977), Distribución y aspectos ecologicos de los peces de las cuencas hidrograficas de Arenal Bebedero y Tempisque, Costa Rica. *Revista de Biología Tropical*, **25**, 13-37.
- Carrel, G. and Rivier, B. (1996), Distribution of three euryoecious cyprinids in the main channel of the Lower River Rhône. *Archiv Für Hydrobiologie*, **113**, 363-374.
- Cornell, H. V. and Lawton, J. H. (1992), Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology*, **61**, 1-12.
- Danehy, R. J.; Ringler, N. H.; Stehman, S. V. and Hassett, J. M. (1998), Variability of fish densities in a small catchment. *Ecology of Freshwater Fish*, **7**, 36-48.
- Evans, J. W. and Noble, R. L. (1979), The longitudinal distribution of fishes in an east Texas stream. *American Midland Naturalist*, **101**, 333-334.
- Fausch, K. D. and White, R. J. (1981), Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in a Michigan stream. *Canadian Journal of Fish and Aquatic Sciences*, **38**, 1220-1227.
- Fausch, K. D.; Lyons, J.; Karr, J. R. and Angermeier, P. L. (1990), Fish communities as indicators of environmental degradation. In *Biological indicators of stress in fish*. *American Fisheries Society Symposium* 8, Bethesda, Maryland, USA, **8**, 123-144.
- Ferguson, R. G. (1958), The preferred temperature of fish and their midsummer distribution in temperate lakes and streams. *J. Fish. Res. Bd. Can.*, **15**, 607-624.
- Fialho, A. P. (2002), Ecologia da comunidade ictiofaunística da bacia do rio Meia Ponte. Master thesis. Universidade Federal de Goiás. 60 p.
- Freeman, M. C.; Crawford, M. K.; Barrett, J. C.; Facey, D. E.; Flood, M. G.; Hill, J.; Stouder, D. J. and Grossman, G. D. (1988), Fish assemblage stability in a Southern Appalachian stream. *Canadian Journal of Fish and Aquatic Sciences*, **45**, 1949-1958.
- Ganasan, V. and Hugues, R. M. (1998), Application of an index of biological integrity (IBI) to fish assemblages of the rivers Khan and Kshipra (Madhya Pradesh), India. *Freshwater Biology*, **40**, 367-383.
- Gido, K. B. and Brown, J. H. (1999), Invasion of North American drainages by alien fish species. *Freshwater Biology*, **42**, 387-399.
- Gorman, O. T. and Karr, J. R. (1978), Habitat structure and stream fish communities. *Ecology*, **59**, 507-515.
- Gorman, O. T. (1988), An experimental study of habitat use in an assemblage of Ozark minnows. *Ecology*, **69**, 1239-1250.
- Grossman, G. D. (1982), Dynamics and organization of a rocky intertidal fish assemblage: the persistence and resilience of taxocene structure. *American Naturalist*, **119**, 611-637.
- Grossman, G. D.; Dowd, J. F. and Crawford, M. (1990), Assemblage stability in stream fishes: a review. *Environmental Management*, **5**, 661-671.

- Grossman, G. D.; Freeman, M. C.; Moyle, P. B. and Whittaker, J. O. (1985), Stochasticity and assemblage organization in an Indiana stream fish assemblage. *American Naturalist*, **126**, 275-285.
- Grossman, G. D.; Moyle, P. B. and Whittaker, J. O. (1982), Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. *American Naturalist*, **120**, 423-454.
- Grossman, G.; Ratajczak, R. E.; Crawford, M. and Freeman, M. C. (1998), Assemblage organization in stream fishes: effects of environmental variation and interspecific interactions. *Ecological Monographs*, **68**, 395-420.
- Gutierrez, M. A. R. (1994), Utilización de la ictiofauna como indicadora de la integridad biótica de los ríos Guache y Guanare, Estado Portuguesa, Venezuela. Master thesis. Universidad Nacional Experimental de los Llanos Occidentales "Ezequiel Zamora". 144 pp.
- Harris, J. H. (1995), The use of fish in ecological assessments. *Australian Journal of Ecology*, **20**, 65-80.
- Hay, C. J.; van Zyl, B. J. and Steyn, G. J. (1996), A quantitative assessment of the biotic integrity of the Okavango River, Namibia, based on fish. *Water SA*, **22**, 263-284.
- Henderson, P. A. and Walker, I. (1990), Spatial organization and population density of the fish community of the litter banks within a central Amazonian blackwater stream. *Journal of Fish Biology*, **37**, 401-411.
- Hocutt, C. H.; Johnson, P. N.; Hay, C. and Van Zyl Ben, J. (1994), Biological basis of water quality assessment: the Kavango River, Namibia. *Rev. Hydrobiol. trop.*, **27** (4), 361-384.
- Horwitz, R. J. (1978), Temporal variability patterns and the distribution patterns of stream fishes. *Ecological Monographs*, **48**, 307-321.
- Huet, M. (1959), Profiles and biology of Western European streams as related to fish management. *Transaction of the American Fisheries Society*, **88**, 155-163.
- Hughes, R. M. and Gammon, J. R. (1987), Longitudinal changes in fish assemblages and water quality in the Willamette River, Oregon. *Transaction of the American Fisheries Society*, **116**, 196-209.
- Hughes, R. M. and Noss, R. F. (1992), Biological diversity and biological integrity: current concerns for lakes and streams. *Fisheries*, **17**, 11-19.
- Hughes, R. M. and Oberdorff, T. (1999), Applications of IBI Concepts and Metrics to Waters Outside the United States and Canada. Pages 79-83. In: Thomas P. Simon (Ed.). *Assessment Approaches for Estimating Biological Integrity using Fish Assemblages*. Lewis Press, Boca Raton, FL, USA.
- Hughes, R. M.; Kaufmann, P. R.; Herlihy, A. T.; Kincaid, T. M.; Reynolds, L. and Larsen, D. P. (1998), A process for developing and evaluating indices of fish assemblage integrity. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 1618-1631.
- Hughes, R. M.; Rexstad, E. and Bond, C. E. (1987), The relationship of aquatic ecoregions, river basins, and physiographic provinces to the ichthyogeographic regions of Oregon. *Copeia*, **1987**, 423-432.
- Hugueny, B. (1990), Richesse des peuplements de poissons dans le Niandan (haut Niger, Afrique) en fonction de la taille de la rivière et de la diversité du milieu. *Revue Hydrobiologie Tropicale*, **23**, 351-364.
- Hugueny, B.; Camara, S.; Samoura, B. and Magassouba, M. (1996), Applying an index of biotic integrity based on fish assemblages in a West African river. *Hydrobiologia*, **331**, 71-78.
- Hugueny, B.; Tito de Morais, L.; Méricoux, S.; Mérona, B. and Ponton, D. (1997), The relationship between local and regional species richness: comparing biotas with different evolutionary histories. *Oikos*, **80**, 583-587.
- Hugueny, B. and Paugy, D. (1995), Unsaturated fish communities in African rivers. *American Naturalist*, **146**, 162-169.
- Ibarra, M. and Stewart, D. J. (1989), Longitudinal zonation of sandy beach fishes in the Napo river basin, Eastern Ecuador. *Copeia*, **2**, 364-389.
- Jackson, D. A.; Peres-Neto, P. R. and Olden, J. D. (2001), What controls who is where in freshwater fish communities – the roles of biotic, abiotic, and spatial factors. *Can. J. Fish. Aquat. Sci.* **58**, 157-170.
- Kamdem-Toham, A. and Teugels, G. G. (1997), Diversity patterns of fish assemblages in the Lower Ntem River basin (Cameroun), with notes on potential effects of deforestation. *Arch. Hydrobiol.*, **141**, 421-426.
- Kamdem-Toham, A. and Teugels, G. G. (1999), First data on an Index of Biotic Integrity (IBI) based on fish assemblages for the assessment of the impact of deforestation in a tropical West African river system. *Hydrobiologia*, **397**, 29-38.
- Karr, J. R.; Fausch, K. D.; Angermeier, P. L.; Yant, P. R. and Schlosser, I. J. (1986), Assessing Biological Integrity in Running Waters: A Method and its Rationale. *Illinois Natural History Survey Special Publication 5*, Champaign, Illinois, USA.
- Karr, J. R. and Chu, E. W. (1999), *Restoring life in running waters: better biological monitoring*. Island Press, Washington, DC, USA.
- Karr, J. R. (1981), Assessment of biotic integrity using fish communities. *Fisheries*, **6**, 21-27.
- Kesminas, V. and Virbickas, T. (2000), Application of an adapted index of biotic integrity to rivers of Lithuania. *Hydrobiologia*, **422/423**, 257-270.

- Kestemont, P.; Didier, J.; Depiereux, E. and Micha, J. C. (2000), Selecting ichthyological metrics to assess river basin ecological quality. *Archiv Für Hydrobiologie*, **121**, 321-348.
- Lamouroux N., Olivier J.M., Persat H., Pouilly M., Souchon Y. and Statzner B. (1999), Predicting community characteristics from habitat conditions: fluvial fish and hydraulics. *Freshwater Biology*, **42**, 275-299.
- Landivar J. (1995), Ecologie de la communauté de poissons et du chame (*Dormitator latifrons*) dans les rivières Vincennes et Babahoyo (Equateur) et leur plaine d'inondation. Master thesis. Université du Québec à Montréal. 69 p.
- Lauzanne L. and Loubens G. (1988), Estudios ictiológicos del convenio ORSTOM-UTB-CORDEBENI en la Amazonia boliviana. *Memorias Sociedad de Ciencias Naturales La Salle*, **48**, 387-407.
- Lauzanne L., Loubens G. and Le Guennec B. (1991), Liste commentée des poissons de l'Amazonie bolivienne. *Revue d'Hydrobiologie Tropicale*, **24**, 61-76.
- Lawton J. H. (2000), Community ecology in a changing world. Ecological Institute, Oldendorf/Luhe, Germany.
- Lyons J. and Schneider D. W. (1990), Factors influencing fish distribution and community structure in a small coastal river in South-Western Costa Rica. *Hydrobiologia*, **203**, 1-14.
- Lyons J. (1996), Patterns in the species composition of fish assemblages among Wisconsin streams. *Environmental Biology of Fishes*, **45**, 329-341.
- Lyons J., Navarro-Pérez S., Cochran P. A., Santana C. E. (1995), Index of Biotic Integrity based on fish assemblages for the conservation of streams and rivers in West-Central Mexico. *Conservation Biology*, **9**(3), 569-584.
- Mahon R. (1984), Divergent structure in fish taxocenes of north temperate streams. *Canadian Journal of Fisheries and Aquatic Sciences*, **41**, 330-350.
- Maret T. R., Robinson C. T. and Minshall G. W. (1997), Fish assemblages and environmental correlates in least-disturbed streams of the upper Snake River basin. *Transactions of the American Fisheries Society*, **126**, 200-216.
- Mastorillo S., Dauba F., Oberdorff T., Guégan J. F. and Lek S. (1998), Predicting local fish species richness in the Garonne River basin. *C. R. Acad. Sci. Paris (Life Sciences)*, **321**, 423-428.
- Matthews E. M. and Matthews W. J. (2000), Geographic, terrestrial and aquatic factors: which most influence the structure of stream fish assemblages in the midwestern United States? *Ecology of Freshwater Fish*, **9**, 9-21.
- Matthews W. J. and Robinson H. W. (1988), The distribution of the fish of Arkansas: a multivariate analysis. *Copeia*, **1988**, 358-374.
- Matthews W. J. and Styron J. T. (1981), Tolerance of headwaters vs. mainstream fishes for abrupt physicochemical changes. *American Midland Naturalist*, **105**, 149-158.
- Mazzoni R. and Lobon-Cervia J. (2000), Longitudinal structure, density and production of a neotropical stream fish assemblage: the river Ubatiba in the Serra do Mar, southeast Brazil. *Ecography*, **23**(5), 588-602.
- Meffe G. K. (1984), Effects of abiotic disturbance on coexistence of predator-prey fish species. *Ecology*, **65**, 1525-1534.
- Mérigoux S., Ponton D. and Mérona B. (1998), Fish richness and species-habitat relationships in two coastal streams of French Guiana, South America. *Environmental Biology of Fishes*, **51**, 25-39.
- Mérona B. (1981), Zonation ichthyologique du bassin du Bandama (Côte-d'Ivoire). *Revue Hydrobiologie Tropicale*, **14**, 63, 75.
- Mérona B. de. (1986), Aspectos ecológicos da ictiofauna no baixo Tocantins. *Acta Amazonica*, **16**/17, 109-124.
- Miller D. L., Leonard P. M., Hughes R. M., Karr J. R., Moyle P. B., Schrader L. H., Thompson B. A., Daniels R. A., Fausch K. D., Fitzhugh G. A., Gammon J. R., Halliwell D. B., Angermeier P. L. and Orth D. J. (1988), Regional applications of an index of biotic integrity for water resource management. *Fisheries*, **13**, 12-30.
- Nelson R. L., Platts W. S., Larsen D. P. and Jensen S. E. (1992), Trout distribution and habitat in relation to geology and geomorphology in the North Fork Humboldt river drainage, northeastern Nevada. *Transactions of the American Fisheries Society*, **121**, 405-426.
- Norris R. H. and Thoms M.C. (1999), What is river health? *Freshwater Biology*, **41**, 197-209.
- Oberdorff T. and Hughes R. M. (1992), Modification of an index of biotic integrity based on fish assemblages to characterize rivers of the Seine Basin, France. *Hydrobiologia*, **228**, 117-130.
- Oberdorff T., Guilbert E. and Luchetta J. C. (1993), Patterns of fish species richness in the Seine River basin, France. *Hydrobiologia*, **259**, 157-167.
- Oberdorff T., Hugueny B. and Guégan J. F. (1997), Is there an influence of historical events on contemporary fish species richness in rivers? Comparisons between Western Europe and North America. *Journal of Biogeography*, **24**, 461-467.
- Oberdorff T., Hugueny B. and Vigneron T. (2001b), Is assemblage variability related to environmental variability? An answer for riverine fish. *Oikos*, **93**, 419-428.
- Oberdorff T., Hugueny B., Compin A. and Belkessam D. (1998), Non-interactive fish communities in the coastal streams of North-Western France. *Journal of Animal Ecology*, **67**, 472-484.

- Oberdorff, T.; Pont, D.; Hugueny, B. and Chessel, D. (2001a), A probabilistic model characterizing riverine fish communities of French rivers: a framework for environmental assessment. *Freshwater Biology*, **46**, 399-415.
- Oberdorff, T.; Pont, D.; Hugueny, B. and Porcher, J. P. (2002), Development and validation of a fish-based index for the assessment of rivers "health" in France. *Freshwater Biology*, **47**, 1720-1735.
- Oberdorff, T. and Porcher, J. P. (1994), An index of biotic integrity to assess biological impacts of salmonid farm effluents on receiving waters. *Aquaculture*, **119**, 219-235.
- Osborne, L. L. and Wiley, M. J. (1992), Influence of tributary spatial position on the structure of warmwater fish communities. *Canadian Journal of Fisheries and Aquatic Science*, **49**, 671-681.
- Paller, M. H. (1994), Relationships between fish assemblage structure and stream order in South Carolina coastal plain stream. *Transactions of the American Fisheries Society*, **123**, 150-161.
- Paugy, D.; Benech, V. and Etou, K. (1988), La faune ichtyologique des bassins du Mono et du lac Togo (Togo). ORSTOM, Bamako, **23**, 1-110.
- Perez, L. E. (1984), Uso del habitat por la comunidad de peces de un rio tropical asociado a un bosque. *Memoria Sociedad Ciencias Naturales La Salle*, **XLIV**, **121**, 143-162.
- Poff, N. L.; Allan, D.; Bain, M. B.; Karr, J. R.; Prestegard, K. L.; Richter, B. D.; Sparks, R. E. and Stromberg J.C. (1997), The natural flow regime. A paradigm for river conservation and restoration. *Bioscience*, **47**, 769-784.
- Poff, N. L. and Allan, J. D. (1995), Functional organization of stream fish assemblages in relation to hydrological variability. *Ecology*, **76**, 606-627.
- Poff, N. L. and Ward, J. V. (1989), Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Can. J. Fish. Aquat. Sci.*, **46**, 1805-1818.
- Pringle, C. M.; Scatena, F. N.; Paaby-Hansen, P. and Núñez-Ferrera. (2000), River conservation in Latin America and the Caribbean. In: Boon, P. J.; Davies, B. R. and Petts, G. E. (Eds.). *Global perspectives on river conservation: science, policy and practice*. John Wiley and Sons. Chichester. 548 pp.
- Rahel, F. J. and Hubert, W. A. (1991), Fish assemblages and habitat gradients in a Rocky Mountain-Great Plains stream: biotic zonation and additive patterns of community change. *Transactions of the American Fisheries Society*, **120**, 319-332.
- Rathert, D.; White, D.; Sifneos, J. C. and Hughes, R. M. (1999), Environmental correlates of species richness for native freshwater fish in Oregon, USA. *Journal of Biogeography*, **26**, 257-274.
- Resetarits Jr., W. J. (1997), Interspecific competition and qualitative competitive asymmetry between two benthic stream fishes. *Oikos*, **78**, 428-439.
- Ricklefs, R. E. (1993), *A. economia da natureza*. Guanabara Koogan S. A., Rio de Janeiro, 470 pp.
- Rodríguez, M. A. and Lewis Jr., W. M. (1994), Regulation and stability in fish assemblages of neotropical floodplain lakes. *Oecologia*, **99**, 166-80.
- Rodríguez, M. A. and Lewis Jr., W. M. (1997), Structure of fish assemblages along environmental gradients in floodplain lakes of the Orinoco River. *Ecological Monographs*, **67** : (1), 109-28.
- Schlosser, I. J. and Angermeier, P. L. (1990), The influence of environmental variability, resource abundance, and predation on juvenile cyprinid and centrarchid fishes. *Polish Archives of Hydrobiology*, **37**, 265-284.
- Schlosser, I. J. and Ebel, K. K. (1989), Effects of flow regime and cyprinid predation on a headwater stream. *Ecological Monographs*, **59**, 41-57.
- Schlosser, I. J. (1982), Fish community structure and function along two habitat gradients in a headwater stream. *Ecological Monographs*, **52**, 395-414.
- Schlosser, I. J. (1985), Flow regime, juvenile abundance, and the assemblage structure of stream fishes. *Ecology*, **66**, 1484-1490.
- Schlosser, I. J. (1987), A conceptual framework for fish communities in small warmwater streams. In: W.J. Matthews and D.C. Heins (eds.) *Community and evolutionary ecology of North American stream fishes*. University of Oklahoma Press, Norman, Oklahoma, USA. pp. 17-24
- Schlosser, I. J. (1995), Critical landscape attributes that influence fish population dynamics in headwater streams. *Hydrobiologia*, **303**, 71-81.
- Schut, J.; De Silva, S. S. and Kortmulder, K. (1984), Habitat, associations and competition of eight *Barbus* (= *Puntitus*) species (Pisces, Cyprinidae) indigenous to Sri Lanka. *Netherlands Journal of Zoology*, **34**, 459-181.
- Sheldon, A. L. (1968), Species diversity and longitudinal succession in stream fishes. *Ecology*, **49**, 193-198.
- Smogor, R. A. and Angermeier, P. L. (1999), Effects of drainage basin and anthropogenic disturbance on relations between stream size and IBI metrics in Virginia. In: Thomas P. Simon, editor. *Assessment Approaches for Estimating Biological Integrity using Fish Assemblages*. Lewis Press, Boca Raton, FL, USA. pp. 249-272.
- Sydenham, D. H. J. (1977), The qualitative composition and longitudinal zonation of the fish fauna of the river Ogun. *Rev. Zool. Afr.*, **91**, 974-996.
- Taylor, C. M. (1996), Abundance and distribution within a guild of benthic stream fishes: local processes and regional patterns. *Freshwater Biology*, **36**, 385-396.

- Taylor, C. M.; Winston, M. R. and Matthews, W. J. (1993), Fish species-environment and abundance relationships in a Great Plain river system. *Ecography*, **16**, 16-23.
- Tejerina-Garro, F. L. (2001), Étude des relations habitat-poissons dans les eaux courantes de Guyane Française pour l'évaluation de la qualité du milieu aquatique. PhD Thesis, University of Montpellier II, France, 243 pp.
- Tito de Moraes, L. and Lauzanne, L. (1994), Zonation longitudinale des peuplements ichthyiques avant mise en eau de la retenue de Petit-Saut (Guyane française). *Rev. Hydrobiol. Trop.*, **27** : (4), 467-483.
- Tito de Moraes, L.; Lointier, M. and Hoff, M. (1995), Extent and role for fish populations of riverine ecotones along the Sinnamary River (French Guiana). *Hydrobiologia*, **303**, 163-179.
- Vannote, R. L.; Minshall, G. W.; Cummins, K. W.; Seddel, J. R. and Cushing, C. E. (1980), The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 130-137.
- Verneaux, J. (1977), Biotypologie de l'écosystème "eau courante". Détermination approchée de l'appartenance typologique d'un peuplement ichthyologique. *Compte Rendu de l'Académie des Sciences* (Paris), **284**, 675-678.
- Waite, I. R. and Carpenter, K. D. (2000), Associations among fish assemblage structure and environmental variables in Willamette Basin streams, Oregon. *Transaction of the American Fisheries Society*, **129**, 754-770.
- Werner, E. E. (1984), The mechanisms of species interactions and community organization in fish. In: Strong Jr., D. R.; Simberloff, D.; Abele, L. G. and Thistle, A. B. (Eds.). *Ecological communities*. Princeton University Press, Princeton, N.J. USA. pp. 360-382.
- Whittier, T. R.; Hughes, R. M. and Larsen, D. P. (1988), The correspondence between ecoregions and spatial patterns in stream ecosystems in Oregon. *Canadian Journal of Fisheries and Aquatic Sciences*, **45**, 1264-1278.
- Wikramanayake, E. D. and Moyle, P. B. (1989), Ecological structure of tropical fish assemblages in wet-zone streams of Sri Lanka. *Journal of Zoology* (London), **218**, 503-526.
- Winemiller, K. O. and Leslie, M. A. (1992), Fish assemblages across a complex, tropical freshwater/marine ecotone. *Environmental Biology of Fishes*, **34**, 29-50.
- Winemiller, K. O. (1983), An introduction to the freshwater fish communities of Corcovado National Park, Costa Rica. *Brenesia*, **21**, 47-66.
- Zaret, T. M. and Rand, A. S. (1971), Competition in tropical stream fishes: support for the competitive exclusion principle. *Ecology*, **52**, 336-342.

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