Alterations of the global water cycle and their effects on river structure, function and services

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Abstract

River structure and functioning are governed naturally by geography and climate but are vulnerable to natural and human-related disturbances, ranging from channel engineering to pollution and biological invasions. Biological communities in river ecosystems are able to respond to disturbances faster than those in most other aquatic systems. However, some extremely strong or lasting disturbances constrain the responses of river organisms and jeopardise their extraordinary resilience. Among these, the artificial alteration of river drainage structure and the intense use of water resources by humans may irreversibly influence these systems. The increased canalisation and damming of river courses interferes with sediment transport, alters biogeochemical cycles and leads to a decrease in biodiversity, both at local and global scales. Furthermore, water abstraction can especially affect the functioning of arid and semi-arid rivers. In particular, interception and assimilation of inorganic nutrients can be detrimental under hydrologically abnormal conditions. Among other effects, abstraction and increased nutrient loading might cause a shift from heterotrophy to autotrophy, through direct effects on primary producers and indirect effects through food webs, even in low-light river systems. The simultaneous desires to conserve and to provide ecosystem services present several challenges, both in research and management.

Keywords: Disturbance; river; nutrient; reservoir; diversity.

Introduction

Due to their complexity, river systems may moderate disturbances much more easily than a simpler, linear system. Human disturbances include a range of possible alterations in river systems. Pollution, waste disposal, riparian simplification, bank alteration, straightening and dam construction – human actions increasingly driven by our demands for energy – all affect river ecosystems. Hydrological connectivity is at the base of the organism's

capacity to survive disturbances. In most parts of the world's watercourses, particularly dramatic modifications have occurred as a consequence of their intensive use by human societies (Sala et al., 2000). Typical examples of these changes include the elimination of meanders, lagoons and oxbows, while water is increasingly transferred between catchments. The simplification of the channel network and the alteration of water fluxes have an impact upon the capacity of fluvial systems to recover from disturbances, because of their irreversible character.

Of particular interest are the small-order streams (orders 1 to 3), as they account for 90 % of the drainage length and for up to one third of the surface area of networks (Tockner & Stanford, 2002). Their influence on global biogeochemistry and in the preservation of biodiversity is therefore remarkable. However, human impacts on stream hydrology, such as those that derive from regulating their flow or by affecting their channel geomorphology, affect the functional organisation of streams and lead to the simplification and impoverishment of these ecosystems.

This review explores two main aspects. In the first, I focus on global water fluxes and how interfering with them at local and global scales could affect river ecosystem structure and functioning. In the second, I reflect on the challenges we face as ecologists to provide society with concepts that merge (and make compatible) the uses and services that aquatic systems offer, with the measures needed for their conservation and improvement.

The ecological state of river systems in the context of global water fluxes

Today, about 15 % of the world's total runoff ($40\,000\text{ km}^3\text{ y}^{-1}$) is retained in 45 000 large dams, greater than 15 m in height (Nilsson et al., 2005), and a further 10 % is abstracted (Vörösmarty & Sahagian, 2000). As a result of these manipulations and subsequent irrigation, up to 6 % is evaporated (Dynesius & Nilsson, 1994). A total of 52 % of the surface area connected by large river systems (discharge over $350\text{ m}^3\text{ s}^{-1}$) is heavily modified, Europe containing the highest fraction of altered river segments.

Engineering and managing river flow through the construction of dams, aqueducts and pipelines has been termed the *hard-path* approach (Gleick, 2003), as opposed to the *soft-path* approach of strategies aimed at sustainable management. There are many examples of the consequences of following the hard-path approach, particularly in arid and semi-arid systems. Seasonal flows in the Yellow River in China, for example, fall virtually to zero along extensive sections of the river (Fu et al., 2004); in 1997, a particularly dry year, the length

without flow extended for 700 km and remained dry for 330 days. Similarly, for long periods some sections of the Colorado and Grande rivers in the US South West are without discharge (Molles et al., 1998), affecting ecosystem viability or simply altering ecological integrity; this is in spite of international conventions that govern water abstraction from these rivers. The alternative, soft-path approach, is instead aimed at avoiding irreversible effects on ecosystems, while seeking 'healthier' (more sustainable) human attitudes to the use of water. In essence, this approach seeks greater efficiency of water use, through implementation of changed policies at, at least, local and regional scales (Dietz et al., 2003). This will become all the more critical as population increase (up to 8.9 billion people in the world by 2050; Cohen, 2003), together with the associated rising demand for water (Gleick, 2003), suggest that pressure on water resources is going to increase significantly, though the distribution of water resources among various areas of the globe will remain uneven.

Water abstraction may compound the effect of natural fluctuations in global runoff, runoff ultimately responding to global dynamics (Beckmann et al., 2005). Current estimates suggest that, globally, annual runoff is increasing on average (Labat et al., 2004), with greater fluctuations in regional and local runoff. Nijssen et al. (2001) applied the predictions of several Global Change Models and determined that hydrologic sensitivity to global rising temperatures could be higher in snow-dominated basins of mid- and higher-latitudes. These high-latitude catchments could experience an increase in runoff, whereas tropical and mid-latitude watercourses could experience a reduction. As an example, the Arctic Ocean now receives 7 % more surface inflow from the land than it did 60 years ago (Peterson et al., 2002). These variations are driven by smaller-scale, local events but they contribute to effects on the regional climate (e.g. in the Amazon; Gordon et al., 2005). Altogether, climate-related variations in water flow and hydrology could reinforce the ever-increasing abstraction by humans, the two resulting in alterations in runoff. The predictions of the Intergovernmental Panel on Climate Change (IPCC, 2007) indicate that annual

average river runoff might increase by 10–40 % at higher latitudes, and decrease by 10–30 % over some dry regions.

Changes in hydrological pathways, particularly frequent in technologically advanced countries, can result in decreased water residence time in the catchments, because of agricultural uses and higher soil imperviousness (Wang et al., 2000). Streams draining human-dominated catchments affected by increased use of impervious surfaces (buildings, greenhouses, concrete, asphalt) are hydrologically 'flashy', carry high concentrations of nutrients and pollutants, show diminished nutrient retention, and have altered morphology and channel instability (Walsh et al., 2005).

Greater river regulation, may however, increase the residence time of running waters, leading to an average 'ageing' of the water they contain (Vörösmarty & Sahagian, 2000): water residence time may shift from 16–26 days in unregulated rivers to 60 days in regulated conditions. This transformation of the habitat character of rivers in the direction from lotic to lentic (which I propose to call *lentification*) may contribute to higher evaporative losses (especially in arid and semi-arid areas), as well as to changes in river structure and function. A perturbing consequence of dams in river systems is that they intercept, and cause the accumulation of, sediments and carbon (Vericat & Batalla, 2005). Sediment transport has changed significantly between pre-human and present times (Syvitski et al., 2005). An estimated pre-human load of $14\,030 \times 10^{12} \text{ g y}^{-1}$ to world oceans has decreased to $12\,610 \times 10^{12} \text{ g y}^{-1}$, the 10 % difference being retained in reservoirs. It is an apparent paradox that the world's rivers are transporting more sediment (because of human practices) yet less of it reaches the sea because of its interception and settlement in reservoirs (Syvitski et al., 2005). Significant alterations to the carbon flux may also be related to the loss of wetlands, resulting in a significant decrease in the delivery of young dissolved organic carbon (DOC) to the ocean (Raymond et al., 2004). Alteration to fluxes from large watersheds could have unexpected effects on the biogeochemistry of rivers, favouring higher rates of denitrification and methanogenesis,

with unwelcome consequences from the release of greenhouse gases to the atmosphere (Freeman et al., 2004).

Effects of river-system lentification can be drastic for biological communities. Damming causes major difficulties for the dispersal of organisms and affects diversity, both downstream and upstream of the dam (Pringle, 1997). Regulation may cause decreased peak flows and, therefore, a loss of the hydrological variability (Vörösmarty & Sahagian, 2000) that directly affects the colonising abilities of successive generations of organisms inhabiting the systems. Artificial damming of natural hydrological conditions, by definition, reduces the strength and frequency of flooding and of meander migration, lowering the incidence of post-disturbance succession (Margalef, 1997) and the opportunities for colonist species to re-establish from elsewhere. Some habitat changes associated with lentification can produce positive effects for some macroinvertebrate components (Strayer, 2006): species that are intolerant of desiccation or are relatively immobile (e.g. unionid mussels) face greater dangers in lotic systems than those that can fly or produce resting stages (several insect groups). Certain invasive species can also take advantage of stabilised hydrological conditions: in the lower River Ebro (northern Spain), reduced flow has favoured the proliferation of the zebra mussel *Dreissena polymorpha*, the trematode *Phyllodistomum folium* that infects zebra mussels, and the Asian bivalve, *Corbicula fluminea*.

In terms of the functioning of river systems, a shift in the metabolism of rivers is one of the consequences that might arise from the alteration of water fluxes. Aquatic ecosystems tend, on balance, to be heterotrophic (del Giorgio & Williams, 2004), since they process large inputs of allochthonous organic matter, despite low nutrient availability in many instances (Fisher & Likens, 1973; Vannote et al., 1980; Mulholland, 1992). Evidence suggests, however, that nutrient enrichment and hydrological alteration may favour a shift towards autotrophy in aquatic ecosystems (e.g. Kemp et al., 1997). The decrease of water flow may result in shallower water depths and lead to more underwater light penetrating to the bottom. The potential decrease of the water table in the riparian zone may impair the riparian vegetation, trees being

replaced by herbs, with lower leaf-litter input and – again – allowing higher light penetration. Together with higher nutrient concentrations (lower dilution), the scenario can therefore become favourable to autotrophic organisms, shifting the balance towards autotrophic metabolism but also causing a higher imbalance with respirational demands, particularly at night (Sabater et al., 2000).

Challenges for conservation and provision of services by river ecosystems

There is a growing need to assess physical (geomorphological, hydrological) and biological (community composition and abundance) components in determining the ecological state of inland waters. In Europe, this is now a statutory requirement for systems circumscribed by the EC Water Framework Directive (European Commission, 2000); guidelines issued by the United States Environmental Protection Agency (EPA) seek similar compliances. These characteristics shape the function and performance of biological communities in their environments. In reality, the structure and function of an ecosystem are mutually interdependent (Fig. 1). In practical terms, both need to be assessed in order to predict the response of an ecosystem to known or likely stressors.

Fig. 1. Hierarchy of irreversible effects in river ecosystems associated with the alteration of the global water cycle.

The functions that biological communities perform result from the interactions between the component species, and between the species and environmental parameters. Among the several functions for which the biological communities are responsible are those that directly affect the ecological state of the system (including the use of nutrients, sequestration of toxicants, oxygen production and consumption, and mineralisation of organic matter). Accordingly, some of these functions are recognised as ‘*Services of the Ecosystem*’ (Costanza et al., 1997; Millennium Ecosystem Assessment, 2005; Table 1), and as such their value is fully acknowledged.

Though most ecosystem services are delivered at the local scale, their supply is influenced by regional or global-scale processes. Therefore it is essential to make accountable estimates of the service potential in these systems as well as of the possible constraints caused by disturbances occurring at intermediate scales. The ability to predict thresholds for such processes is hampered, however, by the large heterogeneity of aquatic ecosystems and their processes and by the difficulties in predicting the probability of their consequences. Despite advances in monitoring, there is still a deficiency of uninterrupted time-series of sufficient length and quality to support such extrapolations. Further, there is a dearth of basic information on such topics as the distribution and areas of wetlands (in the widest sense); the biodiversity responses to decreasing hydrological connectivity within river systems; population stocks and fluctuations (for example, for freshwater fisheries); and the connections between human systems and ecosystems (Millennium Ecosystem Assessment, 2005). The use of ecological assessments for the conservation and management of aquatic ecosystems therefore shows many gaps that need to be addressed.

Determining the true pressure on freshwater ecosystems associated with water use

The impacts on river ecosystems caused by water flow abstraction or reduction can be readily illustrated by comparing the water demands and resources in individual river basins, as can be shown by reference to several cases

Table 1. Functions and services of river ecosystems. Classification according to the Millennium Ecosystem Assessment (2005).

<i>Provisioning values</i>
Water resources
Food production
Energy production
<i>Regulating & supporting values</i>
Gas regulation
Climate regulation
Disturbance regulation
Nutrient recycling
Material processing
<i>Cultural values</i>
Aesthetic & spiritual
Educational

in the Iberian Peninsula (Fig. 2). The northern part of the peninsula has an Atlantic climate and, hence, a sufficiency of resource supply. The percentage use of water in this region accounts for between 4 % and 7 % of the total resource available. However, demands increase to between 30 % and 80 % of the total resource in the rest of the peninsula, following the gradient of decreasing precipitation from north-west to south-east Spain. In the Segura basin, at the extreme south-east corner of the Iberian Peninsula, current demands, equivalent to 224 % of the supply, are satisfied only by transferring water from other basins (especially the Tajo). The Segura river does not carry water in most of its network, especially in the lower section and particularly during the summer months. The only water carried by these lower reaches at such times is treated sewage effluent and, hence, of poor chemical and biological quality.

A similar analysis has recently been undertaken at the global scale by Oki & Kanae (2006). They refer to the percentage of available water resources abstracted for human use as the *water stress index*, which they have used to assess the global distribution of water scarcity. Estimates at both regional and local scales are less precise, because they can be distorted by several factors. The *true* extent of groundwater resources is difficult to estimate

as, in many agricultural and industrialised areas, much is of poor quality and cannot be used directly (Llamas, 2005). In many areas of the globe, for political, economic and practical reasons, apparent resources (both surface- and groundwater) are not available for direct use by stakeholders; an extreme example is the difficulties in sharing of Israeli and Palestinian resources (Tal, 2006). In systems where the seasonal and interannual variability is high (this being the case in Mediterranean systems; Gasith & Resh, 1999), as well as in many other arid or semi-arid areas, the availability of resources is unpredictable and the estimation of the impacts on river systems caused by water abstraction is unreliable. In all such cases, there is a critical relationship between water demand and the available resources beyond which the ecosystem structure and function is likely to be compromised. In order to assess this threshold, the services offered by the river ecosystems need to be assessed at a regional scale.

The relevance of hydrology to ecosystem structure and function can be exemplified by comparisons among river systems all over the world. Freezing and thawing in the Alps produces strong variations in river discharge (Ward & Uehlinger, 2003) that result in the contraction and expansion of the drainage network, in variations in sediment transport and in the organisation of the biotic system (Robinson et al., 2003). Floodplain streams, such as those in the Argentinean Pampa, are of low slope, and have silty or sandy sediments (Bonetto & Wais, 1995). These streams lack riparian vegetation but they are functionally dominated by an extremely high abundance of macrophytes (Feijó et al., 1996) and large detritivores (Rodrigues Capítulo et al., 2002) that, under hydrological conditions obtaining elsewhere, might be washed away. In Mediterranean systems, litter inputs are smaller but occur over longer periods than experienced in temperate systems (Elosegi et al., 2002; Sabater et al., 2008), with the result that riparian vegetation is subject to severe stress during summer (Bernal et al., 2003). In some areas, the occurrence of floods and droughts is responsible for large changes in the structure of the fluvial macroinvertebrate communities (Grimm & Fisher, 1989; Acuña et al., 2005). During periods of low flow, biotic interactions can govern the

Fig. 2. Water use in the main river watersheds of the Iberian Peninsula, as a proportion of the total resource available. Colours identify the precipitation range (mm per year). Data used in this figure were derived from the Libro Blanco del Agua en España (Ministerio Medio Ambiente, 2000).

community structure (Power, 1992) but, as the dry season is progressively extended, the aquatic environment becomes increasingly harsh; in the case of temporary streams, it disappears altogether (Boulton & Lake, 1992).

Such cases exemplify the extreme relevance of the hydrological regime to the biological functioning of the system. The combined effects of climate change and those related to human use may greatly modify the characteristic function of each ecosystem and even lead to its malfunction.

Predicting responses and thresholds in river ecosystems

Nonlinearity is one of the most salient features of complex systems, and ecosystems are amongst them (Nicolis & Prigogine, 1989). Nonlinearity applies to many ecosystem properties, including those emanating from biogeochemical processes and those consequential upon food-web

organisation and the operation of constituent biological communities. In practice, it means that many processes and functions in river ecosystems do not follow linear patterns and their action may be subject to abrupt thresholds. As an example of this emerging characteristic, having higher nutrient availability does not mean that primary productivity will *always* increase. There is thus a difficulty in predicting the responses to many processes, in particular at the regional or global scales required to quantify ecosystem services.

Among the several approaches to producing reliable predictions, I will comment on two. The first one is the comparison of a given process between sites and the discernment of common patterns and regularities. This approach is particularly useful for demonstrating whether predictions based on small-scale observations are sustained at large scales. The recent pan-European comparison of riparian zones (NICOLAS project; Burt et al., 2007) showed

that the capacity of riparian zones for removing dissolved nitrogen in surface runoff and in groundwater is a non-linear ecosystem process. Nitrate removal is an identifiable ecosystem service provided by the riparian compartment in river ecosystems, lowering the concentrations eventually entering river waters. For this reason, riparian buffer strips in areas susceptible to the receipt of large amounts of nitrate (e.g. agricultural, urban) provide an excellent means of maintaining river water quality. Furthermore, they constitute biological corridors for terrestrial fauna and flora, and provide particulate organic materials for the river habitat and biota (Elosegi & Johnson, 2003).

Nitrate removal in riparian zones is the result of two separate processes. Bacterial denitrification in the soil releases nitrogen to the atmosphere, while plant uptake and assimilation, though significant, represents a transient pool, unless intact vegetation is harvested effectively. Both processes are closely linked to climatic conditions (Hill, 1996). Denitrification can account for 50 % to 90 % of the total nitrate elimination when soils are water-saturated for most of the time (Nelson et al., 1995), though it may be constrained by low soil temperatures (continental climates) and by low soil moisture (arid or semi-arid climates). The relevance of denitrification and plant uptake shifts according to variations in temperature, water table and nitrate input (Clément et al., 2003; Hefting et al., 2003).

The NICOLAS study showed that the annual nitrate-removal efficiency in the participating European countries was about 10 % to 30 % per metre of forested or herbaceous riparian strip, but removal efficiency decreased to around 5 % per metre in other locations or even to zero in some cases (Sabater et al., 2003). The reason for such differences was not found in the vegetation type, or in the soil characteristics, or in the climate patterns at the various sites. Instead, the large variation in nitrate removal efficiency between the riparian study areas was related to the particular characteristics of individual riparian buffers. Local geomorphological and hydrological conditions tend to provide the most important controls of the nitrogen removal capacity of riparian zones. It has been found that riparian zones in which the water table is close to the soil surface are more effective at removing nitrogen compounds than those

where the water table is lower (Haycock & Pinay, 1993; Hefting et al., 2004). Therefore, sites with a flat riparian zone (floodplain), which allows a high water table to be maintained, were more effective than those sites where the riparian zone is sloping (Burt et al., 2002). Since the actual pathway of water flow through substrates is often complex, as a consequence of varying soil texture and vegetation, the riparian zone contains a mosaic of suitable and unsuitable areas for nitrate removal. As a result, process rates are not simply a function of the riparian surface area but of the length and period of hydrological contact.

Riparian zones are sensitive to nitrogen levels that might approach or exceed those that saturate the system requirements (Aber et al., 1989). In nitrogen-poor systems in the NICOLAS study, removal efficiencies were high and remained unaffected when nitrate input increased (Fig. 3; example from the Mediterranean stream, Fuirosos). However, in nitrate-saturated soils, the efficiency decreases and the nitrogen leaches from the riparian zone. The results of this inter-site comparison (Sabater et al., 2003) showed that nitrate load was also one of the main factors controlling variation in nitrate removal rates between riparian zones. The significance of nitrogen load for nitrate removal was only seen for nitrate concentration inputs higher than 5 mg N L^{-1} , when nitrate removal efficiency was negatively correlated with nitrate input ($r = -0.59$, $p < 0.05$). This relationship followed a pattern of negative exponential decay, with no nitrogen removal by the riparian buffers receiving nitrogen inputs of up to 20 mg L^{-1} nitrate-N. The negative relationship between nitrate load and riparian-zone removal efficiency found at some sites suggests also that there is a saturation effect of long-term nitrate loading, which exceeds the buffering capacity of the riparian zones. Hanson et al. (1994) observed clear symptoms of nitrogen saturation in a forested riparian zone subjected to long-term enrichment. These symptoms consisted of enrichment of total plant and microbial nitrogen pools, as well as an increase in the rates of soil nitrogen processes such as mineralisation and nitrification. The most remarkable example of riparian malfunction in our NICOLAS study was the Dutch forested site (Hefting

Fig. 3. Evolution of the nitrate input to, and output from, the riparian zone of a Mediterranean stream, Fuirosos (NE Spain) during the NICOLAS project study period. Input: exterior of riparian zone; output: last section of the riparian zone, connecting with the river water. The solid arrow indicates the period corresponding to an episode of fertilisation in the adjoining agricultural field. The broken arrow indicates the later arrival of nitrates (from the fertilisation) to the underground water at the input zone of the riparian area.

et al., 2004), located in an area of long-lasting nitrogen enrichment but not performing as a net retainer of nitrogen.

Another possible approach to achieving reliable predictions is through experimental manipulations. This second approach to predicting responses and thresholds in river ecosystems adds some value to inter-site comparisons, though it lacks the wider view provided by the simultaneous comparison of several sites at once. Experimental manipulations are useful in discerning potential causes influencing thresholds. Classical studies in lake ecology, for example, have shown increased phosphorus, and not carbon, to be the principal cause of eutrophication in temperate lakes (Schindler, 1987). Experimental approaches can be useful in analysing the response of the biological structure to a disturbance. These approaches require chemically undisturbed conditions and need careful planning to obtain robust conclusions (Underwood, 1994). If these conditions are fulfilled, such experiments allow accurate cause-effect relationships to be diagnosed. Again, I provide an example of this manipulative approach with the outcome of a short-term (six week) nutrient enrichment experiment in a forested stream, in which N and P concentrations were increased

10-fold (Sabater et al., 2005). The experiment brought both expected and unexpected consequences. Chlorophyll concentration increased (by a factor of about four) in the fertilised reach but effects on bacteria and heterotrophic (exoenzymatic) metabolism were less obvious. A colonisation experiment carried out in parallel to the enrichment (Romaní et al., 2004) showed that chlorophyll and bacterial density on natural substrata (sand and rocks) progressively converged as the nutrient addition was assimilated; after the nutrient addition was completed (44 days), the two habitats showed similar algal and bacterial biomass. It would appear, therefore, that short-term but continuous nutrient enrichment caused

structural changes in the biofilm components, these changes producing uniformity among substrata. The biofilm approached a continuous layer covering the stream substrata, while heterogeneity between habitats decreased. These changes implied a loss of structural heterogeneity in the stream which may be associated with significant modifications of the stream functioning (such as nutrient retention) in the longer term (Mulholland, 1992).

Chronic disturbances are defined as those in which pressure is continuously brought to bear on the ecosystem. This type of pressure can cause lasting simplification of the community structure. A consistent long-term disturbance is produced by sustained nutrient inputs into river systems that may have permanent effects on biofilm structure and functioning: the experiments of Peterson et al. (1993) have demonstrated the occurrence of bottom-up effects on the structure and functioning of river systems. Rivers continuously receiving high nutrient inputs become nutrient-saturated (Bernot & Dodds, 2005) and show functional alteration. In nutrient-saturated rivers, when light is not limiting, the functional complexity that is potentially associated with habitat diversity is partially suppressed by a complete cover of filamentous

algae such as *Cladophora* (Guasch, 1995), resulting in the physical simplification of the stream habitat. Algal-dominated biofilms may also have an impact on the hydrodynamics of stream flow (Mulholland et al., 1994).

Even though the impact of nutrients is a recurring theme in ecology, the capacity of systems to cope with enrichment and the chain of consequent effects are still poorly known, especially in streams and estuaries (Robertson et al., 1999; Sobczak et al., 2005). There remains a question about whether long-term enrichment produces enduring effects when community components are subject to other critical conditions, such as light limitation. In particular, forested streams may frequently be light-limited systems, where the effects of inorganic nutrients are, at first sight, immaterial to the stream structure and functioning. This has been tested through a two-year continued enrichment conducted in a forested reach in Fuirosos, looking at the effects on biofilm structure and metabolism. Basal concentrations of N and P in an experimental reach were increased three-fold during one year, and several biofilm descriptors were compared between the enriched reach and three control (unenriched) reaches upstream. A two- to four-fold increase in chlorophyll-*a* concentration in the enriched reach over those of the control reaches was observed within four months of the experiment starting (Veraart et al., in press). Chlorophyll measurements approached 100 mg m⁻², and differences between the enriched and the control reaches were greatest during late autumn and spring, when light was less of a constraint. Nutrient enrichment also produced a consistent increase in the biomass and the areal cover of the bryophyte community in the fertilised reach. In addition, differences were observed in the percentage of elemental phosphorus accumulated in the biofilm, which became significantly different only after nine months of fertilisation. Finally, effects were detectable in the processing of organic matter in the river, with a significant increase in peptidase activity in the fertilised reach. Peptidase activity is directly related to the heterotrophic catabolism of organic matter of algal origin (Romaní et al., 2004). This consistent increase in enzymatic activity may be taken as an indication

of a shift towards the preferential use of autotrophic organic matter in the stream. It remains to be seen whether other trophic levels (meiofauna, macrofauna) have also been favoured by the nutrient increase.

These various responses to enrichment in Fuirosos do not indicate that nutrient saturation (*sensu* Bernot & Dodds, 2005) developed within the ecosystem. The lag between nutrient addition and the permanent responses in chlorophyll and phosphorus in the biofilm may be an expression of the capacity of the ecosystem to resist additional nutrient inputs before approaching a more saturated state. This moderated response to continuing enrichment may have been compounded by the forested nature of the riparian zone (Sabater et al., 2005) and by the well-developed habitat structure of the system, suggesting that forested systems are better protected against disturbances caused by enhanced nutrient inputs than are others in which light is more available. Despite the slow responses, it is concluded that consistent trends towards system autotrophy are driven by inorganic nutrient enrichment, even in stable, light-regulated habitats.

Scaling up local processes to the ecosystem scale

Observations in space and time performed at the local scale need to be scaled up in order to account accurately for the processes and services of river ecosystems. Our perception and ability to detect the effect of disturbances is also a matter of the observation scale (Strayer et al., 2003). Rivers are not simply uniform transport channels but are complex and heterogeneous systems. Within this complexity, we need to take into consideration that different geomorphological, hydrological and biological scales are operating in river ecosystems (Frissell et al., 1986). For instance, at the habitat scale of individual organisms (a patch size of diameter between 0.1 m and 1 m), there may be variations in velocity, shear stress, substratum and incoming irradiance. However, at the reach scale (10 m to 50 m), differences appear between riffles and pools, between the littoral and central part of the channel, and also because of the presence of natural obstacles such as debris or beaver dams. Those structures

visible at the reach scale are compounded from those at the habitat scale. The connection between structure and functioning, which is detectable at the habitat scale, is also expressed at the reach scale in the stream. The reach scale is obviously relevant to the understanding of many of the processes occurring in a river (Fig. 1). Sweeney et al. (2004) observed that benthic habitat quality differs substantially between forested and unforested reaches, these differences affecting functioning (biogeochemical and metabolic) within the streams. Finally, at the stream and river system scale (> 1000 m), the complexity includes the influence of tributaries on the main channel and of secondary channel structures, such as former meanders or oxbow lakes.

Processes occurring generally in rivers cannot be separated from this hierarchical structure. Hierarchies exist in ecological systems because they are more stable than the random grouping of assemblages; they match the theories of dissipative structure and stratified stability (D'Angelo et al., 1997). Dependent upon their hierarchical organisation, downstream conditions may be translocated to upstream conditions, producing functional variability (Power & Dietrich, 2002). As an example, fine sediments and deeper waters, typical of the lower river sections, may occur in upstream reaches as a consequence of the formation of debris dams. The effects of animals (beavers, hippopotamus), landslides, or man-made structures are obvious in the context of hierarchically structured river systems (McCarthy et al., 1998; Halley & Rosell, 2002), and favour the creation of conditions which otherwise would depend on hydrological (and ultimately climatic) processes (Margalef, 1983). The resulting complexity of this hierarchic network may produce a buffer to disturbances, since refuges for organisms may be more numerous than in a simple linear channel system (Power & Dietrich, 2002).

Upscaling is therefore required in order to translate structure and function from the local process to the complexity of entire regions. Upscaling is a necessary step in achieving accountable assessments of the ecosystem services that are socially acceptable. Basic information is always an essential ingredient to making relevant projections. These may include: the length of stream channel (by order) per watershed, the wetland

and riparian surface area, the habitat quality and losses, and the habitat relevance with respect to a function.

Conclusions

Most human-induced disturbances promote the physical uniformity of river systems and the decrease of biological diversity in streams and rivers. The structure and functioning of heavily impacted river systems become mutually and strikingly similar, irrespective of the river's origin and the climate. The more intense and persistent is the disturbance, so the resemblance is greater. On the other hand, river organisms use resources most efficiently in spatially heterogeneous channels, and under moderate disturbance frequencies, rather than in steady conditions, to which they are not adapted.

Disturbances (both natural and anthropogenic) that increase nutrient concentration may cause the river biological components and metabolism to shift from natural heterotrophy towards autotrophy, even in relatively pristine rivers. River ecosystems are generally heterotrophic unless alterations/manipulations promote greater autotrophy. Enforced hydrological stability or increased nutrient loading, among many other disturbances, may cause pronounced changes in system metabolism. Several lines of evidence indicate that a shift from heterotrophy to autotrophy may occur even in shaded, low-light systems with flourishing benthic habitats, following persistent addition of nutrients.

Rising human pressure on water resources and the likely effects of climate change will probably affect the hydrological and geomorphological state of river systems in many areas of the globe. Hydrological variations will lead to a chain of effects in the structure and functioning of river systems and will make difficult the estimation of the ecosystem services that they can sustain. This will be especially relevant in arid and semi-arid areas, and in those systems where water use is very intense.

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