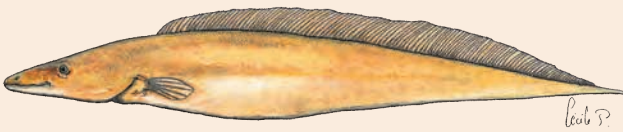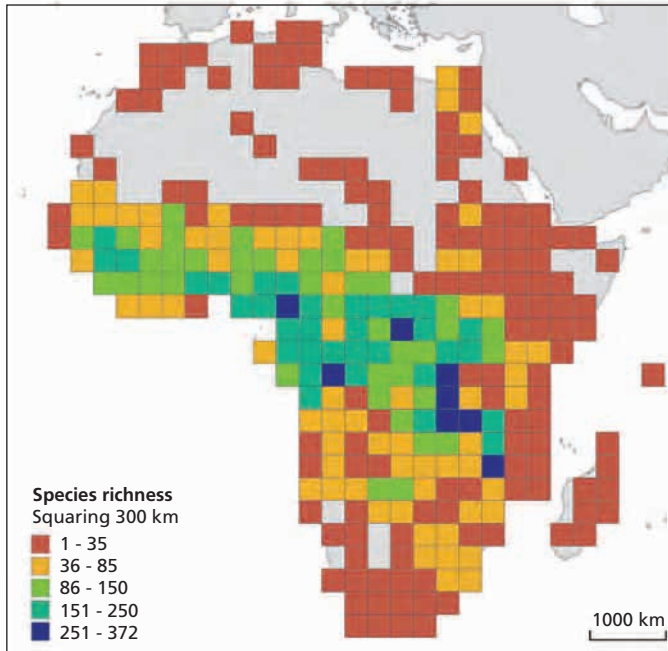# Species richness of fish communities

BERNARD HUGUENY

Introduction

Freshwater habitats from Africa and Madagascar harbour about 3,255 fish species (Lévêque *et al.*, 2008). This is of course not a definitive figure because new species are still described and taxonomic revisions occur regularly. That means that about a quarter of all known freshwater fishes live in Africa, an expected pattern considering that biodiversity peaks in tropical biomes for most taxonomic groups. Indeed, other biogeographic realms with a large extent of tropical climate (Neotropical and Oriental) also display great freshwater fish diversity (3,000-4,000 species) in comparison with more temperate ones (about 2,000 species in Nearctic and Palaearctic). However, high biodiversity at a continental scale does not necessarily translate to high biodiversity at a smaller, regional, scale, a pattern clearly shown by the number of species recorded per 300*300 km quadrat in the FAUNAFRI database (an updated storage of fish distribution in Africa) which exhibits a high spatial variability with both "cold" (e.g. Maghreb) and "hot" (e.g. Congo) spots of diversity (figure 15.1). Similarly, the number of fishes encountered in rivers of comparable catchment area may differ greatly if we compare for instance the Nile (fewer than 200 species, Witte *et al.*, 2009) and the Congo (more than 700 species, Teugels & Thieme, 2005). At a smaller scale, species richness in similarly sized river sections may differ within the same drainage. This chapter is about how and, possibly, why species richness differs among localities, rivers or provinces, whether it scales down or scales up between different hierarchical spatial levels, and whether past climatic or orogenic events have left an imprint on present fish assemblages. Provided sufficient information, other components of biodiversity such as biological traits will be considered as well. Before describing the conceptual framework used to organize the existing knowledge about fish biodiversity in Africa, a description is given of the broad patterns obtained by analysing the FAUNAFRI database.

Broad patterns in fish diversity

Geographically Madagascar is included in Africa, but with regard to faunal affinities, and particularly considering freshwater fishes, this island clearly stands apart, reflecting its complex biogeographical history. In particular, none of the fish families endemic to continental Africa occur there, and most of the species belong to widespread families that can stand saline water and could have colonized the island on several occasions. Considering that it has been isolated for a long time, it is not surprising that relatively few freshwater species (135) have been recorded in this island despite its large size, many of them being endemics (Lévêque *et al.*, 2008). Other islands occur off the African coast, all are small and have not been colonized by strictly freshwater fishes due to a lack of connection with the continent in the past. As a result they harbour only a reduced number of brackish or migratory species. One notable exception is Bioko Island (off the coast of Cameroon) which was connected to the continent thanks to a lower sea level during the Quaternary and is now inhabited by 43 species, including strictly freshwater species (Castelo, 1994).

From a biogeographic point of view, continental Africa is generally divided into two realms. The Maghreb belongs to the Palearctic realm and is very depauperate, inhabited by only 47 species. The remaining part of continental Africa constitutes a biogeographic realm on its own, the Afrotropical realm, and takes the lion's share of fish biodiversity. This realm has been broken down into several ichthyological provinces of different shapes and numbers depending on the authors. Here we will use the provinces recognized in the FAUNAFRI database:

Nilo-Sudan, Upper Guinea, Lower Guinea, Congolese, Angolan, Zambezi, East Coast, Ethiopian, Cape and Karoo. To reduce the number of small provinces, we included the Ethiopian province into the Nilo-Sudan one and regrouped the Cape and Karoo regions into a Sourthern province (as in Lévêque *et al.*, 2008).

In addition, due to their specific evolutionary history dominated by adaptive radiations, we considered the lakes and their tributaries of the rift valleys as a separate entity, despite the fact that some of them are hydrologically connected to one of the abovementioned provinces. Strictly freshwater fish species richness per province span a range of one order of magnitude (from 70 species for the Southern province to 947 species for the Congo basin, according to the FAUNAFRI database), reflecting a diverse array of evolutionary histories shaped by past climates, orogenic and tectonic events, hydrological connections, extensions and retractions of active catchments, and sea level changes. It is worth noting however that these provinces also differ greatly with regard to our knowledge about fish distribution. Considering that regions for which identification guides exist are the best known, then the most reliable biodiversity patterns probably came from West Africa (Paugy *et al.*, 2003a, b), Lower Guinea (Stiassny *et al.*, 2007a, b), and South Africa (Skelton, 1993).

Not surprisingly, the great majority of African fish species are encountered in permanent rivers and lakes, but even temporary water bodies are not entirely devoid of fishes (inhabited by more than 500 species) as some species evolved specific life history strategies to cope with these extreme habitats. Fishes can also be encountered in deserts conditioned upon the existence of permanent water pockets that have been connected in the past to neighbour river basins. Due to the high seasonality of many African rivers, estuaries could be highly dynamic with regard to salinity and, depending on the season, are inhabited by strictly freshwater or marine species that add to a pool of brackish species. This explains the great number of species (about 600 are known to occur – sometimes temporarily – in African estuaries).

The African fish fauna is well-known for the multiple adaptive radiations that took place in lakes of the rift valleys (e. g. Victoria Lake), particularly within the Cichlidae family, leading to high species richness and endemism and motivating numerous studies to elucidate the factors underlying such outstanding biodiversity. About 1,850 fish species have been recorded so far in lakes and their tributaries within this part of Africa, but many more await scientific description (table 15.I). A large part of these species are not encountered outside the rift valley. Other cases of lacustrine adaptive radiation are known in Africa outside this region; among the most notable are Tana Lake (Ethiopia) with its cyprinid species flock and some small crater lakes in Cameroon (Barombi Mbo, Bermin) that provide some of the strongest support of sympatric speciation ever reported (Schliewen *et al.*, 1994).

Differences among biogeographic provinces suggest that biodiversity of freshwater fish is not distributed at random over Africa, a pattern also shown by the number of species recorded per 300*300 km quadrats in the FAUNAFRI database (figure 15.1). Depauperate regions are those with very low drainage density (Maghreb, Sahara, Sahel, Kalahari) while hot spots of diversity tend to

Lakes	Tanganyika	Malawi	Victoria	Kivu
Non cichlids	124	53	63	10
Cichlids	250 +	800 +	500 +	17
Total	374 +	853 +	563 +	27

occur in regions with very high rainfall and co-occur with rain forest. One hotspot, in the rift valleys, is not related to the presence of rain forest and reflects the high number of endemic lacustrine species encountered there.

A conceptual framework

In this framework a pivotal role is given to the river basin mainly because it can be treated as a biogeographical island. From this level, scaling down to the local community requires the concept of ecological filter, and for scaling up to the biogeographical province the concept of spatial turnover is needed. These three important concepts: biogeographical island; ecological filter; and spatial turnover are introduced in the following.

River basins draining into the ocean and endorheic basins are isolated units for strictly freshwater fishes within an ecological time frame as no dispersal occurs between them due to impassable barriers (sea water or dry land). Within a geological timeframe, events such as river capture or overflow from one basin to another may allow faunal exchange, but these events are rare and primarily depend on major climatic or geological changes (Craw *et al.*, 2006). Consequently, most coastal rivers probably have been isolated since at least the end of the Pleistocene, the last period of great geological and climatic changes. River basins, as defined in this chapter, are biogeographical islands (Hugueny,1989), but they do not conform to the dynamic equilibrium hypothesis of MacArthur and Wilson (1967) because extinctions cannot be balanced by a continuous colonization within an ecological time scale. Without *in situ* cladogenetic speciation (a species splitting into two or more daughter species), the fate of species richness is to decrease in a river basin as long as no connection exists with a neighbour. *In situ* speciation may slow down this process or even take over.

Over an ecological time scale (10-1000 years) a river is a closed system (no immigration, no emigration) and over such a narrow time window speciation could be neglected. Consequently, the species richness of a locality cannot be higher than the total number of species encountered in the river catchment it belongs to. From this pool of species available for colonization, only a fraction will be encountered in a given locality because some species may fail to pass through one of a series of filters (Poff, 1997). First the species should have the opportunity to disperse from a source to the locality, then to find there environmental conditions that fit its niche requirements, then to cope success-

fully with competitors, pathogens and predators already present. In rivers, a major factor modulating the strength of these different filters is the position along the upstream-downstream gradient.

The species richness of a province cannot be lower than the one of its most speciose river basin. So this lower bound in species is set by the factors that contribute to the richness of a river basin, for instance its area. From this starting point, regional species richness increases as new river basins are added, up to the final list of rivers constituting the province. The increase in total species richness as new spatial units are added is known as spatial turnover (or spatial beta diversity). A rapid increase corresponds to a high turnover. Spatial turnover occurs mainly because most of the time basins are isolated and their faunal composition changes with the accumulation of extinction and speciation events occurring independently in each of them. When basins get connected again, faunal exchange will partly – rarely totally – erase spatial turnover.

Patterns among rivers

Species-area relationship

One of the few quasi-universal laws of ecology is the so-called species-area relationship (SAR) describing an increase of the number of species of a community or a fauna/flora with the surface area it occupies, and its quantitative modelling as a power relationship goes back to Arrhenius (1921). Daget & Iltis (1965) pioneered its use for riverine organisms by relating species richness of fish communities to the catchment area in a sample of 13 rivers, mostly from Côte d'Ivoire. More comprehensive studies by Welcomme (1979) and Hugueny (1989) estimated SAR over Africa as a whole and confirmed that a power relationship accounted for a great variability in species richness among rivers (table 15.II; figure 15.2).

Relationships between the number of fish species and the catchment area (in km^2). A comparison is made between African and European rivers.
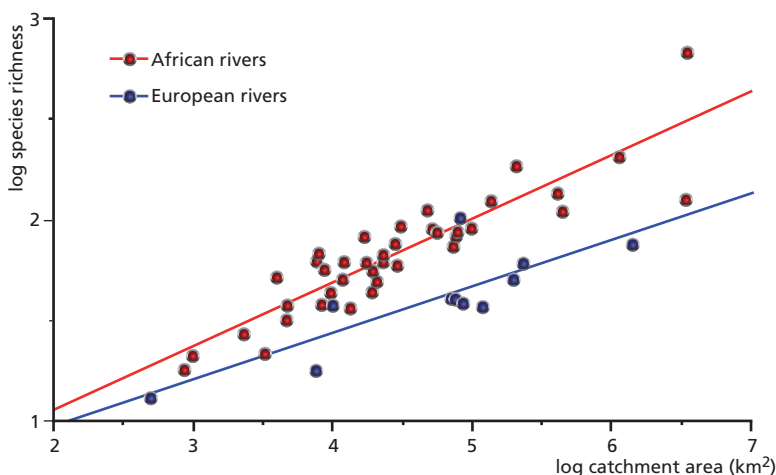
Rivers	Species richness	Surface (km^2)	Mean annual discharge (m^{3}s-^{1})	Rivers	Species richness	Surface (km^2)	Mean annual discharge (m^{3}s-^{1})
Congo	1068	3 457 000	40 487	Cess	76	11 920	
Nile	156	3 349 000	2 640	Bia	64	9 730	81
Niger	335	1 125 000	6 100	Agnébi	81	8 520	50
Senegal	195	441 000	687	Mano	53	8 260	
Volta	199	398 371	1 260	Jong	114	7 750	
Bandama	123	97 000	392	Kolenté	102	7 540	
Comoé	130	78 000	206	Boubo	48	4 690	32
Gambia	135	77 000	170	Mé	50	3 920	32
Sassandra	95	75 000	513	San Pedro	46	3 310	31
Ouémé	157	50 000	220	Néro	25	985	16
Cross	223	48 000		Dodo	18	850	
Cavally	88	28 850	384	Mungo	38	4 570	
Tominé	75	23 200		Wouri	157	11 500	308
Ogun	110	22 370		Sanaga	224	135 000	2 060
Mono	87	22 000	104	Nyong	145	27 800	443
Sewa	75	19 050		Lobé	52	2 305	102
Moa	93	18 760		Ntem	194	31 000	348
St Paul	96	18 180		Ogowe	344	205 000	4 758
Konkouré	99	16 470	353	Niari	200	56 000	913
Loffa	78	13 190					

TABLE 15.II.

Species richness, area and mean annual discharge for different African river basins.

Three nonexclusive explanations have been put forward to explain the species-area relationship: (1) area-dependent extinction rate (MacArthur & Wilson, 1967), (2) the area-dependent speciation rate (Losos & Schluter, 2000), and (3) the influence of habitat diversity (Williamson 1988). Area-dependent extinction assumes that probability of extinction of a species increases with a reduction of its population size, which in turn is a function of the surface area of the catchment. The fact that the lifetime of a population increases with its size has been supported by numerous empirical studies. In particular, an empirical relationship between population extinction rate and surface area has been established for Holarctic fishes (Hugueny *et al.*, 2011) and there is no reason to suspect African fishes differ in this regard. According to this relationship, population lifetime in a huge river basin such as the Congo is predicted to be about a few million years, a value not different from the average lifetime of a fish species evaluated on a global scale. Such a comparison suggests that very large river basins are biogeographically more like continents. Besides harbouring large populations, a large basin is probably able to maintain more persistent populations by being buffered against climatic variability. Conversely, small basins are expected to react quickly to environmental changes and a good example is provided by the Casamance, a small coastal river in West Africa. Following a period of drought, the salinity of the Casamance River in 1984-85 was higher than in the open ocean for the first time since the beginning of the

century. Salinity followed an increasing upstream gradient at the end of the rainy season, and values above 90‰ were observed in the upper reaches (Albaret, 1987). Along this gradient, the total fish species richness, estimated from commercial and experimental catches, decreased dramatically and only the two brackish water cichlids *Sarotherodon melanotheron* and *Tilapia guineensis*, were recorded in the most extreme environmental conditions. A dramatic impact of this new ecological situation is the assumed disappearance from the Casamance River of many freshwater species which were previously recorded. That is the case for *Hepsetus odoe*, a few cyprinids including *Labeo* and *Barbus*, mormyrids, characids (*Alestes* and *Brycinus*), citharinids, *Malapterurus electricus*, etc. which were recorded by Pellegrin (1904), and still observed by fishermen in the river before the drought (Albaret, 1987). It is unlikely that those species were able to survive in refuge zones, given that most of the upper reaches dried out during the dry season. Only a few species such as *Hemichromis bimaculatus*, some Cyprinodonts and *Clarias,* were sampled in the upper reaches.

Area-dependent speciation assumes a positive effect of area on speciation rate by exposing species to greater ecological heterogeneity and/or geographical barriers (Rosenzweig, 1995). This hypothesis is quite old but received empirical support only recently thanks to phylogenetic studies of insular biotas (e.g. Losos & Schulter, 2000). Similarly, there is phylogenetic evidence that many endemic species of some large river basins originated by *in situ* cladogenesis (a species splitting into two or more species). For instance, entire clades of *Synodontis* species probably originated in the Congo basin as revealed by phylogenetic studies of this specious genus distributed all over tropical Africa (Day *et al.*, 2013, Pinton *et al.*, 2013). However, for most river systems and taxa such phylogenetic information is lacking and we have to rely on the taxonomic hierarchy to assess the likelihood of *in situ* cladogenesis. As a first approximation let us assume, following Tedesco *et al.* (2012), that the existence in a river basin of two or more endemic species within the same genus could be the result of a cladogenetic event. In figure 15.3 the proportion of such species is plotted against catchment area and this value is quasi-null up to an area of about 8,000 km^2. That means that species extinction could be balanced by *in situ* speciation only in large or very large basins such that they can maintain or possibly increase their species richness even in complete isolation. In contrast, small rivers are in a disequilibrium state, losing species through time because of species extinctions that are not balanced by speciation or immigration. It is worth noting that catchment area is not sufficient to explain the observed pattern, as for the same area the percentage of endemism depends on the biogeographic provinces (see below for the possible contribution of drainage density to this pattern).

The habitat diversity explanation suggests that habitat heterogeneity and diversity of available trophic resources increase with area, thus offering more available niches and consequently favouring the existence of a large number of species. For instance Hugueny (1989) attempted to test this hypothesis in a sample of African rivers by considering the diversity of terrestrial vegetation over the river catchment, based on the observation made by Daget & Iltis
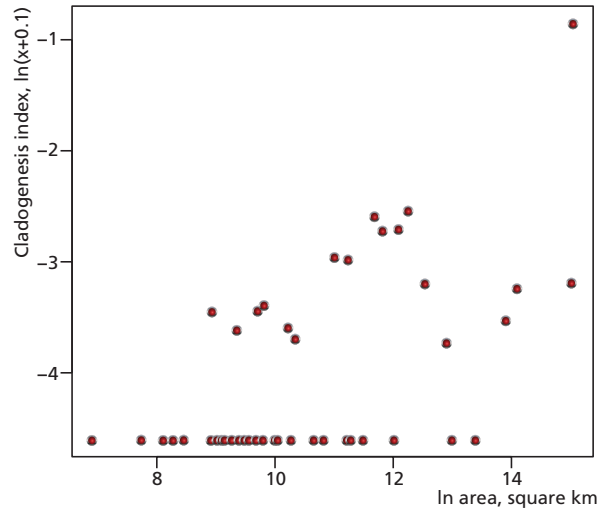
(1965) that some species were associated with forested areas and others with
savannah. No clear signature of vegetation diversity on species richness was
observed, suggesting a loose relationship between terrestrial landscape and
fish distribution. Another important pattern in this context is that hydrological
and geomorphic features of a river change along the upstream-downstream
gradient in a more or less predictable way and species are not distributed at
random along this gradient. The consequence is that some habitats encoun-
tered in the lower courses of a large river may be absent from small river
basins. Thus, a positive species-area relationship may be observed just
because habitat diversity is truncated in small rivers in comparison with larger
ones. To illustrate this hypothesis let us consider two species with contrasting
distribution along the upstream-downstream gradient. As shown in figure 15.4,
Brycinus longipinnis occurs preferentially in low order streams (small tributaries)
while *Lates niloticus* is more likely to be observed in high order streams (down-
stream sections of the river). In a small river basin, high order river sections are
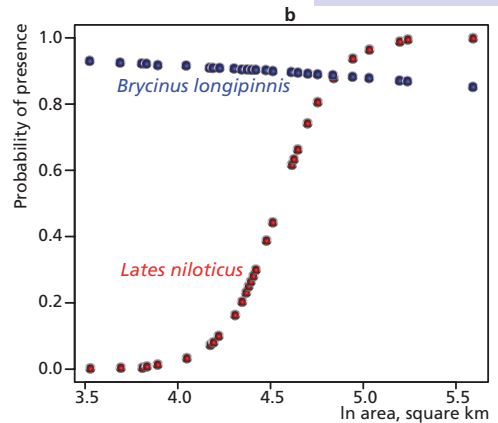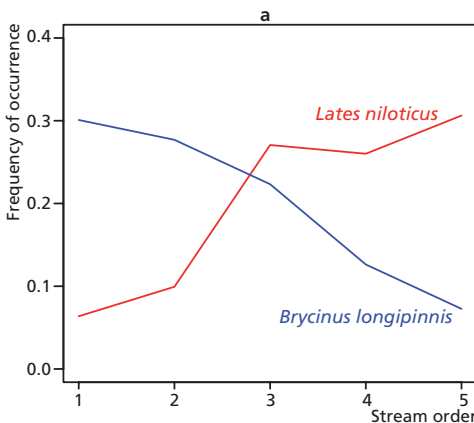
not encountered while both low and high order streams occur in a large one. On this basis we expect *B. longipinnis* to be present in both small and large river basins, while the probability of presence of *L. niloticus* should be very low in small rivers due to the absence of high order streams. The distribution patterns of these two species in West Africa fit this expectation (figure 15.4), suggesting that the dendritic structure of river networks could be an important component of SAR among river basins.

The role of discharge

Once the important role of area is controlled for, the action of other factors underlying species diversity may appear more clearly. For instance the Nile River, as already pointed out by Greenwood (1976), has considerably fewer fish species than the Congo (128 against more than 700; see section 2, "Broad patterns in fish diversity") despite very comparable catchment areas. To explain this pattern, Livingstone *et al.* (1982) suggested that discharge at a river's mouth could be a better predictor of species richness than catchment surface area. This was confirmed in their study of the fish fauna from some African rivers and by subsequent works in West Africa (Hugueny, 1989; figure 15.5). Models including both surface area and discharge are better predictors of species richness than models using one of these variables alone. At least two explanations could account for this successful use of discharge as a predictor variable. First, discharge is a better surrogate for the total surface area of habitat available for fishes than catchment area since drainage density varies with precipitation (de Wit & Stankiewicz, 2006). For the same catchment area, a river with a high discharge will have a higher number of perennial streams than a river with a lower discharge. This is particularly striking when maps of the Nile and Congo river networks are compared. Another explanation for the association between discharge and species richness, formulated by Livingstone *et al.* (1982), was that discharge also reflects productivity of the terrestrial vegetation within the river basin. This is a variation of the so-called species-energy hypothesis that we will discuss below.

Relationship between the number of freshwater fish species recorded in one river catchment and the corresponding mean annual discharge at the river mouth (in $m^3 s^{-1}$) (from Hugueny, 1989).
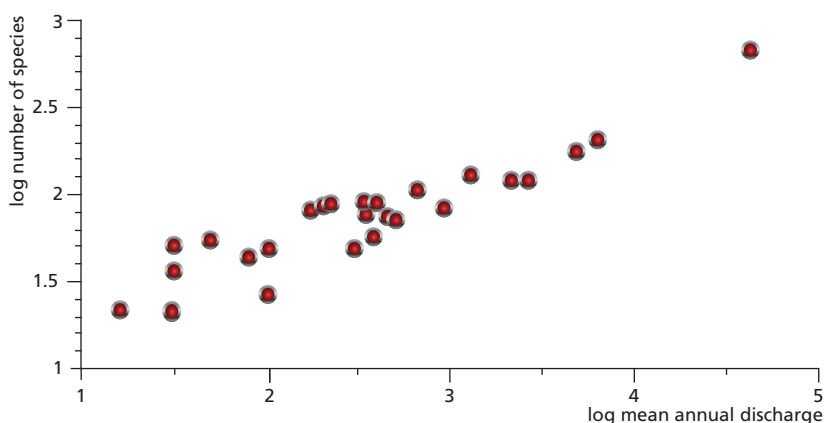
Species-energy relationship

The species-energy hypothesis (Wright, 1983) predicts a positive correlation between species richness and the energy available within an island, or in our case a river catchment. The rationale is that a river catchment with great energy output (primary productivity) should sustain more dense animal populations than those located on a river catchment of the same but less productive area. As a result, population sizes are higher, extinction rates lower and species richness higher in the more productive river basin. The species-energy hypothesis has been supported by studies that used terrestrial net primary productivity (NPP) as a surrogate for the available energy for fish (Oberdorff *et al.*, 1995). It is worth noting that these studies conducted at a global scale included African rivers and that the effect of NPP was significant even when discharge had been accounted for, suggesting that the discharge does not act only through the available energy. The species-energy theory as originally developed by Wright (1983) has been modified by postulating that diversity is controlled directly by the effect of climate on organism energetics and its consequences on individual performances (growth, reproduction, etc.). The recent "metabolic theory of ecology" (Brown *et al.,* 2004) predicts, for ectotherms, a positive association between speciation rate and ambient temperature (Allen *et al.*, 2006). When the sample size is restricted to African rivers, NPP does not add much to discharge in explaining species richness and therefore it is difficult to disentangle the effect of available habitat (river network density) from the energy contribution in this part of the world, and *a fortiori* to test competitive hypotheses dealing with the species-energy relationship.

Historical factors

Considering the low dispersal ability of obligate freshwater fishes, it seems logical that the influence of historical events should be detectable for riverine fish assemblages in terms of species richness. African river discharge was greatly affected by dramatic climatic changes during the Quaternary, and during dry periods a number of fish species, unable to survive extreme conditions or face habitat shrinkage, could have disappeared in the rivers most affected by drought. Recovery of the presumed original richness needs either time for speciation, or reshaping of the hydrological network to permit immigration from other river basins. For most rivers the elapsed time since the last dry period (Last Glacial Maximum, LGM) has been too short to allow speciation and, to a lesser extent, colonization and therefore extinction rates should have been higher for river basins affected by drought (through a decrease in discharge and available habitat) than for river basins located within one of the rain forest refuges that persisted during the LGM. Currently, presence of rain forest refuges during the LGM is associated with high contemporary species richness in African rivers (Tedesco *et al.*, 2005). Past configurations of hydrological networks,

when they are known, may shed light on present fish distributional patterns. For instance, in Southern Africa the presence of a lake that vanished about 2,000 years ago probably explains the high diversity of Haplochromines (Cichlidae) presently observed in rivers formerly connected to the lake (Joyce *et al.*, 2005). The Haplochromines are well known for their propensity to diversify quickly within lacustrine habitats and the former lake may have acted as a regional cradle for this group.

Global gradients

It is usually assumed that species diversity increases from high to low latitudes for most of the major groups of plants and animals and that biodiversity peaks in tropical and equatorial Africa, South America and Asia. This pattern holds true for freshwater fishes. For instance a comparison between species richness in African and European rivers shows that the fish species richness is significantly lower for the same catchment area in European than in African rivers (figure 15.1). Among the numerous hypotheses that have been proposed to explain the latitudinal gradient, only a few have been tested and received empirical support from studies comparing fish species richness in rivers distributed all over the globe. One is the species-energy hypothesis stating that rivers receiving higher energy input per unit area (tropics) should sustain richer communities than rivers with low input (temperate). The same data are also compatible with the metabolic theory postulating higher speciation rate for poikilotherms in warmer habitats and hence a positive relationship between temperature and species richness. The relationship between "energy" (NPP or temperature) and fish diversity per river basin is empirically established but the underlying mechanisms are still poorly known. The species-energy theory as originally developed by Wright (1983) posits a positive relationship between species richness and energy availability because of a reduction in population extinctions due to higher population densities. This hypothesis could be further tested if population density data were available along an energy gradient, or along a crude surrogate such as a latitudinal gradient. According to the few studies available for fishes (Knouft, 2002; Randall *et al.*, 1995; Mazzoni & Lobón-Cerviá, 2000), average density per species is not related to latitude. Similarly the relationship between temperature and speciation rate which underlies the metabolic theory still lacks empirical support for freshwater fishes. Moreover, among tropical biomes differences persist that cannot be attributed to differences in available energy, and for instance rivers in South America harbour more fish species than in Africa for the same area and energy input. The existence of a continental effect not explained by present features of rivers leads to the conclusion that unknown historical factors, maybe particular to each geographical region, are responsible for differences in fish diversity between Africa and South America and only palaeontological or phylogenetic data could provide some insights on these factors.

Biological traits

While major species richness patterns are well identified for African rivers, very little is known about the relationship between assemblage structure (quantified by using some biological traits) and river basin characteristics. For example, Tedesco *et al.* (2008) tested the hypothesis that hydrological regime within a river basin should be linked to life-history strategies of fish species. In particular, according to the scheme proposed by Winemiller & Rose (1992), species known as "periodic" (highly fecund, small eggs, no parental care) should have a higher probability of presence within river basins with marked seasonal floods. This hypothesis was confirmed for a set of West African rivers and by results obtained using river (seasonal) versus lake (stable) comparisons in the same biogeographic area (Bruton & Merron, 1990). In a global analysis Blanchet *et al.* (2010) observed that river basins with high species richness tend to be inhabited by a larger proportion of small species. For instance in Africa, the median body length of species inhabiting the Congo River is one of the lowest observed in African rivers. Many processes may explain such a pattern. First, speciation rate is expected to be higher for small, short-lived species than for large species with longer generation times. Second, large species with low population density and slow recovery after disturbance are likely to have high extinction rates. In support of these hypotheses, diversification rate (speciation minus extinction) tends to be inversely correlated to body size in fish families endemic to Africa (figure 15.6). Third, large species are expected to have better dispersal abilities than small ones. In support of this hypothesis, there is in West Africa a significantly positive correlation between fish body size and the geographic range of that species' distribution, estimated as the number of catchments where the species is present (Hugueny, 1990a). As a whole such processes should lead to an accumulation of small species in speciose river basins that experienced few population extinctions and many speciation events. It is also expected that single river endemic species should be of small size, a pattern that is observed for African fishes and at a global scale as well.
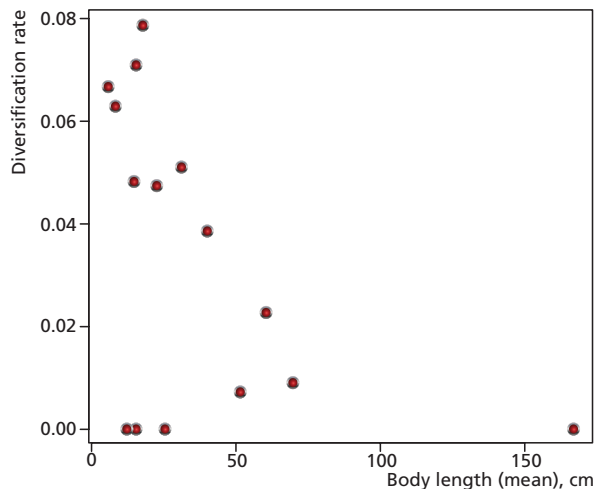

FIGURE 15.6.

Diversification rate (log number of species/age in million years) and average body size for 15 African endemic families (from Tedesco *et al.*, unpublished).

Patterns within rivers

Local-regional richness relationship

Most models integrating regional dispersal predict that local species richness directly depends on the number of species that are regionally available for colonization or, in other words, that the local features of the habitat (e.g., productivity and complexity) do not set a limit to the number of species that can coexist even if competition occurs, in contrast with what could have been anticipated from a strict interpretation of the niche theory. A positive relationship between local and regional richness is the rule more than the exception (Cornell & Karlson, 1997), provided that local communities occur in comparable habitats in terms of area, productivity and complexity. For riverine fishes, the number of species available for colonizing a local habitat is given, in first approximation, by the total number of species encountered within the catchment because there is no possible dispersal from adjacent river basins. Within this framework, Hugueny & Paugy (1995) tested for the existence of a local-regional species richness relationship by comparing local communities from similar habitat ("pool") in rivers from Côte d'Ivoire spanning a large gradient in their total species richness (20-90 species). As expected, the average local species richness is correlated with the river species richness, as shown in figure 15.7. Note that the proportional increase in local vs. regional species richness observed in this example was formerly interpreted as the signature of non-interactive communities, but the present wisdom is now to consider that the shape of the local-regional species richness conveys little information about the strength and nature of species interactions. The salient conclusion is that processes affecting species richness per basin and acting over large spatial and temporal scale such as extinction, speciation and dispersal among rivers, scale down to the local communities. In the present example, analysis of the data led to the conclusion that the area of the river catchment governs the

FIGURE 15.7.

Relationship between the average local fish species richness per basin and the total number of species encountered per basin (regional richness) for rivers in Côte d'Ivoire (From Hugueny & Paugy, 1995).
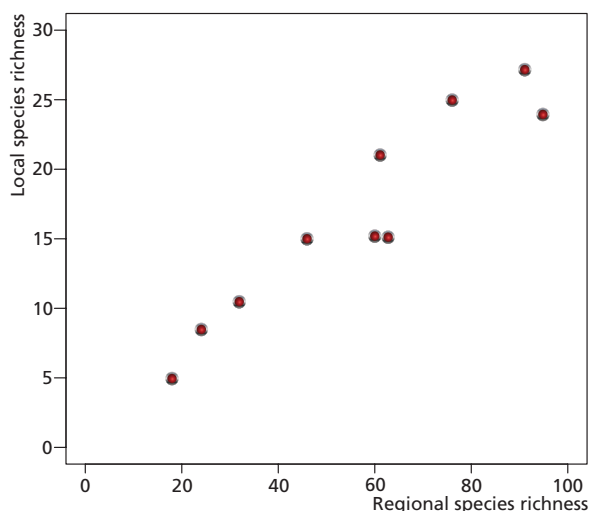
number of species present in the catchment which in turn governs the average local species richness of the pool assemblages. Interpreting how local species richness varies among basins should go hand in hand with finding out what mechanisms are responsible for the species-area relationships observed in aquatic systems.

Upstream-downstream gradient

The previous section focused on local communities from the same habitat compared among different rivers to emphasize the role of regional factors on local community structure. The objective of the present section is to discuss the relationship between local communities and local habitat features within the same river basin, and in particular in light of a major structuring agent of river systems, namely the longitudinal gradient. Changes in physical conditions of streams and rivers from upstream to downstream reaches are generally assumed to favour an increase in species richness through increasing habitat heterogeneity and habitat volume (Schlosser, 1987; McGarvey & Hughes, 2008) or decreasing hydrological variability (Horwitz, 1978). An increase of fish richness along a longitudinal gradient has been reported in Africa from the Mono (Paugy & Bénech, 1989), the Ogun (Sydenham, 1977) and the Nyagui (Kadye & Marshall, 2006) rivers to provide selected examples. In the Mono, fish species richness increases rapidly with increasing distance from the source, and then becomes asymptotic. It is therefore important to carefully investigate the headwaters in order to show an upstream-downstream gradient. It is worth noting that the existence of a longitudinal gradient in species richness is not as frequent in Africa as in other parts of the world, because many rivers flow through very flat landscapes that do not generate great environmental dissimilarity along the river course, as observed for the Bandama for instance (Mérona, 1981).

There were different attempts to explain the above observations. Gorman & Karr (1978) explained the increasing richness with river size by increasing habitat diversity. It is a general observation in community ecology that habitat diversity or complexity is correlated with species richness because of more ecological niches and an easier coexistence of competitors, preys and predators. For stream ecosystems, the depth, current velocity, and the nature of substrate have been the most widely used to characterize habitat diversity (Gorman & Karr, 1978) to account for the major role of hydraulics in habitat selection by species, refuge from predation and distribution of food resources. As expected, a positive relationship between habitat diversity and species richness has been observed in some African rivers. For instance, the upstream-downstream gradient in species richness is explained by a parallel gradient in habitat diversity in the Nyagui River in the Zambezi catchment (Kadye & Marshall, 2006).

Schlosser (1982) pointed out that deep "pools" are absent or rare in the upper streams, and that explains the absence of the fish species inhabiting these deep and quiet habitats. In support of this hypothesis, a positive relationship between richness and maximum depth has been reported in the Niandan River and the Ogowe River (figure 15.8), suggesting that localities with both deep and shallow habitats are inhabited by more species. Note that at the same

depth, species richness in the Ogowe is higher than in Niandan, as expected on the basis of the higher species richness of the Ogowe with respect to the Niger (figure 15.8).
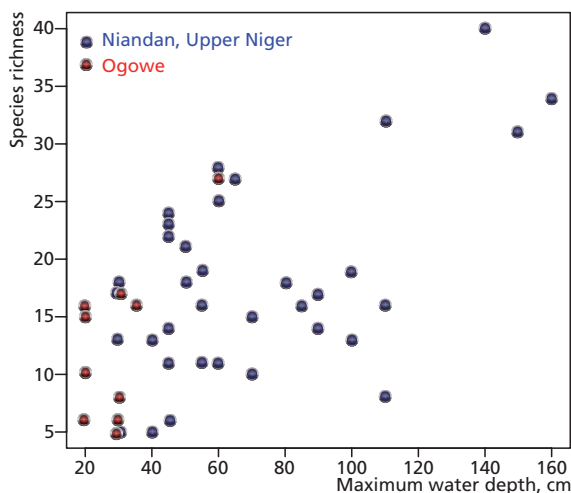
Another hypothesis for explaining longitudinal gradients is that the greater hydrological variability upstream results in the extinction of populations and thus in a lower species richness (Horwitz, 1978). No study has explicitly tested this hypothesis in African rivers but the fact that in some rivers headwaters are temporary (e.g. Bandama) certainly contributes to reduce species richness upstream.

Besides species richness, other community descriptors may change along the longitudinal gradient such as the trophic structure. For instance in the Ogowe river Ibañez et al. (2009) observed an increase in the percentage of omnivores (both individuals and species) and a decrease in the percentage of invertivores (both individuals and species) as stream size increases. Observed trophic differences along the longitudinal gradient were also consistent with many other studies that described a longitudinal progression in fish trophic guilds that generally begins upstream with generalized invertivores and ends downstream with omnivores, detritivores, herbivores and piscivores (Angermeier & Karr, 1983; Schlosser, 1987; Oberdorff et al., 1993; McGarvey & Hughes, 2008). Some of these trends are expected under the River Continuum Concept (Vannote et al., 1980). The greater importance of herbivory/detritivory as a river becomes larger follows the prediction of increasing endogenous primary production and the accumulation of fine particulate detritus.

Mahon & Portt (1985) considered that each species, according to its size and behaviour, needed a minimal water depth to survive. As a result, the shallow waters could only be colonized by small species or juveniles of larger ones (Angermeier & Karr, 1983). This hypothesis was supported by a positive correlation between the length of the largest individual collected and maximal depth of the sampling station in the Niandan (Hugueny, 1990b).

Patterns among provinces

Distance species decay

From one river to another, fish species lists are rarely, if ever, identical, even within the same biogeographic region; some species are encountered in one river basin but not in the second and contribute to spatial turnover. Different indices exist to assess the similarity between two species lists, the most frequently used being Jaccard or Sorenson. Conversely, distances (according to axes of an ordination for instance) could also be used in this aim. A general pattern observed in community ecology and biogeography is the distance species decay (Soininen *et al.*, 2007) which describes a decrease in similarity between two communities with the geographical distance that separates them. Basically two processes may explain this pattern. The first is dispersal limitation. Two communities are increasingly unlikely to exchange individuals through dispersal as geographical distance increases between them. The second is a negative relationship between similarity in environmental features and geographical distance. If the environmental conditions that fit the requirement of a given species are present in a locality, then they are more likely to be found in close localities than in remote ones. For strictly freshwater fishes distributed in isolated river basins, dispersal took place mainly between adjacent basins when a freshwater connection is created by climatic changes (e.g. spillover due to high floods during the last humid period, 8,000 years ago) or orogenic or tectonic events (e.g. river capture). In this context of stepping stone colonization, a convenient way of expressing spatial distance between two river basins is to count the minimum number of river divides that should have been crossed by a species to go from one basin to the other. In West Africa, there is a clear increase in species dissimilarity between two river basins along such a stepping stone distance (figure 15.9). The relative contribution of dispersal and environmental heterogeneity to a species decay pattern is generally difficult to assess, but it can be expected that two recently connected basins should be more similar in species composition than an average pair of adjacent basins. In West Africa Hugueny & Lévêque (1994) listed four pairs of basins for which there is geographical evidence that they had been recently connected (Quaternary). These authors also listed river basins connected via coastal brackish creeks and lagoons. For species that can tolerate brackish water this is a possible dispersal route between river basins. For the other, less tolerant, species such exchanges could have been facilitated during past pluvial periods when high freshwater inputs may have diluted the brackish waters. For these pairs of basins that had been recently connected and maybe still are for some of them, the faunal similarity is higher than for other pairs of adjacent basins (figure 15.9). Finally, exchanges between rivers may have occurred during periods of lower sea level than at present. For instance, during the LGM drop in sea levels (up to 120 m), river mouths progressed through kilometres of exposed marine shelves before reaching the ocean, which sometimes resulted in a connection between previously isolated drainage basins. Dias *et al.* (2014) reconstructed such palaeo-connections at the global scale and compared pairs of river basins connected during the LGM with pairs that were not, to assess whether ancient

connections left an imprint on present faunal similarities. At the global scale the response is yes, but restricting the analysis to African rivers leads to a statistically non-significant result despite the fact that, as expected, the existence of palaeo-connection results in higher faunal similarity. The narrow continental shelf of the Afrotropical realm resulted in a very limited number of palaeo-connected rivers under low-sea-level conditions and may explain, by lack of statistical power, the absence of a significant pattern. To conclude, when information is available it appears that recent connections between basins have favoured faunal exchanges that resulted in a greater faunal similarity between them. Such connections, by homogeneizing ichthyofaunas among basins, contributed to shaping biogeographical provinces. For instance all the connections through river capture, overflow, or brackish creeks listed by Hugueny & Lévêque (1994) occur between rivers located within the same province (Nilo-Sudan or Upper Guinea). The fact that the recent known connections occurred between basins that are considerably larger in the Nilo-Sudan than in the Upper Guinea resulted in provinces differing greatly in their spatial extent.

Freshwater fish faunal dissimilarity between two rivers increases with the geographical distance separating them. A geographic distance of zero is for two contiguous river basins, one when they are separated by one river catchment and so on. For comparison, the faunal dissimilarities between pairs of rivers connected by a recent river capture or through a coastal creek network are shown (from Hugueny & Lévêque, 1994).
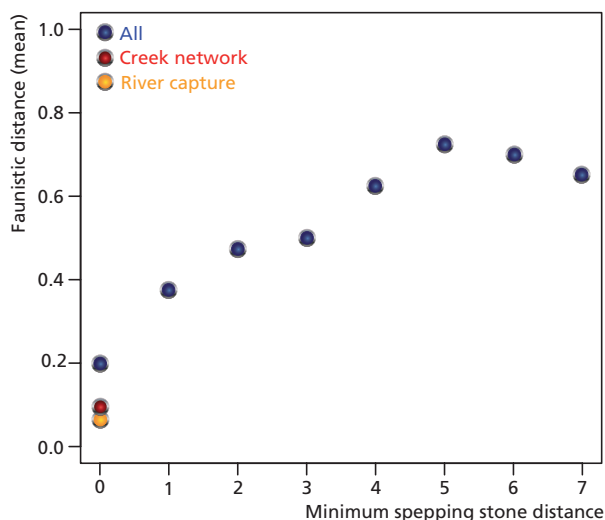
Provincial biodiversity

The species richness of a province is a combination of the richness of its most specious river basin and spatial turnover. To graphically represent these two components, species richness increments from the most specious river to the province is plotted as a function of area, the slope connecting the two points being an index of species turnover, the higher the slope the higher the turnover. Such river-to-province species-area relationships are depicted in figure 15.10 for all provinces but Congo (one river) and Maghreb (no reliable species richness estimates per river).
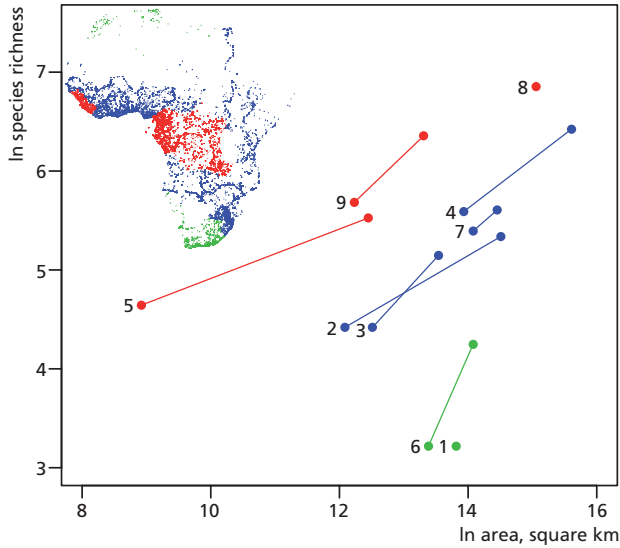
The most salient result is that the species richness of a province is highly correlated to the richness of its most specious river (91% of the variability is explained in log-log space) so that spatial turnover has a very low contribution. We can distinguish three groups with regard to species area-relationships. The first includes the three regions (Upper Guinea, Lower Guinea, Congo) that are mostly located within the rain forest biome and have harboured one or several rain forest refuges during the Last Glacial Maximum. Rivers and regions belonging to this group have the highest richness for a given area. In contrast a group of two regions located in arid climatic zones display the lowest species richness for a given area. The remaining regions are intermediate. Grossly, the main factor explaining why a river basin harbours a rich fish fauna irrespective of its area, namely precipitations that remained high during the Quaternary despite the alternation of dry and humid phases, scales up and also explains biodiversity patterns at the regional scale. Species-rich provinces are rich just because of the aggregation of species-rich river basins. The disparity observed in spatial turnover among regions is not sufficient to blur this simple pattern. For instance the highest spatial turnover is observed for the Austral province, yet this region is very depauperate considering its area. Interpreting the differences in spatial turnover among provinces is a difficult task because the evolutionary histories of the lineages (speciation, extinction, dispersal) and past changes in the geographic and climatic setting may have been complex, and, unfortunately, frequently imperfectly known. According to an analysis conducted at the global scale (Leprieur *et al.*, 2011), basins located in mountainous areas are more likely to be dissimilar in species composition than when located within flat areas, probably because river capture and overflow are more likely to occur between catchments separated by low elevation river divide. However the observed pattern in Africa does not fit this expectation. For instance the Upper Guinea has a low spatial turnover while being in a high elevation region.

The Inland Water Fishes of Africa

Diversity, Ecology and Human Use

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