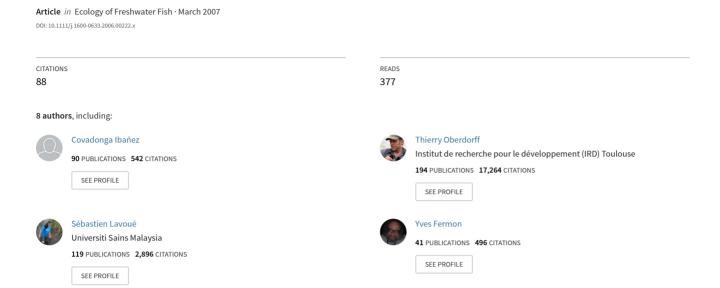
## Fish assemblages structure and function along environmental gradients in rivers of Gabon (Africa)



### ECOLOGY OF FRESHWATER FISH

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

Ibanez C, Oberdorff T, Teugels G, Mamononekene V, Lavoué S, Fermon Y, Paugy D, Toham AK. Fish assemblages structure and function along environmental gradients in rivers of Gabon (Africa). Ecology of Freshwater Fish 2007: 16: 315–334. © 2007 The Authors. Journal compilation © 2007 Blackwell Munksgaard

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; Mérigoux et al. 1998; Ibarra & Stewart 1989; Tito de Morais & 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; Mérigoux 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 Ogowe 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 Ogowe Basin (32) sites; total drainage area of the basin 205,000 km<sup>2</sup>), the Nyanga Basin (10 sites: total drainage area of the basin 20,062 km<sup>2</sup>), the Ntem Basin (four sites; total drainage area of the basin 31,000 km<sup>2</sup>), the Komo Basin (three sites; total drainage area of the basin 7900 km<sup>2</sup>), the Mbini Basin (three sites; total drainage area of the basin 13.694 km<sup>2</sup>) and the Nova Basin (one site; total drainage area of the basin 8500 km<sup>2</sup>); (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.

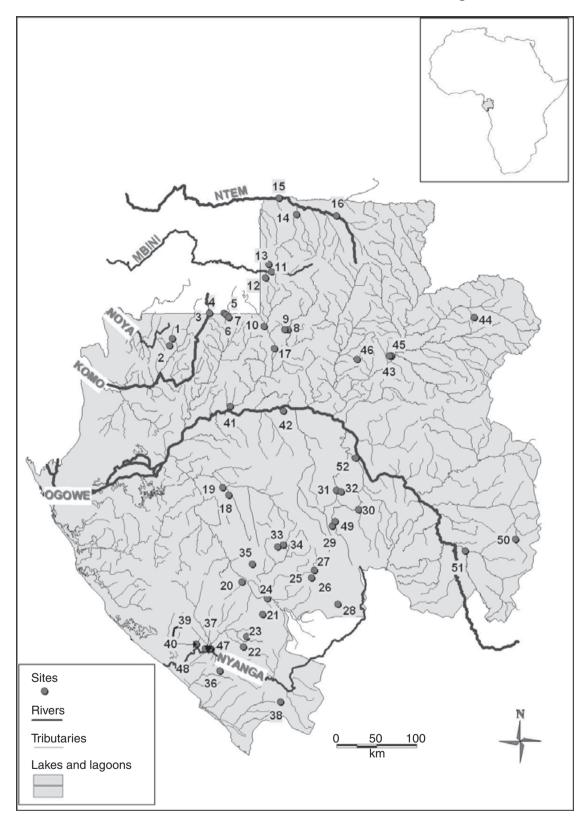


Fig. 1. Map of Gabon showing sites location (see Appendix 1 for sites description).

#### Fish sampling

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  $\leq 10$  m, mean depth = 1 m), as water conductivity (CON) was too low to employ electrofishing, we used the ichtyotoxin 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 ichtyotoxin, was poured out below the second blocking net to eliminate the effect of the later downstream of the sampled site.

For larger streams (mean depth >1 m) a set of seven monofilament gill nets (25 m long by 1.5 m high) of mesh size varying between 8 and 45 mm between knots (i.e., 8, 10, 15, 20, 25, 35 and 45 mm) was deployed for 24 h (i.e., the nets were placed at dawn, checked once just before dusk and definitely removed after 24 h). One net of each mesh size was extended perpendicular across the river channel at each site in a random order with around 10 m maintained between nets.

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).

#### Environmental variables

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

(*DEP*, m), *CON* ( $\mu$ S·cm<sup>-1</sup>) and pH (pH). Two variables were used to describe the site spatial position within the upstream–downstream gradient. These variables were distance of the site from sources (*DIS*, km) and surface area of the drainage (*SAD*, km<sup>2</sup>) basin upstream of the site. One regional scale variable (i.e., Basin unit) was used as a synthetic descriptor of regional environmental constraint for fishes.

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.

#### Trophic groups

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.

#### Data analysis

#### 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).

#### Regression tree analysis

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 brazzai), 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 Parananochromis gabonicus, Paramormyrops gabonensis and Anaspidoglanis 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.

	SAD (Ln)	DIS (Ln)	ELE (Ln)	STW (Ln)	DEP (Ln)	CON (Ln)	pН
SAD (Ln)	1.000						
DIS (Ln)	0.978*	1.000					
ELE (Ln)	-0.398	-0.392	1.000				
STW (Ln)	0.853*	0.846*	-0.220	1.000			
DEP (Ln)	0.725*	0.756*	-0.012	0.875*	1.000		
CON (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

 $<sup>^*</sup>P < 0.001.$ 

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

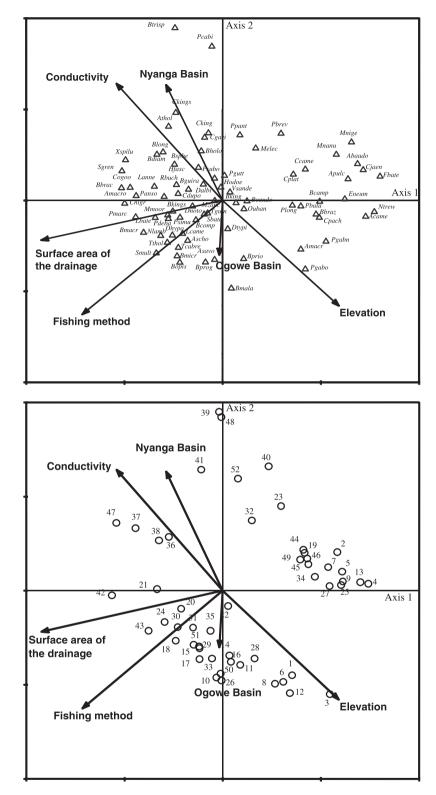


Fig. 2. Canonical correspondence analysis ordination plots showing species and sites distribution in relation to significant environmental variables (see Appendices 1 and 2 for sites and species code).

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

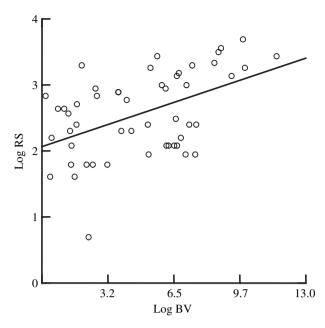


Fig. 3. Effects of stream size (i.e., surface area of the drainage) on local species richness.

with gill nets. The fourth group, (e.g., Schilbe grenfelli, Xenocharax 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  $\leq 7.5$ . 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

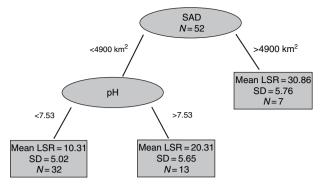


Fig. 4. Regression tree analysis for local species richness (LSR). Ovals show variables used as decision points, and values of decision criteria are indicated along diagonal lines. Rectangles show nodes used in tree construction. Also given are the mean LSR and standard deviation values for each node.

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  $STW \le 5$  m. Cell with STW < 5 m had a mean %INV species of 67.2. Cells with STW > 5 m had a mean %INV of 45.3, and were further split into two groups for which SAD was  $\le 210 \text{ km}^2$ . 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  $DIS \leq 50$  km. Cell with DIS < 50 km had a mean %OMN of 27.7. Cells with DIS > 50 km had a mean %OMN of 37.8, and were further split into two groups for which CON was  $\leq 35~\mu s$ . 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  $STW \le 5$  m. Cell with STW < 5 m had a mean %HER of 2.2. Cells with STW > 5 m had a mean %HER of 16.6, and were

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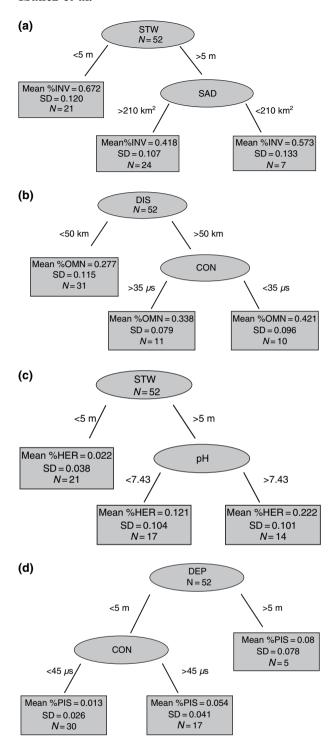


Fig. 5. Regression tree analysis for %INV (a), %OMN (b), %HER (c) and %PIS (d) (see legend Fig. 4 for explanations and text for abbreviations).

further split into two groups for which pH was  $\lesssim 7.43$ . 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 extend 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 km<sup>2</sup>) 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 I	Axis 2	Axis 3
Correlations of environmental variables with ordination	is axes		
Ogowe	-0.015	-0.303	0.008
SAD	-0.921	-0.214	-0.083
FIM	-0.716	-0.627	0.056
CON	-0.542	0.637	0.005
Nyanga	-0.289	0.627	0.458
ELE	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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Order and family	Species	Species code†
Characiformes		
Alestiidae	Alestes macrophthalmus Günther, 1867	Amacro
	Brycinus schoutedeni Boulenger, 1912	Ascho
	Brycinus taeniurus Günther, 1867	
	Brycinus tholloni Pellegrin, 1901	Athol
	Brycinus intermedius (Boulenger, 1903)	Distant
	Brycinus kingsleyae (Günther, 1896) Brycinus longipinnis (Günther, 1864)	Bkings Blong
	Brycinus nongipinins (duniner, 1864) Brycinus macrolepidotus Valenciennes, 1850	Bopis
	Brycinus opisthotaenia (Boulenger, 1903)	Боріз
	Brycinus sp. (7 species)	
	Bryconaethiops macrops Boulenger, 1920	Bmacr
	Bryconaethiops microstoma Günther, 1873	Bmicr
	Bryconaethiops sp. (1 species)	
	Nannopetersius lamberti Poll, 1967	Nlamb
	Phenacogrammus ansorgii (Boulenger, 1910)	Panso
	Phenacogrammus gabonensis (Poll, 1967)	
	Phenacogrammus major (Boulenger, 1903)	
Distinhadantidas	Phenacogrammus sp. (1 species)	Dhuno
Distichodontidae	Distichodus hypostomatus Pellegrin, 1900 Distichodus notospilus Günther, 1867	Dhypo Dnoto
	Hemistichodus vaillanti Pellegrin, 1900	Diloto
	Nannaethiops unitaeniatus Günther, 1872	
	Nannocharax fasciatus Günther, 1867	
	Nannocharax parvus Pellegrin, 1906	
	Nannocharax sp. (1 species)	
	Neolebias kerguennae Daget, 1980	
	Neolebias trewavasae Poll & Gosse, 1963	Ntrew
	Neolebias unifasciatus Steindachner, 1894	
	Xenocharax spilurus Günther, 1867	Xspilu
Hepsitidae	Hepsetus odoe (Bloch, 1794)	Hodoe
Clupeiformes	Odavathriaga angaraii Daylangar 1010	
Clupeidae	Odaxothrissa ansorgii Boulenger, 1910 Pellonula leonensis Boulenger, 1916	
	Pellonula vorax Günther, 1868	
Cyprinodontiformes	Tenonula votax duninel, 1000	
Aplocheilidae	Aphyosemion cameronense (Bouleneger, 1903)	Acame
•	Aphyosemion joergenscheeli Huber & Radda, 1977	
	Aphyosemion ocellatum Huber & Radda, 1977	
	Aphyosemion ssp. (4 species)	
	Epiplatys neumanni Berkenkamp, 1993	Eneum
	Aphyosemion batesii (Boulenger, 1911)	Fbate
Poeciliidae	Plataplochilus cabindae (Boulenger, 1911)	Pcabi
Cunviniformes	Plataplochilus terveri (Huber, 1981)	
<b>Cypriniformes</b> Cyprinidae	Barbus aloyi Roman, 1970	
бурттаас	Labeobarbus batesii Boulenger, 1903	
	Barbus brazzai Pellegrin, 1901	Bbraz
	Barbus brichardi Poll & Lambert, 1959	Bolaz
	Barbus camptacanthus (Bleeker, 1863)	Bcamp
	Barbus caudovittatus Boulenger, 1902	Bcaudo
	Labeobarbus compiniei (Sauvage, 1879)	Bcomp
	Barbus diamouanganai Teugels & Mamonekene, 1992	Bdiam
	Barbus guirali Thominot, 1886	Bguira
	Barbus holotaenia Boulenger, 1904	Bholo
	Barbus jae Boulenger, 1903	5 .
	Labeobarbus malacanthus Pappenheim, 1911	Bmala
	Barbus martorelli Roman, 1970	
	Barbus micronema Boulenger, 1904	Davia
	Barbus prionacanthus Mahnert & Géry, 1982 Barbus progenys Boulenger, 1903	Bprio Bprog
	Labeobarbus rubrostigma Poll & Lambert, 1964	υμισα
	Barbus trispilomimus Boulenger, 1907	Btrisp
	San San Chapman Million Doublingon, 1001	Striop

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

Order and family	Species	Species code†
Mugilidae	Liza falcipinnis (Valenciennes, 1836)	
Polynemidae	Polydactylus quadrifilis (Cuvier, 1829)	
Sciaenidae	Pseudotolithus elongatus (Bowdich, 1825)	
Siluriformes		
Amphiliidae	Paramphilius baudoni Pellegrin, 1928	Abaudo
	Amphilius brevis Boulenger, 1902	
	Amphilius longirostris (Boulenger, 1901)	
	Amphilius pulcher Pellegrin, 1929	Apulc
	Doumea typica Sauvage, 1879	Dtypi
	Phractura brevicauda Boulenger, 1911	Pbrev
	Phractura intermedia Boulenger, 1911	
	Phractura longicauda Boulenger, 1903	
	Phractura sp. (1 species)	
Claroteidae	Anaspidoglanis macrostoma (Pellegrin, 1909)	Amacr
	Anaspidoglanis ssp. (2 species)	
	Chrysichthys auratus auratus (Geoffroy Saint-Hilaire, 1809)	
	Chrysichthys nigrodigitatus (Lacepède, 1803)	Cnigr
	Chrysichthys ogooensis (Pellegrin, 1900)	Cogoo
	Chrysichthys thysi Risch, 1985	· ·
	Chrysichthys ssp. (4 species)	
	Parauchenoglanis balayi (Sauvage, 1879)	Pbala
	Parauchenoglanis guttatus (Lönnberg, 1895)	Pgutt
	Parauchenoglanis pantherinus (Pellegrin, 1929)	Ppant
	Parauchenoglanis ssp. (4 species)	
Clariidae	Clarias camerunensi Lönnberg, 1895	Ccame
	Clarias gariepinus (Burchell, 1822)	Cgari
	Clarias jaensis Boulenger, 1909	Cjaen
	Clarias longior Boulenger, 1907	o <sub>j</sub> ao
	Clarias pachynema Boulenger, 1903	Cpach
	Clarias platycephalus Boulenger, 1902	Cplat
	Clarias submarginatus Peters, 1882	Opiat
	Clarias sp. (1 species)	
	Gymnallabes typus Günther, 1867	
Malapteruridae	Malapterurus electricus (Gmelin, 1789)	Melec
Mochokidae	Atopochilus savorgnani Sauvage, 1879	Asavo
Woonokidao	Atopochilus sp. (2 species)	Nouvo
	Synodontis albolineatus Pellegrin, 1924	
	Synodontis aterrimus Poll & Roberts, 1968	
	Synodontis batesii Boulenger, 1907	Sbate
	Synodonius teasmanni Pappenheim, 1911	Shate
	Synodontis tessinamin' appetitetti, 1911 Synodontis ssp. (4 species)	
Schilbeidae	Parailia occidentalis (Pellegrin, 1901)	
Comboldac	Parailia sp. (1species)	
	Pareutropius debauwi (Boulenger, 1900)	Pdeba
	Schilbe grenfelli (Boulenger, 1900)	Sgren
	Schilbe multitaeniatus (Pellegrin, 1913)	Smult
	Schilbe ssp. (2 species)	Siliuit
Synbranchiformes	טטוווטפ פפף. (ב פאפטופפ)	
Mastacembelidae	Mastacembelus marchei (Sauvage, 1879)	
เพลงเลงเทมบิแนลช	Mastacembelus niger Sauvage, 1879	Maigo
	masiacennuenus niger sauvaye, 1019	Mnige

<sup>†</sup>Species code used in the statistic analysis.

#### Ibanez et al.

#### **Appendix**

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

Site code	River basin	Latitude	Longitude	рН	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	Ö	5	0
ST40	Nyanga	2°43.719′S	10°36.621′E	8.05	95.8	14.0	8.0	130	1.0	0.3	0	5	1
ST41	Ogowe	00°02.536′S	11°00.166′E	8.26	91.0	461.0	40.0	79	2	0.4	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	•		12°49.383′E	6.96	49.0	19930.0	195.0	472	250	5.0	1	2	0
	Ogowe	00°31.269′N						522			0	2	1
ST44	Ogowe	00°56.579′N	13°44.795′E	5.19	45.0	4.2 7.1	2.0 3.3	536	3 2	0.3 0.6	0	2	1
ST45	Ogowe	00°31.152′N	12°47.961′E	6.86	25.0	7.1					•		•
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.

Species code         STOS		Site code	one																						
	Species code	ST05			ST07												ST08			ST01 ST	ST39 ST48	.8 ST23	3 ST32	ST12	ST22
Acame	Fbate		-		-			1			-														
Minger Mi	Acame		-			-	_				-								_						
Witter	Mnige	-			<del>-</del>	<b>-</b>		_		•									•	-					
Minimum I	Ntrew		-			_	_	_					-												
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County         County         1 <td< td=""><td>Cjaen</td><td><del>.</del> .</td><td></td><td></td><td></td><td>-</td><td></td><td></td><td></td><td>_</td><td></td><td></td><td>-</td><td>-</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td></td<>	Cjaen	<del>.</del> .				-				_			-	-											
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Patrict   1	Amacr		_				_	_				-		_		_				•			•	_	
Pigatin   1   1   1   1   1   1   1   1   1	Ppani	_ ,	,				,													_			-		
Page Page Page Page Page Page Page Page	Pgabn	_ ,	_ ,			,	_		,	_				,											
Pagato Prigato Prigate Prigato	Plong	_			,	_	,			_				_					•					,	
Opach Baraz         1 <td< td=""><td>Pgabo</td><td></td><td>_</td><td></td><td><del>.</del> -</td><td></td><td>_</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td>-</td><td></td><td></td><td></td><td></td><td>_</td><td></td></td<>	Pgabo		_		<del>.</del> -		_												-					_	
Data	Cpach		<del>.</del> ,	<del>.</del>	<del>.</del>	,		<del>-</del>	<del>.</del>					-	<del>.</del>				_				-	<del>.</del>	
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Eneum         1 <td>Dalbi</td> <td></td> <td>-</td> <td></td> <td>_</td> <td></td> <td>-</td> <td></td> <td></td> <td></td> <td></td>	Dalbi		-																_		-				
Hodoe 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	Eneum		_				_		,-	_			-	-											
Apulc Abulc Abulc Abulc Bkings  Bkings  Bkings  Bkings  Bkings  Bkings  1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	Нодое		-					<del>-</del>									-	<del>-</del>		_	-		-	-	
Bking         1 <td>Apulc</td> <td></td> <td></td> <td><del>-</del></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td>-</td> <td></td> <td>-</td> <td></td>	Apulc			<del>-</del>									-		-										
Pheev         1 <td>Bking</td> <td></td> <td></td> <td><del>.</del> -</td> <td></td> <td></td> <td></td> <td></td> <td></td> <td>_</td> <td></td> <td></td> <td>-</td> <td>-</td> <td><del>-</del></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td><del>.</del> -</td> <td><del>.</del> .</td> <td></td> <td></td>	Bking			<del>.</del> -						_			-	-	<del>-</del>							<del>.</del> -	<del>.</del> .		
Asavo Asavo Bromp Dnoto Brond Dnoto British Brade Brade Ouban Ascho Brade Brad	Pbrev								<del>-</del>				•						<del>-</del>			-	-		
Bcomp         1 <td>Asavo</td> <td></td> <td></td> <td></td> <td></td> <td></td> <td>_</td> <td></td> <td></td> <td></td> <td></td> <td>_</td> <td></td> <td>_</td>	Asavo						_					_													_
Dnoto   Dnot	Всотр						_					-													<del>-</del>
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Melec         1 <td>Bprio</td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td>_</td> <td></td> <td></td> <td>-</td> <td>-</td> <td></td> <td></td> <td></td> <td>-</td> <td></td> <td></td> <td></td> <td></td> <td></td> <td>-</td> <td>-</td> <td>-</td>	Bprio								_			-	-				-						-	-	-
Hasc Braudo  Hasc Braudo  Ouban	Melec									_				-											
Bcaudo         1 <td>Hfasc</td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td>_</td> <td></td> <td></td> <td></td> <td>-</td> <td></td> <td></td> <td>-</td> <td></td> <td>_</td> <td>-</td> <td>-</td> <td></td> <td>-</td> <td>-</td> <td></td>	Hfasc									_				-			-		_	-	-		-	-	
Ascho Ascho Bmala Broad	Bcando										_							_				-			
Ascho Brada Brada Bprog Bprog Dhypo Dhypo Dtypi Pgut Psimu Rbuch Rbuch Bkings 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	Ouban										_	_	-	-			_	_	_				-	-	
Binala         1           Bprog         1           Dhypo         1           Dtypi         1           Pgutt         1           Psimu         1           Rbuch         1           Sbate         1           Bkings         1           Conity         1           Description         1           Des	Ascho											-											-		
Bprog         1           Dhypo         1           Dtypi         1           Pgut         1           Psimu         1           Rbuch         1           Sbate         1           Bking         1           1         1           1         1           1         1           1         1           1         1           1         1           1         1           1         1	Bmala											_													
Dhypo  Dtypi  Pgut  Pgut  Psinu  I  I  I  I  I  I  I  I  I  I  I  I  I	Bprog											_													
Dtypi	Dhypo											-					-								_
Pgutt         1           Psimu         1           Rbuch         1           Sbate         1           Bkings         1           Parties         1	Dtypi											-						-	_						-
Psimu hbuch 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	Pgutt													-					_				-		
Rbuch 1 Sbate 1 Bkings 1	Psimu													-											
Shate Bkings 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	Rbuch													-				-					-		
Bkings Danier 1	Sbate													-											
Danies	Bkings													-										-	
blind	Bguira													-				_	_				-		

	Site code	ode																								
Species code	ST05	ST09	ST25	ST07	ST04	ST03	ST13	ST27	ST44	ST02	ST19	ST06	ST46	ST45	ST34	ST49	ST08	ST40	ST52 8	ST01 8	ST39	ST48 S	ST23 8	ST32 S	ST12 S	ST22
Cgari														-				-								
Mmoor														-												
Bsphe														-												
Mzanc														-												
Psubo																		_							_	
Cdnbo																		_								
Atho/																		_								
Cking																		_	_			_				
Blong																			_		_	_				
Pcabi																					_	_				
Ckings																				•	_	_				
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Tcabre																										
Lbate																										
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Cnigr																										
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Ttho/																										
Sgren																										
Cogoo																										
Bbrac																										
Bopis																										
Fmarc																										
Amacro																										
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 4	43.0	43.0	90.09	65.0 8	82.0	185.0

Appendix 3A. (Continued)

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.

	Site code	de																							
Species code	ST28	ST35	ST20	ST36	ST31	ST41	ST33	ST50	ST29	ST21	ST26	ST38	ST11	ST10	ST51	ST14	ST30	ST16 S	ST17 S	ST18 S	ST37 S	ST24 S	ST15 ST	ST43 ST47	47 ST42
Fbate Abaudo Acame Mnige Ntrew																									
Mnanu Cjaen Cplat Bcamp											-														
Ccame Pbala	-		-							-	<del>-</del>			-		-									
Amacr Ppant				-									-	-	-							,			
Fgabn Plong		-													-			•				_	-		
ryavo Cpach Rhraz									-		-					_		-	-						
Bholo Dalbi		-		-	-								-		-	-	_		-	-		-	-	-	
Eneum Hodoe			-	-	-					-		-		-	-	-			-	-	-				
Apulc Bking Phrev	-	-		-	-			-	-		-	-			-					-			-		-
Asavo Bcomp				-		-			-					-	-		_		-		-	-	-		-
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Bcaudo			-	-	- ,	-	-	-	-	-	-	-			,		. ,	-	- ,	•	•		-	-	,
Ouban Ascho			-	-			,						_		- <del>-</del> ,	_		-			-		-		
Bprog			-		_										_		_		•		•	•			
Dhypo Dtypi	-	-		-	-		-		-		_				-		_		-	-	-	-	_	-	
Pgutt Psimu			-						-			-						_	-	-	-	-		-	-
Rbuch		-			-	-							<del>.</del>				_		_	-	-		-	-	-
Spate Bkings					-					_		-					_		-	-	-	-	-	-	-

Appendix 3B. (Continued)

Za	0150 0100	2	0010	S131	ST41	ST33 S	ST50 ST	ST29 ST21	:1 ST26	ST38	ST11 S	ST10 8	ST51 S	ST14 S	ST30 S	ST16 S	ST17 S	ST18 S	ST37 S	ST24 S	ST15	ST43	ST47	ST42
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		-	-																				_	
Mmoor	-	-	-	-						-				,-	_	_	-	_	,-	-	_	_	_	-
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Amacro																	_	_				_	-	
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SAD, surface area of the drainage.