Community Ecology of River Fishes: A Large-Scale Perspective

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Abstract.—Community ecology increasingly seeks to integrate the influences of regional and historical processes with species interactions within local habitats. This broadened perspective is largely based on comparative approaches that employ "natural experiments" to identify factors shaping community structure. Because coastal rivers are separated from one another by insurmountable barriers (oceans or land), freshwater fishes are particularly well suited for comparative analyses of factors that influence fish community organization. In this chapter, we review how this comparative approach shed light on large-scale biodiversity gradients, community saturation, community convergence, density compensation, and the role of intrinsic and extrinsic factors in community dynamics. The main factors (e.g., river mouth discharge and history) empirically related to species richness of a river are well identified, and metacommunity ecology provides a fruitful conceptual framework for understanding how regional (river) species richness translates into local species richness. Much work remains to identify factors explaining differences among whole river basin assemblages with regard to ecological traits (e.g., trophic status and life history) composition and to assess whether trait-related environmental and biotic local filters act similarly over large spatial scales. One important conclusion that can be drawn from the studies reviewed here is that history cannot be neglected whatever the scale of investigation (global, river, or site). A second conclusion is that historical effects are not strong enough to blur the occurrence of qualitatively repeatable patterns of community structure over large spatial scale, which is encouraging because it suggests development of general predictive models of community structure is an attainable goal.

Introduction

Ecology is an integrative science that investigates processes operating at levels from individual organisms (e.g., behavioral ecology) to the entire biosphere (e.g., biogeochemical cycles) over time scales ranging from a few seconds (e.g., prey choice) to centuries (e.g., ecosystem succession). However, many ecological studies are conducted at local scales (<1 km^2) and during short periods (<3 years) (Blackburn and Gaston 2003). Of course, logistical constraints largely explain this bias toward small-scale investigations; yet, within the field of community ecology, there has been a long-held view that communities are strongly influenced by species interactions operating within habitats. This "theory of local diversity" (Schluter and Ricklefs 1993b) states that

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community diversity is the outcome of competition and predation among its members, depending on environmental conditions such as productivity, disturbance, and structural complexity. A growing number of ecologists now embrace a view that integrates regional and historical processes, as well as species interactions within local habitats (Ricklefs 1987, 2008; Cornell and Lawton 1992; Rosenzweig 1995). This broader perspective has been partly driven by the frequent occurrence of positive relationships between local and regional species richness (Cornell and Karlson 1997), which implies that local communities are affected by factors that operate at large spatial and temporal scales to shape regional diversity. By emphasizing the spatial scale at which dispersal occurs, the recent field of metacommunity ecology (Leibold et al. 2004), or spatial ecology (Tilman and Kareiva 1997), reveals the limitations of concepts restricted to local processes for explaining community structure and dynamics. Most of these recent calls for increasing the spatiotemporal scale of ecological investigations could be encapsulated under the new research field of macroecology (Brown 1995), which urges ecologists to "think big." Macroecology explores the domain where ecology, biogeography, and macroevolution meet. It aims to identify the statistical properties that emerge from complex ecosystems, in order to highlight generalized patterns of observation, particularly at the macroscopic scale. It is thus a nonexperimental, comparative approach that is largely based on "natural experiments" where one potentially important factor varies naturally between communities.

Riverine fishes are particularly well suited to this type of study since river basins are separated from one another by barriers (oceans or land) that are insurmountable for strictly freshwater fish and thus form biogeographical islands. The absence of migration between rivers over large temporal scales implies that extinction and speciation processes are basin-specific. Thus, river basins are, to some extent, independent entities that could be used in comparative analysis to explore the factors that shape fish community organization between and within them. In this chapter, we will use this natural experiment framework to discuss the relative role of local, regional, and continental features in determining community structure. As far as possible and when relevant, the same framework will be applied to community structure described both in terms of number of species and of community composition based on biological traits such as life history strategies, body size, feeding habits, and so forth (see also Infante and Allan 2010; Frimpong and Angermeier 2010; Jones et al. 2010; all this volume). Community richness, composition and dynamics will be discussed in light of past findings and recent advances on several research axes: large-scale biodiversity gradients, local-regional relationships, community convergence, density compensation, and temporal dynamics.

Unless otherwise specified, the term "river basin" will refer to rivers flowing into the ocean. For rivers that are part of a bigger drainage, the term "tributary" will be used. When dealing with spatial scale in ecology, it is convenient to distinguish between "grain" and "extent." Grain size refers to the resolution while the extent refers to the spatial scale involved. In this contribution, we will deal essentially with two grain sizes: entire river basin and river reach (locality). The term "assemblage" will be used to describe the set of species encountered within a river basin and community for a set of species coexisting locally. In a first step, we will describe the biodiversity patterns that emerge by comparing the larger grains (i.e., fish assemblages of entire river basins). Then, we will deal with studies that asked whether local commu-

nities differed between river basins. Finding a "river effect" may suggest dependence between local community and regional (river) assemblage; the patterns identified in the first step should be helpful in explaining those observed in the second (if top-down processes occur). Depending on the hypothesis tested, the extent will be variable, ranging from a set of adjacent rivers to the entire globe.

This chapter is biased toward topics we are familiar with, and we certainly do not pretend to exhaust all the relevant issues raised by the matter of scale in freshwater fish community ecology or macroecology. We nevertheless hope that by discussing these studies, we can identify a coherent and useful framework for future studies.

Biodiversity Patterns at the River-Basin Scale

River basins draining into the ocean (as opposed to tributaries) 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 (seawater or dry land). Within a geological timeframe, events such as river capture or overflow from one basin to another may allow faunal exchange (Craw et al. 2006), but these events are rare and primarily depend on major climatic or geological changes. 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 (retreat of glaciers and sea level rise). River basins, as defined in this paper, are biogeographical islands, but they do not conform to the dynamic equilibrium hypothesis of MacArthur and Wilson (1967) because extinctions cannot be balanced by colonization within an ecological time scale. Because of their well-defined boundaries and isolation, rivers are

ideal "grains" for conducting biogeographical or macroecological comparative studies. In the most comprehensive studies conducted on this topic, Oberdorff et al. (1995) and Guégan et al. (1998) used data from 292 river basins on five different continents to identify factors responsible for variation in fish species richness. A combination of three variables (i.e., the total surface area of the river basin, the mean flow at the river mouth, and the net terrestrial primary productivity within the basin) explained up to 93% of the variance. Possible explanations for the processes underlying the role of these variables are discussed below.

Species–Area Relationships

Differences in species richness among rivers frequently can be explained by species–area relationships (Daget and Iltis 1965; Daget 1968, Eadie et al. 1986; Hugueny 1989). River size can be estimated by calculating catchment area, but this considerably overestimates the true (but generally unknown) surface area that could be inhabited by fishes (but see Eadie et al. 1986). Three nonexclusive explanations have been put forward to explain the species–area relationship: (1) the size-dependent extinction rate (MacArthur and Wilson 1967), (2) the size-dependent speciation rate (Losos and Schluter 2000), and (3) the influence of habitat diversity (Williamson 1988). Size-dependent extinction assumes that probability of extinction of a species increases with a reduction in its population size, which in turn is a function of surface area of the island. Size-dependent speciation assumes a positive effect of area on speciation rate by exposing species to greater ecological heterogeneity and/or geographical barriers (Rosenzweig 1995). The habitat diversity explanation suggests habitat heterogeneity and diversity of available trophic resources increase with island size, thus offering more available niches and consequently

favoring the coexistence of a larger number of species (Williamson 1988).

We are aware of only one study quantifying extinction probability of fish populations as a function of catchment area (Morita and Yamamoto 2002), and this study was conducted at a small scale (around 1 km^2) and may hardly represent patterns at larger scales. However, the inverse relationship between extinction probability and population size is well established for many taxonomic groups (Lande et al. 2003), and there is no reason to suspect freshwater fishes differ in this regard. The hypothesis that a large surface area promotes speciation is quite old but received empirical support only recently thanks to phylogenetic studies of insular lizards (Losos and Schluter 2000) and continental birds (Ricklefs 2006). There is phylogenetic evidence that many endemic species of some large river basins originated by in situ speciation (e.g., the Mississippi River basin, Mayden 1987, 1988), but the speciation–area hypothesis remains to be explicitly tested for riverine fishes.

Regarding habitat heterogeneity, an important pattern is that hydrological and geomorphic features of a river change along the upstream–downstream gradient in a more or less predictable way. The consequence is that some habitats encountered 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 larger river basins offer more habitats. It is difficult to test this hypothesis per se because of the intricate relationship between the cumulative increase in habitat diversity along the longitudinal gradient and the increase in the surface of the drainage area. That coastal rivers harbor less species than similarly sized tributaries (e.g., Sheldon 1988) suggests that the habitat hypothesis is not sufficient to account for species–area relationships, and extinction processes should be also considered.

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), in North America (Xenopoulos and Lodge 2006; McGarvey and Hughes 2008), and at the global or intercontinental scales (Oberdorff et al. 1995, 1997, Xenopoulos et al. 2005). At least two explanations could account for this successful use of discharge as a predictor variable. First, discharge is a better surrogate of the total surface area of habitat available for fishes than catchment area, since drainage density varies with precipitation (de Wit and 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. Moreover, stream density can be a good predictor of fish species richness at a medium spatial scale (640 km2, Rathert et al. 1999). 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.

Species–Energy Relationships

The species–energy hypothesis (Wright 1983) predicts a positive correlation between species richness and the energy available within a system. The rationale is that an island with great energy output (primary productivity) should sustain more dense animal populations than those located on an island of the same, but less productive area. As a result, population sizes are higher, extinction rates lower, and species richness higher on the more productive island. The species–energy hypothesis has been sup-

ported by studies that used terrestrial net primary productivity (NPP) as a surrogate for the available energy for fish (Oberdorff et al. 1995; Guégan et al. 1998).

However, limitations of the study conducted by Oberdorff et al. (1995) were that NPP was estimated for terrestrial vegetation, and aquatic primary productivity was neglected due to a lack of available estimations at a global scale. The limited data gathered by Davies et al. (2008) indicate that aquatic primary productivity (1) is about 10-fold higher in tropical streams and rivers than in their temperate counterparts, (2) is about 10-fold higher in rivers than streams, and (3) represents around 10% of corresponding values for terrestrial productivity within a similar climatic zone. Tropical floodplains are an exception to this pattern. In these systems, aquatic productivity may reach similar or even higher values than observed for tropical forests. If fish biomass is significantly supported by aquatic primary production, this should happen disproportionately in large rivers. However, available evidence seems contradictory because autochthonous components of food webs may (Forsberg et al. 1993; Thorp and Delong 2002) or may not (Zeug and Winemiller 2008) sustain a significant part of fish biomass in these systems. Using estimates of terrestrial primary productivity probably does not underestimate the amount of energy available for river food webs.

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 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 (Randall et al. 1995; Mazzoni and Lobón-Cerviá 2000;

Knouft 2002), average density per species is not related to latitude. More comprehensive studies are thus needed before a definitive conclusion about the relevance of the density–energy hypothesis for river fishes can be assessed. To date, this hypothesis has not been supported by available data.

Greater amounts of energy circulating through food webs may also increase the availability of a resource that could then be exploited by more species (Evans et al. 2005). A possible example is frugivory (Correa et al. 2007), a feeding strategy that is known only for fishes occurring in energy-rich environments such as rivers flowing through tropical forests. Hence, greater productivity may lead to higher species richness by allowing more trophic diversification.

Other explanations for the positive link between species richness and energy could be combined under the label of the "ambient energy hypothesis" (Turner 2004). This hypothesis suggests that diversity is controlled directly by the effect of climate on organism energetics and its consequences on individual performances (growth, reproduction, etc.). For freshwater fishes, the most likely component of climate that could affect individual metabolism is temperature. To explain large-scale diversity patterns, the temperature effect on individual metabolism should translate into speciation and/or extinction rates. 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; see also Rohde 1992). The rationale is that a high metabolism rate increases the mutation rate and, in turn, the speed at which two incipient species may diverge. Temperature or temperature-based variables (e.g., growing degree-day) have been correlated with fish species richness in rivers, at global (Allen et al. 2002) and regional scales (Latta et al. 2008), but only studies based on

phylogenies or paleontological data can provide strong evidence of a link between diversification rates and temperature. Few relevant studies exist for freshwater fishes, and, to our knowledge, no studies compared diversification rates between warm (e.g., tropical) and cool (e.g., temperate) regions, as done, for instance, for birds (Ricklefs 2006).

To sum up, the relationship between "energy" and fish diversity per river basin is empirically established, but the underlying mechanisms are still poorly known. In particular, we need more information about how energy affects diversification rates.

Historical Issues

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 and composition (e.g., percent of good dispersers). Indeed, in both temperate and tropical zones, historical factors have been identified for different continents. Presence of rain forest refuges during the Last Glacial Maximum (LGM) is associated with high contemporary species richness in tropical rivers (Africa and South America, Tedesco et al. 2005). This result is expected as 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 a rain forest refuge. In the Holarctic zone, distance from major aquatic refuges during the LGM (Danube and Mississippi, Mahon 1984; Moyle and Herbold 1987; Banarescu 1989) was found to be negatively linked to river basin species richness (Oberdorff et al. 1997; Griffiths 2006; Reyjol et al. 2006). Surprisingly, basins covered by ice sheets during the LGM did not harbor significantly less species than those that were not, both in Europe and North America (Ober-

dorff et al. 1997). A potential explanation for this weak direct effect of glaciers on species diversity is that their retreat has favored connections between drainages due to the numerous lakes created by ice melting (Bernatchez and Wilson 1998). According to this hypothesis, the extinction of species due to glaciers was compensated by a rapid immigration process. This was confirmed by phylogeographic data (Bernatchez and Wilson 1998).

Besides a predictable effect of past events, history could have a more idiosyncratic role. Data analyzed by Oberdorff et al. (1997) show that after river size and net primary productivity have been factored out, North American river basins are still 1.7 times as species-rich as their European counterparts, and this difference persists when distance to refuge zones is considered. The fact that a "continental" effect is highly significant in the final model leads to the conclusion that other historical factors not taken into account in the study, and maybe particular to each geographical region, are responsible for differences between rivers on the two continents. A complex array of factors is probably involved in this pattern, but speciation events occurred more frequently in North American refugia than in Western European (Mahon 1984). Such continental effects are not restricted to the Holarctic (Oberdorff et al. 1995; 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 Haplochromine (Cichlidae) presently observed in rivers formerly connected to the lake (Joyce et al. 2005). The Haplochromine 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.

Patterns in Biological Trait Composition

While major species-richness patterns are well identified, very little is known about the relationship between assemblage structure (quantified by using some biological traits) and river basins 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 (1989, 1992) and Winemiller and Rose (1992), species known as "periodic" (highly fecund, small eggs, and 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 and Merron 1990). Olden and Kennard (2010, this volume) reported, in both North America and Australia, a greater prevalence of "opportunistic" species (small size, no parental care) in river basins with high hydrologic variability as expected on theoretical grounds. Other approaches suggesting a link between river characteristics (past or present) and biological traits are those that reported changes of biological trait distribution along latitudinal gradients or between continents. For instance, it is well established that the average body size of freshwater fish species within a regional community increases with latitude in North America (McDowall 1994; Knouft 2004) and in Europe (Griffiths 2006). The underlying mechanisms are still unclear and certainly multiple, but Griffiths (2006) provided some evidence for at least one of these. He observed that formerly glaciated areas have been colonized by larger fish species than unglaciated areas, a result compatible with the hypothesis that large fishes are better dispersers. Mahon (1984) performed a very detailed comparison of fish community structure between two comparable rivers, one

in Poland (Europe) and the second in Ontario (North America). In the same vein, Moyle and Herbold (1987) compared western and eastern North American fish assemblages. Results from both studies suggested that the high number of species encountered in eastern North American rivers compared to western North America and Europe is mainly due to highly diversified taxa that occur principally in small streams and have low dispersal abilities (e.g., darters). Mahon (1984) suggested that speciation rates have been higher for stream specialist species in North America and principally in the Pleistocene refuges (Mississippi basin). However, it is unclear why small stream specialists did not undergo similar diversification within European refuges (e.g., Danube). Completing this pattern, in an intercontinental comparison of life history strategies, Vila-Gispert et al. (2002) observed that the North American fish fauna tends to have more species with larger eggs and more parental care (the equilibrium strategy sensu Winemiller 1989, 1992) than European species. Tropical intercontinental comparisons also have been performed. Winemiller et al. (1995) compared cichlids assemblages from three regions (Costa Rica, Venezuela, and Zambia) and found no differences among regions in trophic composition, but, with regard to ecomorphology, a larger relative proportion of fusiform piscivores was observed in Zambia. These comparisons in addition with Olden and Kennard (2010) suggest that both determinism (intercontinental similarities) and contingency (intercontinental dissimilarities) play a role in the ecological structuring of assemblage at a continental scale.

"Contemporary" versus "Historical" Factors

While there is evidence that both species and ecological guild richness may vary among river basins because of river characteristics and historical events, these patterns are nevertheless

best described for species richness. The most likely causal pathways that explain variation in species richness are synthesized in Figure 1. This scheme outlines the importance of area, climatic, and energy-related variables. These variables are also associated with fish species richness in lakes (Amarasinghe and Welcomme 2002) and amphibian richness (Buckley and Jetz 2007). For instance, eastern North America, a glacial refugia and an area receiving high rainfall over recent epochs, was found to be a hotspot of fish and amphibian biodiversity.

Because models integrating contemporary factors (e.g., potential evapotranspiration) explain a large part of terrestrial vertebrate species richness (e.g., mammals) over large geographical gradients (e.g., North America), Currie (1991) argued that the match between environmental factors and species richness have occurred at such a rapid pace that the impact of historical factors (such as the last glaciation) are no longer perceptible or have only a negligible contribution. Similarly, the fact that at a global scale, contemporary factors (area, discharge, and available energy) explain up to 93% of the variance in fish species richness per river basin (Guégan et al. 1998) suggests that historical factors are unlikely to play a prominent role. Nonetheless, to conclude that fish species richness in a river basin is at equilibrium with modern environmental conditions, in particular with climate, could be misleading. Due to their isolation, river basins are not at equilibrium because in situ extinctions are not balanced by colonization from other basins. However, very large basins may be exceptions if in situ speciation compensates for extinction. So, why are contemporary environmental factors so successful in predicting river fish diversity? The reason probably comes from the strong correlation between current and historic climate (and thus energy levels) at large spatial scales. During the LGM, the tropics were warmer and wetter than temperate re-
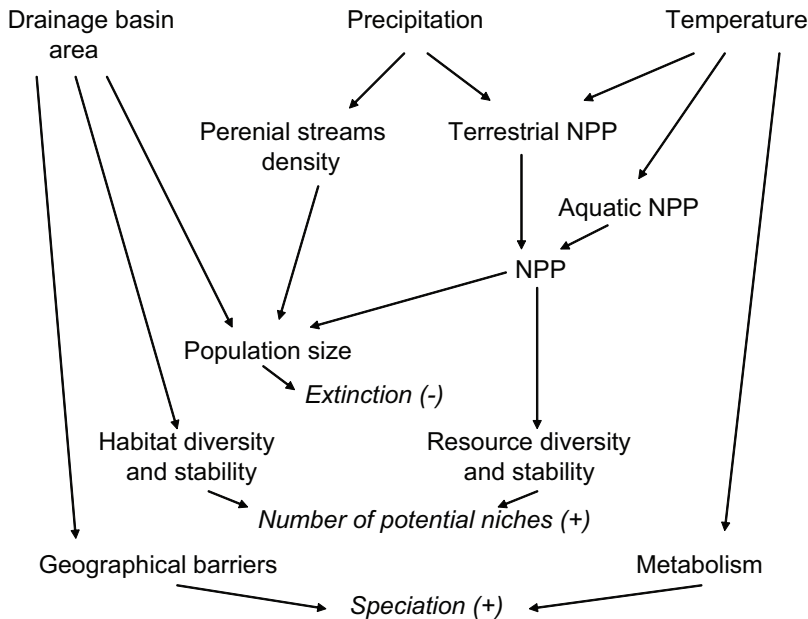

Figure 1. Potential causal pathways between environmental factors and processes increasing (+) or decreasing (−) the species richness of a river basin. NPP is for net primary productivity.

gions, just as they are today (H. Dürr, Utrecht University, Utrecht, Netherlands, unpublished data), and postulated forest refuges are generally located within areas that receive today the highest amount of rainfall. Present climate should be viewed as a surrogate for the average climatic conditions over long time periods that could have affected fish diversity, rather than viewed as the actual causal factor.

Local-Regional Richness Relationships

Because the fish species present within a tributary or within a river reach are a subset of the river basin species pool, local and regional communities are unlikely to be completely independent. We also expect that dispersal along the river network will be an important component of local community structure and dynamics. In the following section, we consider dispersal at the regional scale. This scale cannot be larger than the one defined by the river basin (there is no possible dispersal outside the river basin). However, the scale can be lower for naturally and anthropogenetically disconnected (e.g., due to falls, dams) tributaries or those located within large basins (e.g., Mississippi basin) where dispersal between very distant tributaries is unlikely to take place within ecological time scales, particularly for species with low vagility.

Importance of Dispersal

The role of dispersal in explaining biodiversity patterns within river basins gains importance when species richness is compared between similarly sized tributaries and river basins. Theory predicts that without immigration, species richness within an insular habitat decreases as extinctions accumulate. As a result, species richness in a "disequilibrium" island is predicted to be lower than in a comparable island (or area) where extinction and colonization are balanced. Considering river basins as "disequilibrium" systems, losing species through time leads to the prediction that they should harbor less species of strictly freshwater fish species than similar systems in which extinctions are balanced by immigrations (Hugueny 1989). Tributaries within a larger river basin are systems likely to be near equilibrium, and thus, higher species richness is expected in a tributary than in a comparable isolated river. Sheldon (1988), Hugueny (1989) and Belkessam et al. (1997) revealed patterns supporting this hypothesis for northeastern American, West African, and northern European river fish assemblages, respectively.

Another pattern demonstrating the importance of dispersal is that sites located near the mainstream of the river sustain higher species richness than more remote but comparable sites (Osborne and Wiley 1992; Hitt and Angermeier 2008). The main course of the river likely acts as a source pool for many species that colonize tributaries. Species richness in the mainstream also may be enhanced by immigration of species from a tributary (Fernandes et al. 2004). Overall, these studies (see also Grenouillet et al. 2004; Matthews and Robison 1998) suggest that the river network topology is an important feature for understanding how fish biodiversity is regulated within a river basin (Fagan 2002; Muneepeerakul et al. 2008). Connectedness to the river network is also an important component of fish community structure in lakes and wetlands (e.g., Tonn and Magnuson 1982; Tonn et al. 1995; Olden et al. 2001, Barber et al. 2002; Hershey et al. 2006). At a smaller scale, within a river segment, connectivity and species richness may depend on dispersal barriers or filters (e.g., presence of riffles between pools, Taylor 1997) or on hydrological regime seasonally or episodically connecting and disconnecting habitats (e.g.,

the distance of floodplain lakes from the mainstream, Granado-Lorencio et al. 2005).

A Metacommunity Framework

This prominent role of dispersal at large (between tributaries) and small (within a tributary or a reach) spatial scales is a strong argument for using a metacommunity framework in riverine fish ecology (Muneepeerakul et al. 2008; and Fausch 2010, this volume; Falke and Fausch 2010, this volume; Peres-Neto 2010, this volume; Roberts and Hitt 2010, this volume). Metacommunity ecology (Leibold et al. 2004) emphasizes the importance of dispersal between local communities within a regional landscape and its consequences on multispecies local and regional dynamics. This subdiscipline could be considered an extension of the concept of metapopulation, despite the fact that some metacommunity approaches (e.g., Hubbell 2001) do not require fragmentation of the populations. Metacommunity theory provided new insights on community saturation, in which similar habitats have the same number of species irrespective of the diversity of regional species pools. According to the concept of limiting similarity, a given habitat could be inhabited by few species with large niche breath or a large number of species with narrow niche breath. Because, according to theory, the former community could be invaded by a more specialized species, the habitat should be filled by the largest number of species it can sustain (available resources),while taking into account the evolutionary potential of species to specialize. So given the same habitat characteristics and the same evolutionary potential, community saturation is expected (Figure 2).

In contrast, most metacommunity models 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 with (e.g., Case 1991) or without (e.g., Bell 2003) niche partitioning. Actually, a positive relationship between local and regional richness is the rule more than the exception (Cornell and Karlson 1997), in contrast with what could have been anticipated from a strict interpretation of niche theory.

A positive relationship between local species richness (LSR, site) and regional species richness (RSR, river basin) has been reported repeatedly for river fishes (Hugueny and Paugy 1995; Hugueny et al. 1997; Angermeier and Winston 1998; Matthews and Robison 1998; Oberdorff et al. 1998). The major remaining question is how local richness increases with the size of the regional pool. A simple formalism for the LSR–RSR relationship is LSR = pRSR, with p being the average probability of presence per site per species (Hugueny et al. 2007). If the presence of a species in a site is not affected by the number of coexisting species, then p is independent of RSR and the LSR–RSR relationship is described by a proportional, linear relationship (Figure 2). If the probability of a species presence decreases as the number of competitors increases, then p is an inverse function of RSR and the LSR–RSR relationship is described by a convex curve (Figure 2). Metacommunity models (Caswell and Cohen 1993; Bell 2003; Fukami 2004, Loreau et al. 2005; Hugueny et al. 2007) have shown that the LSR–RSR relationship depends on the relative rates of colonization and extinction and the sensitivity of these rates to competition. In particular, a strong curvilinear relationship implies some kind of species interaction, whereas linear or quasi linear relationships imply noninteractive species and/or interactive species with high colonization and/or extinction rates.
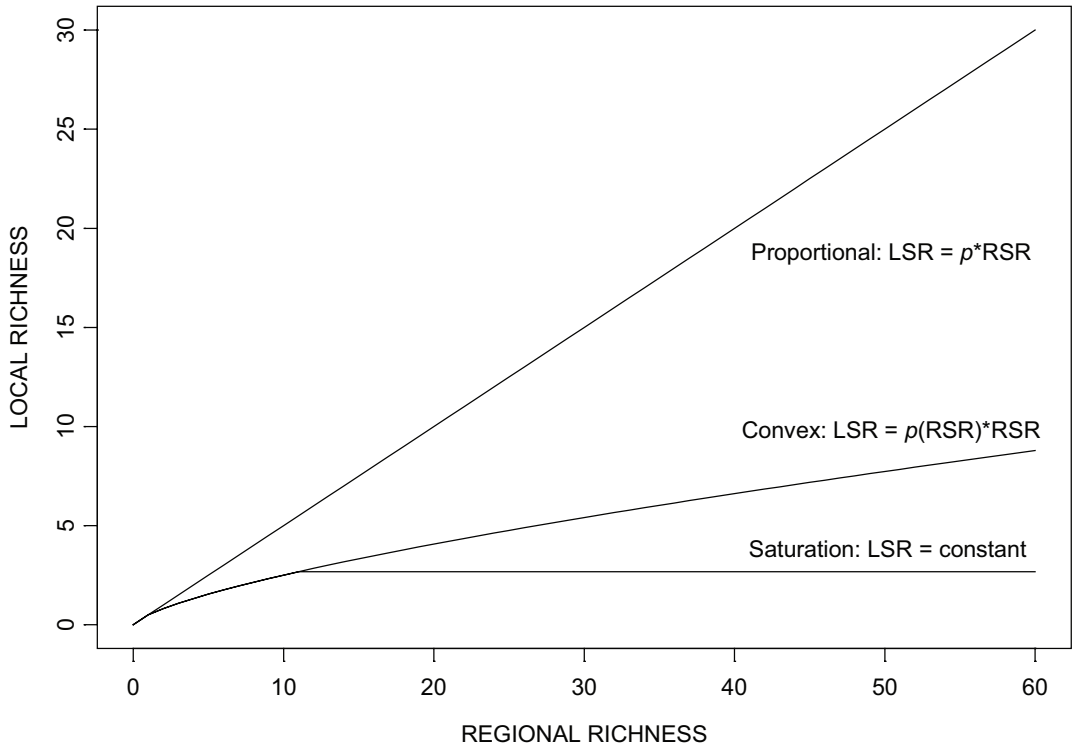
Figure 2. Theoretical relationships between local species richness (LSR) and regional species richness (RSR). The average proportion of sites occupied (or equivalently the probability of presence) per species is designed by p. p(RSR) means that p is a function of RSR, a negative one in the depicted curve.

Despite numerous studies of LSR–RSR relationships for freshwater fishes, no clear pattern emerges. Proportional relationships (Hugueny and Paugy 1995; Griffiths 1997, Hugueny et al. 1997; Oberdorff et al. 1997, Irz et al. 2004) as well as strong convex relationships (Angermeier and Winston 1998; Matthews and Robison 1998; Irz et al. 2004) have been observed for both lacustrine and riverine communities, suggesting that these habitats do not differ in this respect.

For LSR–RSR relationships being affected by species interactions, average colonization or extinction rates per species should be respectively negatively and positively linked to the number of species coexisting locally (Hugueny et al. 2007). Unfortunately, because of logistical constraints (multi-site, long-term surveys),

only a few studies have addressed the role of colonization or extinction rates within riverine fish communities (Gotelli and Taylor 1999; Taylor and Warren 2001; Fagan et al. 2002), and none considered the effect of species interaction on these rates.

Intercontinental Comparisons

Because LSR–RSR relationships are available for different biotas (e.g., European versus North American), it could be informative to assess how much they differ (Hugueny et al. 1997). In the case of two continental biotas, two patterns are expected. First, the same LSR–RSR relationship holds for both continents; thus LSR differs between regions (rivers) due to differences in RSR. Second, different LSR–RSR relationships apply for each continent. A

comparison performed between West Africa and French Guiana gives a possible example of the second pattern (Hugueny et al. 1997). In both continents, a proportional relationship between LSR and RSR is the most parsimonious model, but the slope is higher for West African communities. As a result, for the same RSR, LSR is higher in West African rivers than in Guiana. A possible but untested interpretation is that dispersal rates are lower in neotropical rivers because of a higher number of small species with low vagility. Conversely, when French (coastal rivers of the English Channel) and eastern North American (tributaries of the Mississippi basin, Arkansas) data are analyzed together (Figure 3), intercontinental differences in LSR mainly result from differences in regional richness, which supports the first pat-

tern. So it is tempting to conclude that regional richness of French rivers is too low to make curvature apparent. This suggests that interspecific competition should be absent or weak within French communities and more pronounced within eastern North American communities, which is supported by some data. Within French costal river communities, species mean density and population growth are independent of the number of coexisting species (Oberdorff et al. 1998). In contrast, some studies suggest that interspecific competition plays a significant role in shaping local community structure within tributaries of the Mississippi River. For fish communities in Oklahoma, Taylor (1996) reported a negative relationship between total density and number of species, suggesting the appropriation of resources by
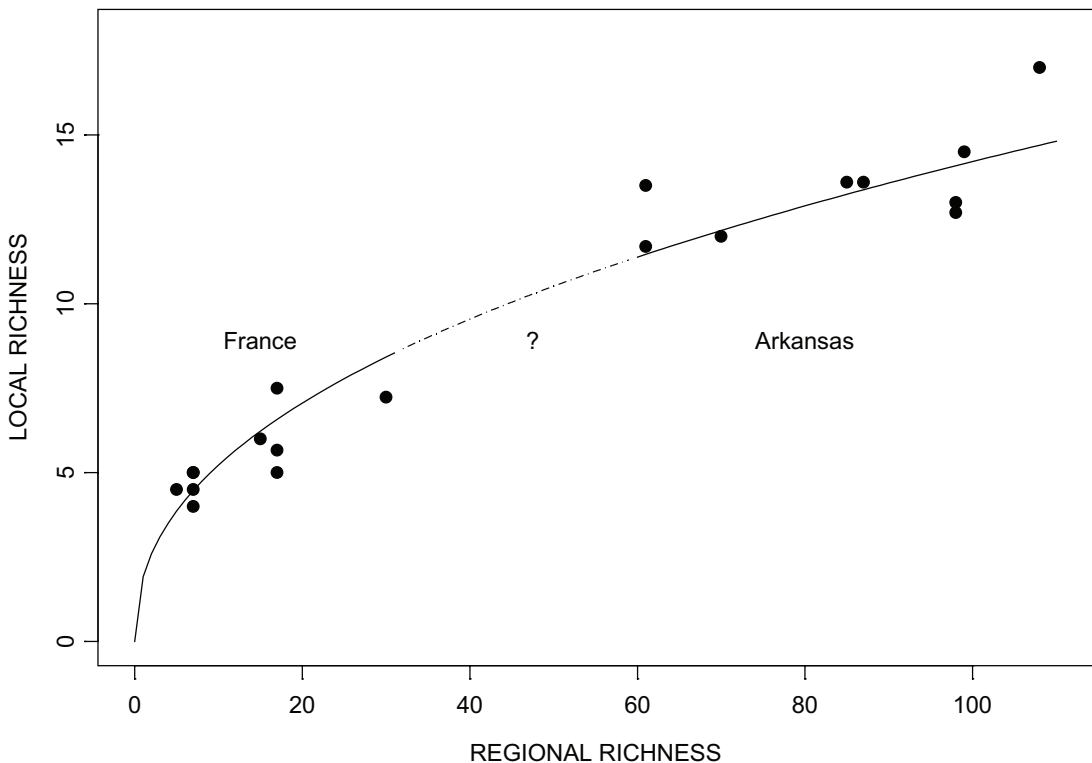

Figure 3. Figure depicting a possible common relationship between local and regional species richness for European (France) and North American (Arkansas) stream fish communities.

some dominant species, and Winston (1995) demonstrated that morphologically similar minnows species in Oklahoma tend to coexist less frequently than expected by chance, probably because they have the same niche and are more likely to exclude each other.

The few available intercontinental comparisons of the LSR–RSR relationship reveal that all the components of diversity could be affected by history. For instance, LSR (alpha diversity) is lower in French coastal rivers than in eastern North America, as is RSR (gamma diversity, see section above, Biodiversity Patterns at the River Basin Scale). The patterns of beta-diversity are also very different between these continents as exemplified by the RSR/LSR ratios (a measure of beta diversity), such that fish communities within eastern North America are more diverse (4.5–7.7), than their European equivalents (1.1–4.2).

Community Convergence

The hypothesis of community convergence predicts that under comparable environmental conditions, the structure of communities should be similar (MacArthur 1972; Schluter 1986). Hence, the hypothesis of convergence supports the deterministic view that community structure can be predicted (at least partly) from the environment. If this hypothesis is true, convergence testing could be a powerful method to assess the generality of community patterns observed and of the processes causing these patterns (Lawton 1999; Schluter and Ricklefs 1993a). Convergence is more convincing when the communities compared have diverged a long time ago such that they can be considered as independent replicates of the ecological and evolutionary processes shaping community structure. But obviously, if a community–habitat relationship is general, then it is expected to occur regardless of the phylogenetic relatedness of the compared communities.

Community convergence is generally tested by checking similar relationship between a descriptor of community structure and an environmental gradient in geographically distinct areas (Schluter 1986). Different ways of quantifying community convergence have been proposed (e.g., Schluter 1986), but for the sake of simplicity, we will consider only two extreme cases of convergence (see also Irz et al. 2007; Figure 4). The first one is quantitative, perfect convergence in which there are no regional differences in community–habitat relationship. The knowledge of the community–environment relationship in one region allows a perfect quantitative prediction of this relationship in a second region (e.g., for habitat diversity x, species richness is y). The second one, qualitative convergence, occurs when community–habitat relationships differ between regions but are described by a common trend. In this case, only qualitative prediction is transferable from region to region (e.g., the relationship between habitat diversity and species richness is positive). Because within the framework of niche theory species interactions have been formerly assumed to be strong drivers of community convergence, studies dealing with this topic generally used local grain (sampling unit) size. However, a test of community or assemblage convergence could be conducted using grains larger than localities or sites. For instance, there is qualitative convergence between Europe and North American fish assemblages with regard to species–energy relationships established among river basins (Oberdorff et al. 1997). As these comparisons between river basins have been discussed above (Biodiversity Patterns at the River Basin Scale), in the following we will focus exclusively on local community convergence. Another approach for assessing how communities are similarly
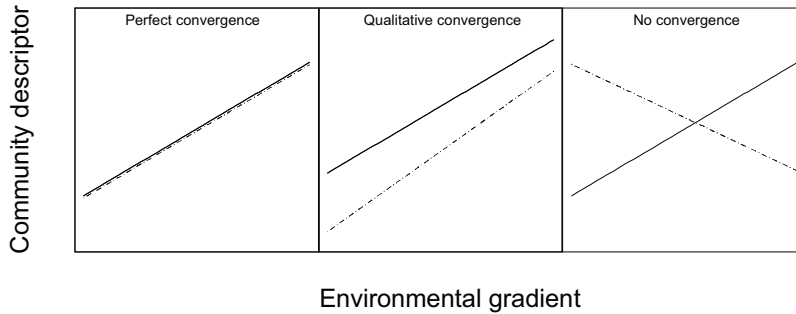
Figure 4. Different types of community convergence based on the relationships between a community descriptor (e.g., species richness) and the same habitat gradient in two different regions (plain and dotted lines).

structured in different parts of the world is to contrast environmental variables explaining biological gradients within regions. For instance Tonn et al. (1995) identified (using canonical correspondence analysis) variables explaining fish composition of lakes within four regions, two in Europe (Finland and Sweden) and two in North America (Wisconsin and Alberta). They considered two groups of variables, those linked to extinction processes (e.g., lake area) and those linked to immigration processes (e.g., distance to nearest lake). They found that extinction-related variables accounted for a very similar percentage of the explained variation within each region (between 60% and 78%), suggesting a prominent role of extinction in the four studied regions. We are not aware of similar approaches applied to river fish communities. Other studies (e.g., Winemiller and Adite 1997) used river fish assemblages from different continents for testing the hypothesis that phylogenetically unrelated species occupying the same ecological niche (e.g., benthic invertivore) should display morphological similarity in some key features (e.g., mouth structure). Because these studies did not deal with emergent assemblage descriptors (e.g., species richness) but with species properties, they are not considered in detail in this section.

Convergence in Species Richness

Because of the positive relationship observed between LSR and RSR, quantitative convergence in local species richness is unlikely to be found as long as regions (rivers) that differ greatly in their species richness are compared. It is expected that for the same position along a habitat gradient, local species richness should be higher in the region having the highest number of species. Studies that compared river fish species richness along environmental gradients provided mixed results with respect to this prediction.

Angermeier and Schlosser (1989) compared species–area relationships for two habitats (riffles and pools) among three different geographic areas (Minnesota, Illinois, and Panama). Water volume was found to be a better predictor of species richness than surface area sampled, and species–volume relationships were very similar among regions and between habitats. Once the volume was accounted for, pools and riffles from Panama contained more species than their temperate counterparts. This result was not expected because more species are encountered regionally in Illinois. One explanation suggested by Angermeier and Schlosser (1989) was that fish communities in Panama were less variable from year to

year than in temperate communities. Studies reporting a negative link between community variability through time and species richness provide support for this hypothesis (Horwitz 1978; Oberdorff et al. 2001).

Changes in physical conditions of streams and rivers from upstream to downstream reaches are generally assumed to favor an increase in species richness (Grossman et al. 2010, this volume; Roberts and Hitt 2010) because of increasing habitat heterogeneity and habitat volume (Schlosser 1987; McGarvey and Hughes 2008) or decreasing hydrological variability (Horwitz 1978). Ibañez et al. (in press) compared local species richness between four zoogeographic regions (South America, Europe, North America, and Africa) with the general objective of testing whether the relationship between species richness and position along the longitudinal gradient was convergent among regions. Increasing richness along the upstream–downstream gradient was observed alongside with strong regional effects, in which tropical regions with richer regional pools have systematically higher local species richness than temperate streams along the gradient. These two studies have thus demonstrated qualitative convergence between species richness and habitat size and between species richness and longitudinal gradient, but an inconsistent effect of regional richness on local richness.

Convergence in Community Structure

Hydrological constraints in rivers may be strong and probably shape fish community structure and dynamics. Lamouroux et al. (2002) tested the convergence of stream fish communities between Europe (France) and North America (Virginia) in stream habitats positioned along the same hydraulic (Froude number) or geomorphic (percentage of pools) gradient. The Froude number integrates water velocity and water depth, is a good predictor of fish community patterns (Lamouroux et al. 1999), and is inversely linked to the percentage of pools in a stream reach. In both continents, habitats with low Froude number tended to contain proportionally fewer benthic, large, fecund, long-lived, nonstreamlined, and weak swimmers (inefficient at swimming in strong currents). Interestingly, continental effects were largely explained by differences in trait distribution between the two regional pools. For instance, the percentage of individuals belonging to large species decreased with the Froude number in both regions but was systematically higher in France than in Virginia. This was probably due to the higher proportion of large species in France (48%) than in Virginia (18%).

In another intercontinental study, Ibañez et al. (in press) tested for convergence in trophic structure along a stream-size gradient between fish communities from Europe (France), North America (Appalachia), Africa (Gabon), and South America (Bolivia). They found evidence of qualitative convergence in trophic structure mainly described by 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. There was no clear relationship between a continental effect and trophic structure of the regional pools (defined as the species encountered at least in one site per region). For instance, a higher proportion of omnivores was observed in the European regional pool, but within localities a higher proportion of omnivores occurred in Bolivia. The strength of convergence was higher within than among climatic zones. Temperate communities had a higher percentage of invertivores (both individuals and species) than tropical ones, and the converse was true for omnivores. Moreover trophic diver-

sity was higher in tropical communities where more detritivore/herbivore and piscivore species occur. With temperature and solar energy being higher in the tropics than in temperate areas, energy input should be greater for tropical than temperate streams. In particular, there is some evidence that endogenous primary productivity is higher in tropical than in temperate streams, where food webs are mainly initiated by allochtonous production (Davies et al. 2008). The greater availability and diversity of plant material (particulate organic matter, aquatic macrophytes, and periphyton) in the tropics (Winemiller and Jepsen 1998) may explain the greater proportion of fishes consuming this resource, as observed in Gabon and Bolivia compared to Europe and North America. A similar trend has been found by Wootton and Oemke (1992), comparing tropical (mainly neotropics) and temperate (North America) fish communities. This higher proportion of herbivory/detritivory within tropical fish assemblages shortens the length of food chains (Layman et al. 2005; Winemiller et al. 2008) and may explain the higher proportion of piscivores observed in Gabon and Bolivia. In European and North American streams and rivers, detritivores/herbivores and piscivores appear farther downstream where the amount of available energy is sufficient to maintain viable populations (Matthews 1998; Oberdorff et al. 1993). It should be noted however, that the high degree of convergence observed between temperate fish assemblages could be due to phylogenetic relatedness between North America and Europe (29% of families in common).

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 and Karr 1983; Schlosser 1987; Oberdorff et al. 1993, 2001; McGarvey and 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.

Related Studies

Although not explicitly testing the existence of community convergence, other studies suggest that some community structure–environment associations are repeatable irrespective of community composition. Poff and Allan (1995) found that hydrologically variable streams contained more trophic and habitat generalists and more tolerant species than did stable ones, a finding consistent with the habitat template concept (Townsend and Hildrew 1994). The relationships observed were independent from the strong zoogeographic pattern observed in fish community composition over the spatial scale of the study (Wisconsin and Minnesota). Hoeinghaus et al. (2007) also reported an association between functional community structure and environmental descriptors largely decoupled from the zoogeographical pattern observed for streams in Texas. Rodriguez and Lewis (1997) suggested that fish community structure in Orinoco River floodplain lakes is tightly linked to lake water transparency, which is controlled by lake morphometry. They predicted that along a gradient of increasing water transparency, the abundance of species with sensory adaptations for low visibility will decline and species that are visually oriented will increase. This pattern has been observed in three Neotropical river systems (Rodriguez and Lewis 1997; Tejerina-Garro et al. 1998; Pouilly and Rodriguez 2004).

Environmental and Biotic Filters

All the studies discussed above, testing community convergence with riverine fish, reported occurrence of qualitative convergence and confirmed the conclusions reached by Schluter and Ricklefs (1993a) that "at least some convergence is the rule rather than the exception" and that "habitats exert repeatable effects" on community structure. The degree of community convergence obviously depends on historical contingencies (Schluter and Ricklefs 1993a) underlying regional species pool composition, but is also strongly influenced by constraints imposed by the environmental filters. For example, the physical environment of lotic ecosystems exert strong selection on body forms, locomotion, and habitat use (Vannote et al. 1980; Statzner et al. 1988, Junk et al. 1989; Townsend and Hildrew 1994). Thus, some degree of community convergence in lotic fish community structure would be expected.

A primary challenge raised by the study of community convergence is to identify unique regional and historical influences. Species with certain traits are more likely to be present in specific habitats (environmental filters sensu Poff 1997), but the matching degree of these patterns between regions depends on the history of adaptive evolution, colonization, and extinction of regional species pools (Lamouroux et al. 2002).

Weiher and Keddy (1995) proposed a conceptual framework in which two opposing forces regulate interfaunal phenotypic similarity. Environmental filters cause species with similar traits to occur in similar habitats. Alternatively, species exclusion may occur when species sharing the same trait have the same ecological niche. In the latter case, fewer species having similar traits coexist in a given habitat than expected from environmental filter alone. The relative importance of biological filters in the convergence studies discussed above is dif-

ficult to assess. Moreover, testing the relative role of environment and species interactions in the co-occurrence of species with regard to their similarity in some biological traits is problematic and needs carefully designed null models. For example, Peres-Neto (2004) ruled out competitive exclusion as a structuring mechanism and concluded that morphologically similar fish species in neotropical streams tend to co-occur because of similar habitat use (but see Winston 1995 for an opposite conclusion for stream fishes).

Density Compensation and Ecological Release

Because of historical reasons (e.g., extinction or speciation events linked to river basin size or time since isolation), adjacent rivers with different species richness offer the opportunity to test how properties of communities are affected by species interactions while keeping constant key environmental factors (natural experiment protocol). Species in low diversity communities potentially experience reduced competition and/or predation, a process known as ecological release (e.g., Terborgh and Faaborg 1973). For species having similar resource uses, one consequence of ecological release is density compensation (MacArthur et al. 1972; i.e., species "compensate" for the absence of competitors by increasing their density). Within a guild of competitive species, total density of individuals in the community (or total biomass if species differ much in body size) is determined by resource productivity. Then, similar habitats colonized by a different number of competing species should have more or less the same total density (or biomass). More generally, if ecological release exists, an inverse relationship between average density (or biomass) of species in a community and species richness is expected.

Density Compensation

The influence of density compensation on the structure of freshwater fish communities has been addressed specifically in French coastal rivers (Oberdorff et al. 1998) and in Oklahoma streams (Taylor 1996). Oberdorff et al. (1998) compared sites among rivers with similar habitat and a gradient of local species richness ranging from three to seven species and found a positive relationship between total density and local richness, a result not compatible with the occurrence of strict density compensation. Moreover, species densities were not inversely related to the number of coexisting species. Local species richness varied among sites because of differences in regional richness, and not a priori because of differences in habitat features. A limitation of this study was that the species studied cannot be considered as representative of the same guild, even if they all depend on benthic invertebrates as a major trophic resource and strong competitive interactions may be limited to a few pairs of species highly similar in their resource use. However, even considering species by pairs did not reveal significant negative covariation in their population dynamics. Another potential limitation of this study is that the range of species richness may not be sufficient for cumulative detrimental effects of competitors to be perceptible. The study by Taylor (1996) reached the opposite conclusion for riffle fish communities in streams across northeastern Oklahoma. Once habitat features were accounted for, a negative relationship between local species richness and total density was observed, suggesting density compensation and even overcompensation. An explanation for these contrasting results may be due to average ecological similarity among species. If it is assumed that congeneric species have similar ecological niches, then they should be strong competitors and density adjustments should

occur more often among congeneric species than in more distantly related ones. Probably as a consequence of its low diversity, the ichthyofauna from western Europe is constituted by genera having generally one or few species, in contrast with the occurrence of species-rich genera in eastern North America. Everything else being equal, stronger species interactions is then expected within North American communities.

Related Patterns

Compensatory dynamics can stabilize total density of competing species through time as low abundances of some species are compensated by high abundances of the others (Houlahan et al. 2007). However, tests of compensatory dynamics are based on the unlikely assumption that total density is constant irrespective of temporal fluctuation of the environment (e.g., climatic variation, see Spatial Synchrony in Community Dynamics below).

Species richness could be a poor indicator of the intensity of interspecific interactions if community dynamics are mainly affected by some key predator fishes. There is some evidence that a handful of fish predator species may affect local fish community structure and dynamics. Examples of such key predators are *Hydrocynus* spp. and piranha for African and Neotropical rivers, respectively (Winemiller et al. 2008). While many rivers harbor no or few piscivores, community change due to natural predation release is largely unexplored in contrast with studies devoted to the evolutionary changes (morphological, coloration, life histories strategies) induced by the presence or absence of predation (e.g., Reznick et al. 2001; Langerhans and DeWitt 2004).

Ecological release could also lead to niche broadening, and, to our knowledge, one study (Changeux 1998) confirmed this hypothesis by reporting that niche breath of brown trout

Salmo trutta was wider in streams from Corsica Island than in similar continental streams, the latter being about twice as rich than the former.

Extrinsic and Intrinsic Factors in Community Dynamics

The existence of community regulation resulting from dynamical feedbacks that maintain an equilibrium state is a key question in ecology. Within this framework, some empirical studies have attempted to classify stream communities on the basis of their temporal dynamics to identify the underlying processes. For instance, Grossman et al. (1982) described two types of communities: stochastic communities, in which species rank abundances change through time, and deterministic communities in which rank abundances are stable. According to these authors, the latter are assumed to be controlled by strong species interactions leading to equilibrium of species abundances, while the former are mainly controlled by environmental, extrinsic variation (Grossman and Sabo 2010, this volume). Grossman et al. (1982) suggested that temperate stream fish assemblages were generally near the stochastic end of the continuum and hence are not strongly regulated by interspecific competition, a proposal that was challenged by other fish ecologists (Herbold 1984; Rahel et al. 1984; Yant et al. 1984). DeAngelis and Waterhouse (1987) warned against the interpretation that biotic interactions always lead to equilibrium and low variability in ecological systems. It is thus likely that little can be inferred about the processes underlying the structure of a community from its temporal variability. However, comparative studies of temporal community dynamics over a regional scale can be used to assess how much community variability is affected by intrinsic and extrinsic processes

(Stenseth et al. 2002). Community-intrinsic processes are defined as those introducing temporal autocorrelation in some community descriptors (e.g., species richness). Community-extrinsic processes may affect community properties but are not affected in turn by community state. Intrinsic and extrinsic processes overlap greatly with biotic and abiotic processes respectively. The existence of intrinsic processes may lead to community regulation, but not necessarily.

Spatial Synchrony in Community Dynamics

Moran (1953) has suggested synchronous environmental fluctuations as an explanation to population synchrony over large geographic regions. The role of dispersal has also been emphasized in recent models as an explanation for regional population synchrony (Ranta et al. 1995). The conceptual framework of the "Moran effect," mainly restricted to the study of spatiotemporal dynamics of populations, can now be applied to multispecies dynamics. Within this framework, a community-wide Moran effect could be defined as spatial synchrony in community parameters (e.g., species richness) not driven by dispersal, but by extrinsic factors (e.g., climate).

Strictly freshwater fish in the same geographic area are good candidates for such studies because of restricted dispersal among river basins. Many studies demonstrated spatial synchrony in freshwater fish population dynamics at different scales. Myers et al. (1997) proposed that the typical spatial scale of synchrony for freshwater fishes was about 50 km, but subsequent studies reported synchrony among river fish populations separated by more than 100 km (Grenouillet et al. 2001; Cattanéo et al. 2003, Tedesco et al. 2004). For most of these studies, regional climatic variability played a significant role (e.g., temperature [Grenouillet

et al. 2001] or hydrology [Cattanéo et al. 2003; Lobón-Cerviá 2004; Tedesco et al. 2004; Ruetz et al. 2005]).

As exemplified by these studies, climate variability can influence regional fish population dynamics, but the evidence for a similar effect on fish community dynamics has not been adequately studied. In Ivory Coast streams, Tedesco et al. (2004) reported interspecific spatial synchronies (correlated population trajectories of two different species in two different rivers). This suggests that aggregate properties of communities, such as total abundance, could also be synchronous because most species will tend to be abundant at the same time in different rivers. Both immigration and extinction

rates were strongly associated with mean abundance in a temperate North American stream fish community: species with high local abundances had higher immigration rates and lower extinction rates than species with low local abundances (Taylor and Warren 2001). Thus, a climatic factor that synchronizes species abundances should also synchronize species richness through extinction and colonization rates. Spatial synchrony in both abundance and species richness was observed in Ivory Coast in two sites separated by about 200 km having similar habitats (large pools) and located in two different river basins of similar species richness (95 and 91, see Hugueny and Paugy 1995; Figure 5). Because freshwater fishes were incapable of
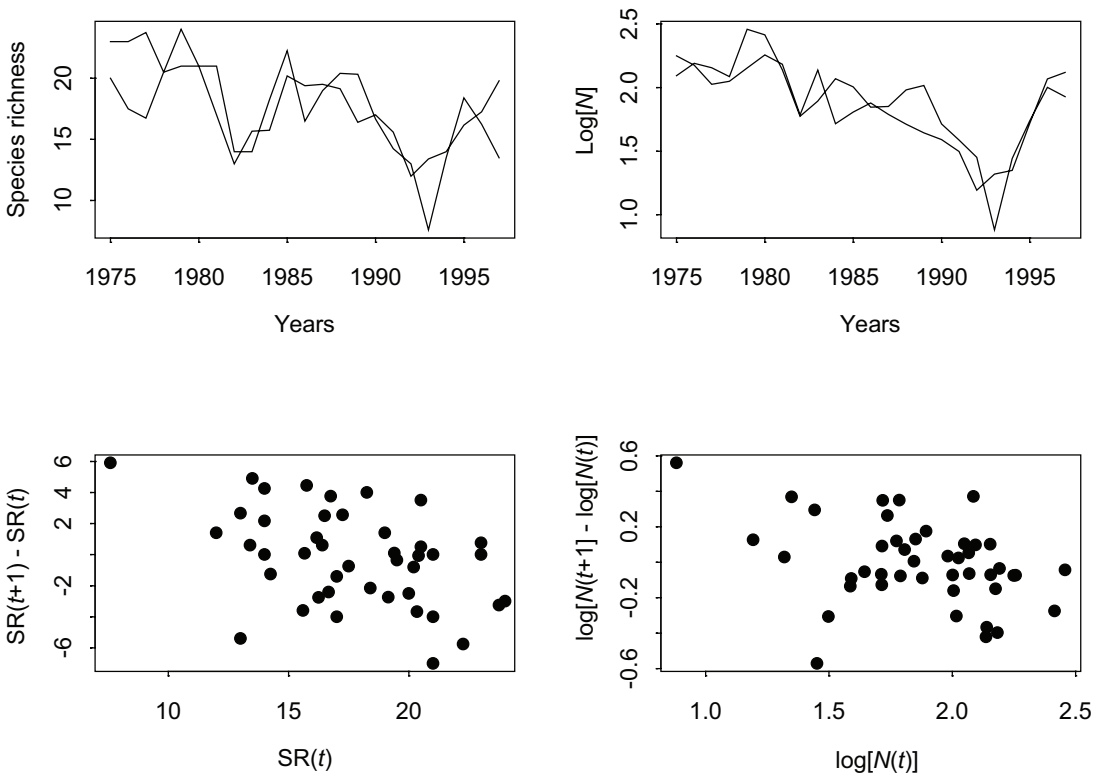

Figure 5.   Top: Spatial synchrony in species richness and total abundance (log[N]) for two fish communities in two different river basins (Comoe and Bandama, Ivory Coast, Africa; Hugueny et al., unpublished data). Bottom: interannual rate of increase in species richness (SR) and total abundance as a function of the value 1 year before. The two sites are considered together.

dispersing between river basins, the observed spatial synchrony in community dynamics is a clear demonstration of a community-wide Moran effect.

Interannual variation in discharge can result in a synchronous lag response in stream fish populations, as shown in Ivoirian rivers (B. Hugueny, T. Oberdorff, and P. A. Tedescco, unpublished data; see also Tedesco et al. 2004). Strong correlations among some measures of flood intensity and abundance in subsequent years are frequently observed in fisheries (Welcomme and Halls 2004) because an increase in flood level and duration improves spawning success, growth, and survival of fishes. Further argument in support of the synchronizing role of hydrology is provided by Tedesco and Hugueny (2006), who demonstrated for Ivorian fishes higher synchrony for species adapted to reproduce during floods (periodic species, sensu Winemiller 1989) than for species more likely to reproduce throughout the year (equilibrium species).In contrast, hydrology is weakly related to temporal changes in species richness within the communities studied in Ivory Coast (Hugueny and coauthors, unpublished). The reason is probably that hydrology indirectly affects species richness through species abundances, which in turn affects extinction and colonization rates.

It is worth noting that a strong effect of regional climate on community dynamics does not preclude the action of biotic, regulatory processes. Because many species produce young stages that feed mainly on zooplankton (Høberg et al. 2002) at the same place (floodplain) and at the same time (during flooding), it can be assumed that interspecific and intraspecific competition will take place and community-wide regulatory processes could occur (juvenile bottleneck, Werner 1986). In favor to this hypothesis, negative density dependence has been observed at the com-

munity level for fishes of the Ivory Coast. As shown in Figure 5, log total abundance change from year t to year $t + 1$ is negatively linked to total abundance at year t, as expected for a regulated dynamic. The same relationship is observed for species richness (untransformed). Although regulatory processes are present, they are weak, suggesting a rather low contribution of intrinsic factors to the overall community variability. Intrinsic factors (log total abundance at year $t - 1$) contribute to 50% of the variance in log total abundance at year t, and this value reaches 88% when regional extrinsic factors are added (as a categorical year effect). For species richness, the percent of variation explained was 40% and 83%, respectively. In both cases, a strong contribution of regional extrinsic factors was identified. With this preliminary analysis, it cannot be assessed if regulatory processes result from intraspecific regulation alone (demonstrated for some species of the community, Tedesco et al. 2004) or if interspecific processes are also implied. Stenseth et al. (2002) also reported fish community dynamics resulting from both intrinsic and extrinsic factors for the coasts of Norway, but with the exception of Grossman and Sabo (2010), we are unaware of similar studies for freshwater fish communities.

Importance of Climate

Daufresne and Boët (2007) synthesized long-term surveys from three river basins in France to assess climate change impacts on structure and diversity of fish communities. During the past 15–25 years, they found consistent increasing trends of species richness, total abundance, and proportion of warmwater species across sites. During the same period, as a result of global warming, temperature regularly increased and resulted in positive correlations between annual average temperature during reproduction (April–June) and the three com-

munity metrics. It is also possible that higher temperature led to higher recruitment success through improved growth of most cyprinid species, particularly for the more tolerant species to high temperature.

According to the above-cited studies from the Ivory Coast and Europe, regional climate is likely to have induced spatial synchrony or common long-term trends in community attributes. However, the major underlying climatic factor differed between the two studies: hydrology for West Africa and temperature for Europe. It seems that the increase in temperature that could be attributed to global warming differentially affects the dynamics of temperate and tropical fish communities. Despite a clear increase in temperature (about +1°) over the study period (1976–1997) in Ivory Coast rivers, the observed community changes could hardly be linked to climatic warming (Hugueny and coauthors, unpublished). If these results

have some generality, it could be anticipated that predicting the effect of global climatic changes will be more difficult for tropical river fishes than for temperate ones because of their dependence on factors, such as hydrology, that are less well forecasted and because of a weaker and perhaps more complex relationship with temperature.

A Synthetic Framework

Here, we propose a conceptual framework that links local and regional richness and summarizes many of the studies discussed in this chapter (Figure 6). According to this framework, local processes are nested within processes that occur at larger spatial and temporal scales. This scheme relates to metacommunity dynamics, as it assumes that local species richness is a balance between extinction and colonization (see also Roberts and Hitt 2010). Local pro-

Average
Local richness   =   fraction of sites occupied   x   Regional richness
per species

Dispersal

River network topology

Number of competitors/predators

Extinction

Local habitat features (e.g., structural complexity)

Strength of pairwise interactions
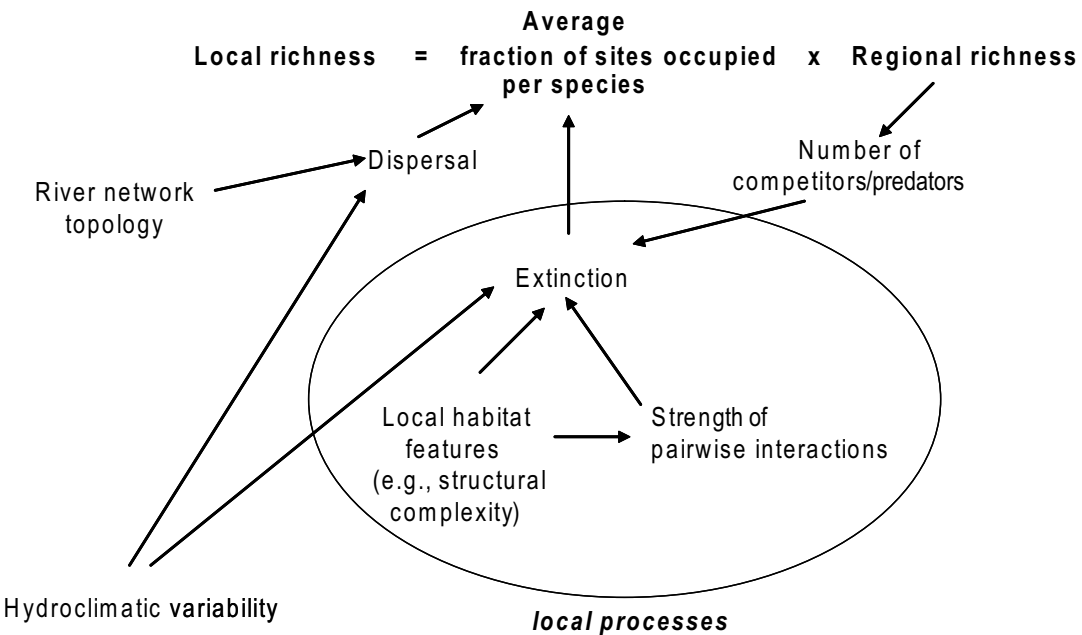
Hydroclimatic variability

local processes

Figure 6. Local and regional factors and processes that contribute to determine the number of fish species observed within a locality. Regional species richness is the total number of species that could colonize the target locality.

cesses act through local population extinctions, which depend on local habitat factors and interspecific interactions (competition, predation). We assume that extinction rate of focal species depends on two components: the effect (strength of competition/predation) and number of each interacting species. It is important to consider the strength of interactions independently from the number of coexisting species because the former could be influenced by local habitat features. For example, a complex habitat offering many refuges can lower competition and predation intensity.

Three types of regional effects have been integrated in this chapter: (1) the regional surrounding that determines dispersal processes (e.g., number of colonization sources, topology of the river network), (2) factors that affect extinction or colonization rates in synchrony over all sites (e.g., climate, hydrology), and (3) richness and composition of the regional species pool that constrains local diversity. These regional effects are briefly discussed below.

Stream fish ecologists are increasingly aware that dispersal (and its associated factors) is a key process for fish population and community dynamics, and particularly within the context of conservation biology (Fausch et al. 2002; Lowe et al. 2006). Studies dealing with this topic accumulate quickly and are discussed in other chapters of this book (Fausch 2010; Rodriguez 2010, this volume; Falke and Fausch 2010; Peres-Neto 2010), so we will not discuss this point further.

Effects of climate and/or hydrology on local species richness is well established (e.g., Horwitz 1978; Angermeier and Schlosser 1989; Oberdorff et al. 2001; Taylor and Warren 2001). These studies have generally reported that increasing environmental variability increase community turnover. Some questions are still largely unanswered, such as (1) what is the contribution of regional variability and

in particular climate to local community variability?, and (2) at which spatial scale are community dynamics synchronized by climate? Looking for spatial synchrony in community dynamic may help in answering these questions which are essential for understanding global warming potential impacts.

A third regional effect results from the fact that local communities are constrained to be a subset of the regional pool. For noninteractive communities put into similar environments (i.e., similar average "connectedness" among sites, hydroclimatic conditions, and local habitat features), the relationship between local and regional richness is simply proportional. If the extinction rate of a population (through competition or predation) increases as the number of interacting species increases, then a convex relationship is expected. Because of the positive relationship between regional and local species richness (either linear of convex), strict community convergence is not expected between regions that differ in the size of the regional pool. Empirical evidence suggests that strict community convergence in species richness rarely occurs for lotic fish communities.

The proposed scheme does not depart much from other conceptual frameworks based on the action of environmental and biotic "filters" (Poff 1997; Weiher and Keddy 1995) because all the species in the regional pool are not expected to be present at the same time in a given locality. In other words, a filter operates between the region and the locality. A step toward a less simplified scheme is to deal with species traits (e.g., Infante and Allan 2010; Frimpong and Angermeier 2010; Jones et al. 2010; all this volume) by considering how some traits increase (environmental filters) or decrease (biotic filters), the co-occurrence of species in a given habitat respectively by shared adaptive features and by higher niche overlap. Studies of lotic fish community convergence

revealed that some environmental filters acted similarly (same traits favored in similar habitat among regions) within different fish biotas. However, the relative contribution of environmental and biotic filters to lotic fish community convergence is still unclear due to the few available studies.

The proposed conceptual framework obviously oversimplifies many processes and neglects others. For instance, it assumes that no species have a disproportionate effect on population extinction rates, such as a very efficient predator. In this case, population extinction rates could be unrelated to the number of coexisting species, but could rather depend on the presence or absence of one particular species. Furthermore, ontogenetic or temporal habitat and diet changes, frequently observed for freshwater fishes, were not explicitly considered (see Schlosser 1995). We hope, however, that the simplicity of our scheme will help in interpreting regional effects on fish communities. While we do not expect this framework to be easily tested (estimating colonization and local extinction rates as a function of both habitat and species richness requires a multi-site and multi-year survey), it could be useful in devising empirical models of fish community diversity over a large spatial scale. There is an increasing need of such models for assessing human impact on river fish communities.

Conclusion

Comparative studies discussed in this chapter revealed that riverine fish community structure and dynamics cannot be predicted or understood entirely on the basis of local biotic interactions and habitat features. These studies provide strong support for a broader perspective on community ecology integrating multiple spatial scales and historical processes. It is frequently assumed that as spatial scale increases, the imprint of history becomes more apparent (Ricklefs and Schluter 1993). This does not seem to apply to river fish communities. Continental effects on biodiversity are as obvious at the level of local communities (e.g., Lamouroux et al. 2002) as when entire river assemblages are compared (e.g., Mahon 1984). One important conclusion that can be drawn from the studies reviewed here is that history cannot be neglected whatever the scale of investigation. A second conclusion is that historical effects are not strong enough to blur the occurrence of qualitatively repeatable patterns of community structure over large spatial scales. These points are illustrated in Table 1, synthesizing Europe–North America comparisons.

The role of history in shaping fish communities is revealed by approaches other than intercontinental comparisons. Mayden (1987) illustrated how the use of phylogenies within a community ecology context could help in estimating the contribution of common ancestry, on one hand, and compositional (e.g., species exclusion) or evolutionary (e.g., character displacement) ecological processes, on the other. A study of niche partitioning within minnow assemblages integrating phylogenetic information has provided evidences for both historical and ecological processes (Gorman 1992).

The regular occurrence of both local and regional or historical effects on river fish communities gives credit to those advocating a hierarchical approach in freshwater ecology (Smith and Powell 1971; Tonn 1990; Poff 1997; Matthews 1998; Jackson et al. 2001). Because of top–down processes, a requisite for explaining local community structure is to understand how communities are organized at higher spatial scales, and particularly at the river basin scale. Thanks to comparative studies conducted at the global scale, the main factors empirically related to species richness of

Table 1. Comparison of fish community patterns observed in Europe and Eastern North America at two spatial scales.

	Convergence	Continental effect
		In comparison with Europe, eastern North America has the following:

Regional	Species–area relationship
	Species–energy relationship
	Species richness decreases from major Pleistocene refuge
	Rapid recolonization of glaciated area
	More large species at higher latitudes
		More species in similarly sized rivers
		Proportionally more
		  small species,
		  stream specialist species, and
		  equilibrium species (parental care, large eggs).

Local	Morphology and life-history versus hydraulic gradient
	Species richness, trophic structure vs. river size gradient
	Local–regional richness relationship?
		Higher alpha and beta diversity
		More competitive species exclusions?
		Proportionally more
		  small species and
		  benthic species.

a river basin are well identified (Figure 1) and metacommunity ecology provides a fruitful conceptual framework for understanding how regional (river) species richness translates into local species richness (Figure 6).

Unfortunately, the processes underlying most of the patterns observed at the river-basin scale (e.g., species–energy relationship) are poorly known and presence–absence data per basin are generally not sufficient to discriminate among concurrent hypotheses. Progress will come from phylogenetic studies that should help identifying the factors that, within a basin, and within a lineage, favor species diversification (see also Douglas and Douglas 2010, this volume). Considering the poor knowledge available on the biology of many fish species, there are still too few empirical studies to propose a general scheme explaining why species having particular traits are more abundant in river basins with particular features. The absence of such knowledge prevents a full understanding of regional effects in studies seeking for convergence between local communities. According to some studies, environmental filters act similarly in different regions, which is encouraging because it suggests development

of general predictive models of community structure is an attainable goal. However, the hypothesis that environmental filters act similarly within different regional contexts remains to be tested explicitly in a greater number of cases.

Rivers belong to the most intensively human influenced ecosystems on Earth partly due to their position in the landscape and the fact that human population densities and associated activities are highest along river courses (Poff et al. 1997; Dudgeon et al. 2005). As a result, the projected mean future decline in freshwater biodiversity, for example, is about five times greater than the average species extinction rate for terrestrial fauna, rivaling projected rates of decline for tropical forest communities (Safina 2001). Under these circumstances, our understanding of the factors and processes that determine species richness at different spatial scales is of extreme importance if we want to answer the questions that are currently being asked by society, including the present and future effects of spread of alien invasive species (Rahel 2010; Copp et al. 2010; both this volume), the effects of global climate changes (Buisson et al. 2010, this vol-

ume), natural habitats fragmentation (Rodriguez 2010), and hydrological alteration (Taylor 2010, this volume; Infante and Allan 2010) on the maintenance of aquatic biodiversity.

Acknowledgments

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