Effects of Hydrologic Alterations on the Ecological Quality of River Ecosystems

Sergi Sabater and Klement Tockner

Abstract In most of the world's watercourses, dramatic modifications have occurred as a consequence of intensive use by human societies. 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 consequences. However, human impacts on river hydrology, such as those that derive from regulating their flow or by affecting their channel geomorphology, affect the functional organisation of streams, as well as the ecosystem services that derive from them, and lead to the simplification and impoverishment of these ecosystems.

Keywords Biodiversity, Biogeochemistry, Drought, Intermittent, Stream

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S. Sabater and D. Barceló (eds.), *Water Scarcity in the Mediterranean: Perspectives Under Global Change,* Hdb Env Chem (2010) 8: 15–39, DOI 10.1007/698_2009_24,

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1 Water Scarcity, Water Stress and Drought, Expressions of Change in River Ecosystems

In most of the world's watercourses, dramatic modifications have occurred as a consequence of their intensive use by human societies [1]. Pollution, water abstraction, riparian simplification, bank alteration, straightening of watercourses, dam construction, and species introduction are widespread perturbations in river ecosystems. These human-driven alterations are part of *global changes*. The simplification of the channel network and the alteration of water fluxes reduce the capacity of fluvial systems to recover from natural disturbances. Hydrologic alterations affect the functional organisation of streams and rivers, and lead to a simplification and impoverishment of the biota within these ecosystems.

These effects add to the ongoing *climate change*, which results in altered temperature and rainfall in all biomes [2]. Though mostly human-driven, these changes do refer exclusively to the climate. The direct implications of climate change on flow regime are certain. Barnett et al. [3] documented a decrease in water flow of the NW America watercourses and related it to the increase in late winter temperature as well as to the associated lower thickness of the snow pack. Globally, the Mediterranean Basin is one of the regions most vulnerable to climate changes. The Mediterranean climate is subject to complex planetary scale processes and teleconnections, but also to local processes, which are induced by the complex physiography of the region and the influence of the Mediterranean Sea. Consequently, the Mediterranean basin is one of the most prominent "hot spots" for potential changes [4]. Most climate change models indicate that Mediterranean regions will be affected by summer drought and high temperatures. These changes will probably not be limited to the catchments draining into the Mediterranean Sea, but will affect all Mediterranean-type regions worldwide. The relation of these climate alterations to the fate of Mediterranean-type aquatic ecosystems will be expressed in altered flow regimes, increasing frequency and magnitude of floods and enduring and unexpected droughts [99] which will affect the distribution and survival of unique biota, and the associated ecosystem functions.

Nevertheless, the response of water resources will be more complex, as human activities will also change in response to altered climates. The intensity of the pressure put on water resources and aquatic ecosystems by external drivers is related to higher economic income (e.g. expressed by electricity production and consumption) of human societies [5]. The limitation of resources can be qualified by a diversity of terms, varying somewhat in intensity: drought, temporality, and

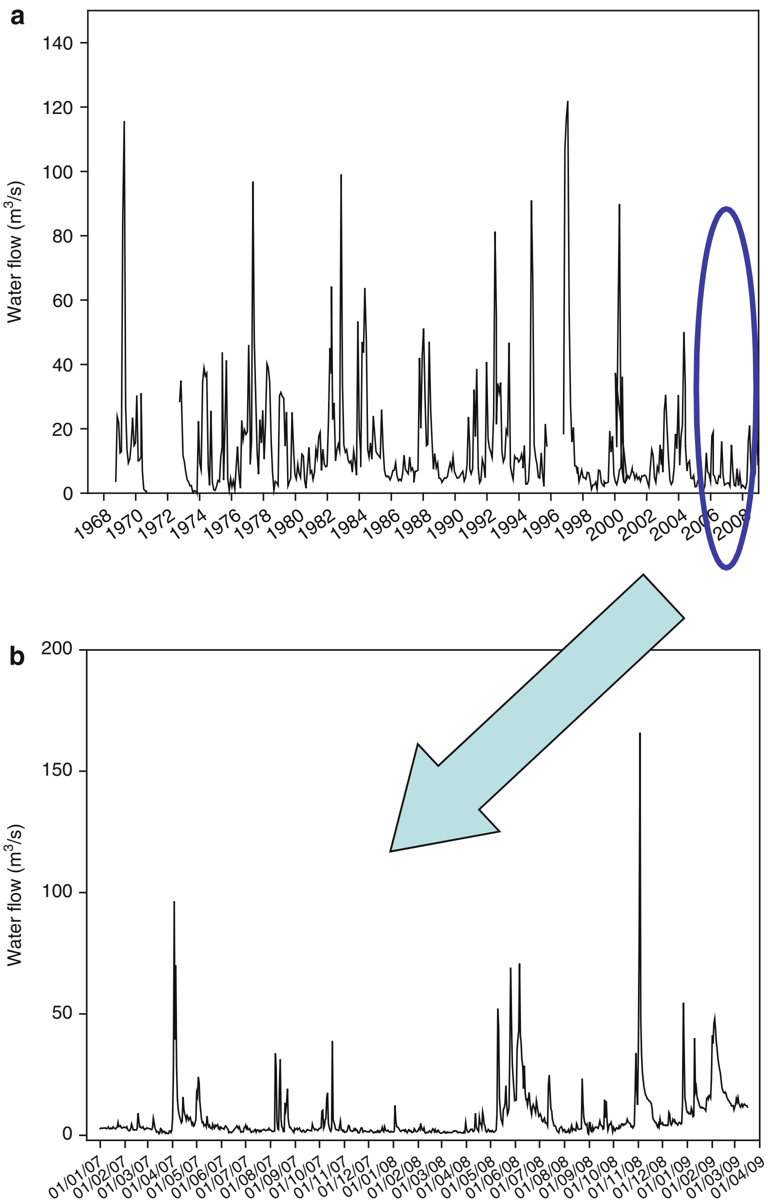

Fig. 1 Water flow dynamics in the Llobregat River (NE Spain) close to its mouth. (**a**) Monthly average flow rates between 1968 and 2008. (**b**) Daily average flow rates in 2007–2008 during a remarkably dry period (data: Catalan Water Agency data base)

water scarcity. Droughts are here defined as persistent periods when the river discharge is below a reference minimum. Droughts can be characterized by the time of occurrence, duration, the minimum flow recorded, and the deficit volume during that episode [6]. Water scarcity is a more structural, persistent drought; it can be properly defined only on the basis of reliable records of drought situations, as well as consistently establishing a drought threshold line. This is a relevant issue to define repetitive drought situations that therefore can be indicative of structural effects. Drought varies in space and time, and therefore the rainfall threshold used to define drought is dependent on the location [7]. Available long-term records can be particularly useful to define these thresholds. Long-term records are available in Mediterranean countries because these events have affected daily life for a long time. Several indicators can be useful to derive this information: tree ring chronology, documentary data (administrative, from local government institutions, both civil and ecclesiastical [8], and even data from rogation ceremonies [7]. To sum up, while *drought* means a temporary decrease in water availability, due for instance to rainfall deficiency, *water scarcity* means that water demand exceeds the water resources exploitable under sustainable conditions (COM2007-414 final).

A mixture of natural and human-driven components causes water temporality. It is obvious that natural influences may be particularly relevant in systems where the seasonal and interannual variability is high, as in the Mediterranean systems; [9]. In the Mediterranean Basin, as well as in many arid or semi-arid areas, temporality naturally associated to the climate leads to drought most usually in summer, followed by extreme autumnal flood episodes (so-called first flush events). For example, the Llobregat River (NE Spain) has an average mean annual discharge of 14 $m^3\ s^{-1}$ (Fig. 1a), but a monthly range from <2 to 130 $m^3\ s^{-1}$. The diel water flow rate is even more variable (Fig. 1b). The hydrological year 2007–2008 was one of the driest years recently recorded, and during 86% of the time the river carried less than the average water flow. During that year, flashy episodes reaching 100–180 $m^3\ s^{-1}$ occurred, and flow returned very quickly to baseflow afterwards. Catastrophic flood events with 1,500–2,000 $m^3\ s^{-1}$ can occur on average every 9–20 years in the Llobregat River [10]. The most painful event occurred on 25th September, 1962 and caused 441 human casualties. These drought–flood patterns have been documented over a long period of time. Thorndycraft et al. [11] analysed paleoflood deposits in the Llobregat River and described that the largest flood in a mid-river location ever recorded in modern times (1971; 2,300 $m^3\ s^{-1}$) was exceeded on five occasions in the past 2,700 years, reaching maximum discharges of 3,700–4,300 $m^3\ s^{-1}$. Therefore, the Llobregat flood events exceed baseflow by up to a factor of 100–300.

2 The Alteration of Water Flows in the Context of Climatic and Global Changes

Global change is an expression of the human footprint on resources, energy and soil uses, directed to larger and less efficient agglomerations, higher use of resources, and a potential higher pressure towards natural ecosystems. As an expression of this global change, ecosystem and societal requirements compete for water resources,

Table 1 Spatial extent of temporary watercourses. Data: Larned et al. (in review), among other sources

Global		~20%
USA	3.2 mill km	~60%
France	70,000 km	25–35%
Tagliamento	1,300 km	~50%
Chatooga	2,800 km	70%
Albujon	820 km	99%
Val Roseg	26 km	80%

and this competition increases with increasing water scarcity. Aquatic ecosystems are impacted in a nonlinear way with increasing water withdrawal. The effects of drought and water scarcity on river ecosystems are evidenced by an extended duration of dry periods as well as by a growing proportion of watercourses being affected (Table 1).

Current estimates predict that on average, the global annual runoff is increasing [12]. However, remarkable variations occur at the regional and local scales. While high-latitude catchments may experience an increase in runoff, tropical and mid-latitude watercourses are expected to experience a reduction in flow. The predictions of the Intergovernmental Panel on Climate Change [2, 13] indicate that annual average river runoff might increase by 10–40% at higher latitudes, and may decrease by 10–30% in dry regions. An increase in flow has already been noticed for Scotland [14]. In Europe, the southern and south-eastern regions already suffer most from water stress and will see a further increase in the frequency and intensity of droughts [15].

The potential impact of water withdrawal on river ecosystems is indicated by the ratio between water demand and available water resources. Though the ecological relevance of this ratio could be stronger if the Q_{90} was used instead of the more general estimate of total resources, it is a simple index easily applicable, using public data sets. For the Iberian Peninsula, the potential ecological effects are demonstrated in Fig. 2. The northern part of the Peninsula exhibits an Atlantic climate with sufficient water supply; the use of water accounts for 4–7% of the total resource available, though this does not prevent severe local shortages in large cities. However, demands increase to 30–80% of the total resource in the remaining catchments of the Peninsula, following the gradient of decreasing precipitation from NW to SE. In the Segura basin, located in the SE corner of the Iberian Peninsula, current demands exceed the supply by 224%, which requires an interbasin transfer of water (especially from the Tajo River). The downstream channel network of the Segura River dries up for several months during summer. When water flows, it consists of treated sewage effluents and, hence, is of poor chemical and biological quality. Figure 2 shows that the quantity attributed to the river (the so-called *minimum flow*) is far from being reasonable where water demand is high [16]. The application of a minimum flow (also called *ecological flow)* regime requires guaranteeing resources to make the ecosystem function. In short, very low water flow implies the inability to carry on with essential ecosystem processes, and complete water absence inhibits even minimum ecosystem function.

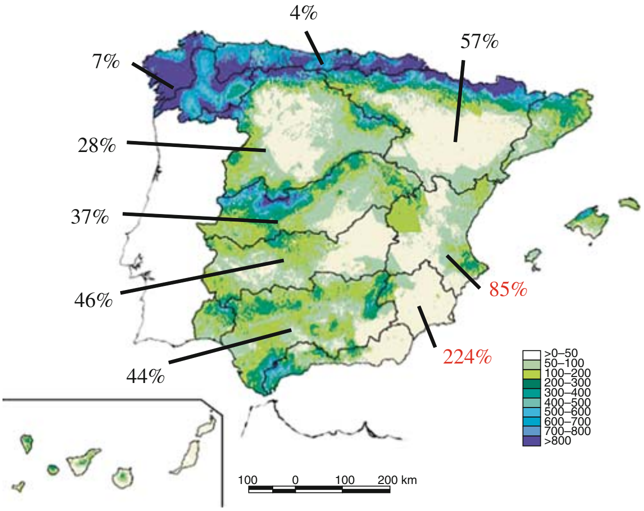

Fig. 2 Relative proportion (%) of water demand in relation to available resources in the main catchments of the Iberian Peninsula (data: derived from Libro Blanco del Agua en España, Spanish Ministry of Environment 2000)

Water withdrawal and scarcity are related to water flow regulation and dam construction. The regions suffering most from water scarcity are those which have a large number of big dams and reservoirs [17]. The global figures are also impressive. About 15% of the world's total runoff (40,000 km^3 yr^{-1}) is retained in 45,000 large dams higher than 15 m [18]. From this retained volume, a further 10% is abstracted [19]. As a result of these manipulations and subsequent irrigation, up to 6% of the resources evaporate [20]. A total of 52% of the surface area connected by large river systems (with a discharge of over 350 m^3 s^{-1}) is heavily modified, Europe containing the highest fraction of altered river segments.

Arid and semi-arid regions are particularly water-thirsty, further increasing the pressure on water resources and causing extended dry river networks. However, this is already a global phenomenon. The Yellow River in China, for example, ceases to flow along extensive reaches [21]. In 1997, during a particularly dry year, more than 700 km of river channel remained dry for 330 days. Similarly, sections of the Lower Colorado and Rio Grande Rivers in SW USA remain dry at the surface for extended periods [22], thereby affecting the ecosystem viability. In the former water-spotted area of Central Spain (La Mancha), the only option for the Tablas de Daimiel wetlands to survive is to transfer water from the distant Tajo River that is hydrologically disconnected from these wetlands. The Tablas de Daimiel wetlands were once fed by ground water that is now exploited for corn production. The steadily increasing water abstraction has caused a decline in the aquifer by up to 35 m [23]. Legal regulations are difficult to enforce because of the resistance by the farmers who exploit ground water for irrigation.

2.1 Potential Effects in Temperate Systems

A recent assessment by the European Environmental Agency indicated that high levels of water stress, both in quantity and quality, exist in many areas throughout Europe, and identified several significant ongoing pressures on water resources. The annual water withdrawal in Europe is projected to rise from 415 km^3 today to ~660 km^3 by 2070 (for comparison: the total annual discharge of the Rhine River is 73 km^3). Overall, the area with severe water stress is predicted to increase from 19% today to 34–36% of entire Europe by 2070. At present about 45% of this water is used for industry, 41% for agriculture, and 14% for domestic needs [24–27]. High water stress and an increase in temporary water are already characteristic phenomena in the Mediterranean area. In Turkey, for example, a significant decrease in discharge has been detected during the past 30 years [100]. The minimum flow during the dry summer months (July to September) is particularly affected by increasing water demands and climate change [28]. Many Balkan rivers have undergone even more dramatic annual discharge reduction during the past 40–45 years; e.g. a 79% discharge reduction for the Evrotas, a 57% reduction for the Axios, and a 48% reduction for the Sperchios [29].

However, the spatial and temporal extent of temporary rivers will not only increase in regions where water is already scarce, but this increase will become a more global phenomenon, mainly as a consequence of climate and land-cover change, increased demand for freshwater for agriculture, and of increasing hydropower generation. Permanent water bodies are shrinking even in areas devoid of human population. Smol and Douglas [30], for example, showed that many shallow ponds in the Arctic region are disappearing, mainly because of increased evaporation/precipitation ratios. For natural ecosystems such as the Yellowstone National Park (USA), Mcmenamin et al. [31] have shown that during the last 16 years the number of permanently dry ponds has increased fourfold, leading to dramatic declines in amphibian population density and species richness. Shallow water bodies and headwater streams are particularly sensitive to small changes in flow alterations; at the same time they are hot spots of biodiversity [32], and their desiccation will have severe ramifications for their structure and function.

In many parts of Europe, dramatic hydrological modifications have occurred during the last few centuries. In the central and eastern plains, for example, the total river network length has increased mainly due to the creation of artificial drainage canals. In addition, a 35,000 km long network of navigation canals in the EU (www.inlandnavigation.org/en/factsandfigures.html) now connects most large rivers across all Europe, from the Rhone River in the west to the Volga River in the east, thereby facilitating the rapid spread of nonnative species. While river basins remain hydrologically separated, they become ecologically more and more connected. At the same time, former permanent rivers are becoming temporary, mainly as a consequence of increasing variation in precipitation and domestic and agricultural use. The Spree River in NE Germany, for example, exhibited a sharp decrease in mean and low discharge during the last decade because of an increase in

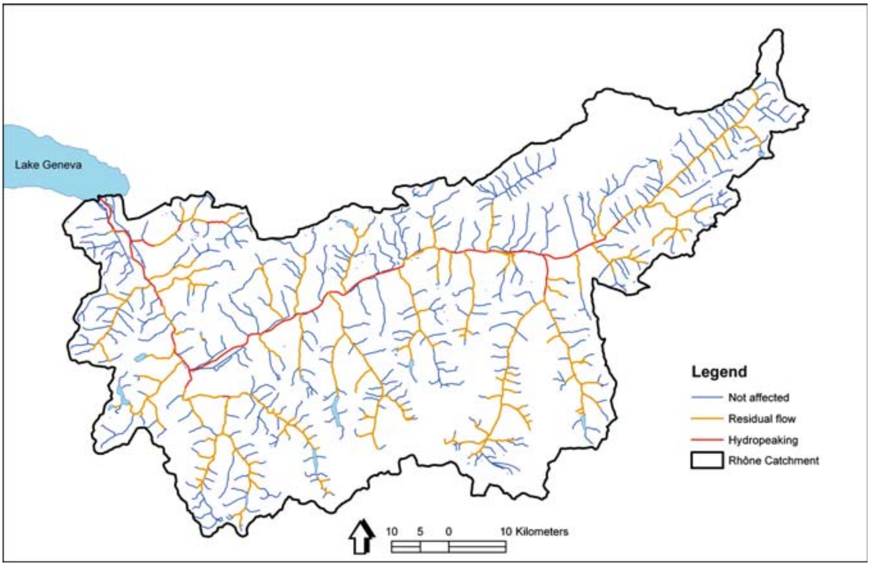

Fig. 3 The hydrological alteration of the river network of the Upper Rhone catchment in Switzerland that drains into Lake Geneva (data: Swiss Federal Hydrological Office)

water abstraction and a decrease in groundwater input. The transformation of permanent waters to temporary waters can be seen as an ultimate threshold for the diversity and the functioning of river ecosystems.

In Alpine countries such as Switzerland, water abstraction for hydropower production creates a network of residual flow channels. Almost all the main rivers in Switzerland and in the Alps are hydrologically altered. For example, the Upper Rhone catchment in Switzerland is extensively exploited for hydropower generation (Fig. 3). Hydropeaking is predominant along the main stem, water abstraction and residual flow conditions are typical for most tributaries, while hydrologically unaffected river segments are fragmented in nature and restricted to the low order sections. As a consequence of flow alteration, biodiversity decreased dramatically along the Rhone River corridor [33].

2.2 Relevance in Mediterranean Ecosystems

Though extremes are part of the normal hydrologic behaviour in Mediterranean-type rivers, a consistent trend of water flow decrease has been described in many of these systems. The Ebro is the largest Iberian river flowing into the Mediterranean Sea. The flow records at its mouth (mean annual runoff 13,408 Mm^3) show a decrease of nearly 40% in mean annual flow in the last 50 years. The forces behind these flow decreases are multiple. Higher water withdrawal, climate change and land use changes have all had an effect [34]. For example, illegal groundwater pumping can be excessive in many areas of the dry Mediterranean (estimated as one million wells in Spain). These practices obviously affect the hydrological behaviour of river systems, and may add an unexpected element for model previsions.

Under these circumstances it is essential to determine the causes of water flow decrease. The *naturalized flow* can be defined as the flow expected under non-direct human influence (e.g. abstraction). This is a useful parameter to be applied in areas subject to strong water withdrawal. One tool to estimate the deficiency of water flow due to human effects is the sacramento soil moisture accounting (SAC–SMA) model, which is based on a rainfall–runoff interaction. Using this model Benejam et al. [35] determined that the Mediterranean river Tordera (NE Spain) dried out for more days (76 per year) than those corresponding to the rainfall–runoff relationship (2 per year). This contrast to the long-term rainfall records in the Tordera watershed, do not show any pattern of decrease that could be causative of the enhanced temporality. The cause of the decrease may be found in the large number of industries and human settlements, which have increased enormously in the basin. More than 30% of the runoff of the Tordera is used by humans (irrigation, urban settlements, industry).

It might be derived from previous suggestions that the river sections below dams can experience even higher stress than those upstream. In the case of the Ter River (NE Spain) during the unusually dry 2007–2008 period, differences were not high

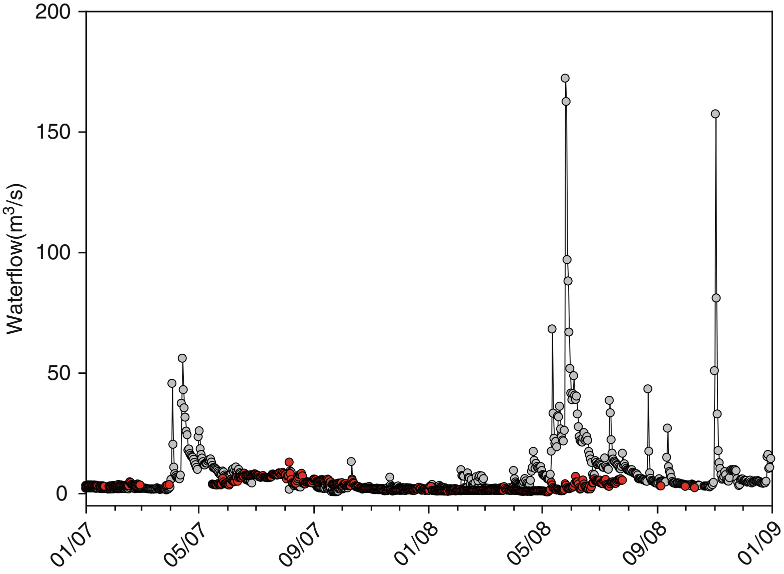

Fig. 4 River Ter (NE Spain) during the dry period 2007–2008. *Grey dots*: River Ter at Ripoll, upstream from the reservoirs of Sau and Susqueda. *Black dots*: River Ter at Girona, downstream from the reservoirs

between the sections upstream and downstream in a series of three reservoirs; however, as soon as rains began, differences rose sharply. The rains in the higher basin (Fig. 4) caused the return of water flow to the river. These waters were stopped by the reservoirs that transferred them to thirsty cities. The river section below the reservoirs was almost not flowing (Fig. 4).

3 Effects of Temporality on In-Stream Biogeochemical Processes and the Structure of Freshwater Communities

Alterations of water flow, independent of the cause, impact the structure and function of aquatic ecosystems. Extended drought produces the loss of hydrologic connectivity between stream compartments, and affects the biota. Therefore, flow cessation triggers a chain of cascading effects, eventually affecting community structure and ecosystem functioning.

The residence time of surface water increases when the discharge decreases, thereby leading to an average "ageing" of water [19]. Alteration of natural hydrological conditions includes reducing the strength and frequency of flooding and of meander migration, abnormally extending the periods of hydrological stability, and lowering the incidence of post-disturbance succession [36], and the opportunities for colonist species to re-establish from elsewhere. Water scarcity may therefore lead to the transformation of the habitat character of rivers in the direction from lotic (moving waters) to lentic (standing waters). This process is known as *lentification* [37], and may promote higher water temperature, with greater evaporative losses, that may be particularly relevant in arid and semi-arid areas [38]. Overall, this produces changes in the biogeochemical processes, as well as in the biological community inhabiting the river.

3.1 Changes in Biogeochemical Processes

The first change produced by decreased flow is the enhanced in-stream retention of particulate organic matter. In forested Mediterranean streams, for example, the falling leaves accumulate on the streambed for 1–3 months until first flooding. During the first flush events, a mass downstream transport of dissolved and particulate material (mainly organic) occurs. In the rehydration of a temporary stream after summer leaf fall deposition, nitrate did not remarkably increase, but the DOC concentration increased two to fourfold [39]. The influence of the pulse of dissolved organic matter extended to baseflow conditions during late summer and autumn. In these pulses after the restart of the flow, the proportion of readily available DOC (BDOC) can be very high (mostly attributed to carbohydrates and peptides; [40]).

Table 2 Summary of effects caused by water scarcity

Water quality descriptor	Effect of low flow	Effect on biota	Affected process
Temperature	Lower oxygen content Higher metabolic rates Combined effects with toxicants and nutrients	Invertebrates Fish All groups All groups	Decrease in oxygen availability Higher primary production Higher respiration rates General effects on structure and metabolism
Conductivity	Enhanced water salinity	All groups	Physiological regulation Changes in community composition
Organic matter	Accumulation of organic matter	Bacteria Primary producers	Slowed down decomposition? High oxygen consumption High mineralization
Sediments	Siltation	Primary producers Invertebrates Fish	Reduced production Changes in community composition Difficulties in gas diffusion
Nutrient	Higher concentration; eutrophication	Primary producers Potential bottom up-effects	Higher gross primary production Lower efficiency on materials processing
Pollutants	Increase of pollutant concentration and enhanced effects on the biota	All groups Complex food web effects	Diversity decrease? Effects on metabolism Effects on material processing

This high availability of materials can also be related to the high enzymatic activities in the water as well as relevant organic carbon uptake by the benthic microorganisms [40, 41].

A subsequent consequence of altered hydrological conditions is the export of solutes, as well as changes of the biogeochemical processes (Table 2) that derive from drought and rewetting. It has been observed that antecedent droughts in wetlands contribute to the oxidation of sulphides stored in the sediment to sulphates, which are mobilized after rewetting [42]. Pinay et al. [43] indicated that the surface area of the water-substratum interface (water-sediment or water-soil interface) is positively correlated with nitrogen retention and uptake rates. This applies both for the sediments in the stream channel as well as for the soils in the floodplain and riparian zones. The stream sediments incorporate the hyporheos, i.e. the zone immediately beneath the stream surface; Fig. 3). This compartment is highly reactive for nutrient cycling [44] because of the hydrated, porous medium that provides exchange and reaction surfaces for the microbes involved in C, N and P cycling. The active riparian area is larger during high flows, but it contracts during the drying periods [45].

The oxic and anoxic phases occurring in the riparian soil and in the hyporheos are therefore related to the variations of flow [43]. Regarding the nitrogen cycle, ammonification can occur during aerobic and anaerobic conditions, while nitrification requires aerobic conditions, and denitrification is favoured by alternating aerobic and anaerobic cycles. Water table fluctuations associated with these processes do not occur during permanently dry conditions; hence the biogeochemical cycle of nitrogen can be expected to be altered with respect to steady flow conditions. Nitrogen processing is limited during the transport from upland to riparian zones in arid areas [46]. Nitrogen processing shifts from the soil (denitrification) to the riparian vegetation (plant uptake) [47], but even this shift can be interrupted under water stress.

Aerobic penetration increases in previously dry sediments, because of better oxygen diffusion compared to saturated conditions; hence, when sediments are exposed to the air, anaerobic zones become aerobic [48]. The oxidation and desiccation affect the microbial assemblages in previously reduced sediments. Drying of sediments will result in an increased sediment affinity for P with reduced availability to biota. The return of the water to a previous dry stream bed is a “hot biogeochemical moment” [49]. Biogeochemical reactions and biological processes; (see Sect. 3.2) restart or accelerate after long quiescent periods. Re-wetted sediments liberate phosphorus and nitrogen, as a consequence of dying-induced microbial cell lysis, that again may enhance in-stream primary productivity. However, opportunistic organisms may be favoured by repeated drying–wetting cycles, which again affect nutrient cycling. In particular, the combined nitrification–denitrification may be severely limited by repeated wetting–drying [48].

Water scarcity increases the concentration of nutrients and pollutants which therefore exert a stronger effect on organisms [50]. Shallow water columns, and higher nutrient concentrations, together with higher temperatures and light availability (these conditions occurring in disturbed watercourses), trigger eutrophic conditions in rivers and coastal zones. An example of these complex relationships was seen in the Oria River (N Spain), where nutrient rich sites with poor riparian cover exhibited high water temperature, high algal biomass, and large dissolved oxygen oscillations [51]. Dissolved oxygen concentrations varied during a diel cycle from 0 to 13 mg O_2 L^{-1}, compared to 8–9 mg O_2 L^{-1} in an adjacent forested site with lower nutrient concentration. The impacted site had a fish community, dominated by cyprinids, more tolerant to hypoxia, while in the forested section salmonids occurred. Occasional fish killings occurred in the eutrophic site because of oxygen fluctuations.

Higher salt concentrations (enhanced water conductivity) from urban and industrial waste waters result in lower dilution. Salinity limits the distribution of sensitive plant and animal taxa, and triggers the abundance of others. The presence of the shrub *Tamarix canariensis* has increased in the saline soils of the low flow affected Tablas de Daimiel (Spain), while the once dominant *Populus alba* retreated.

3.2 Changes in Biological Community Structure

Abnormal hydrological stability homogenizes river habitats, and this obviously affects the performance and distribution of organisms. In some semi-arid and arid-zone streams and rivers, water extraction for human activities may lead to complete and extended dewatering during low flow years, dramatically impairing the freshwater biota [38]. However, many organisms inhabiting naturally temporary rivers have adaptive mechanisms that allow them to survive droughts and to quickly recover after water returns [52]. Microorganisms exhibit physiological adjustments during the gradual drying from permanent to temporal waters. Algal taxa, for example, synthesize energy-storage or osmotically active molecules [53]. Other algae are able to produce resistant structures such as akinetes, cysts, or zygotes, which can reactivate and grow upon rewetting [54]. The physiological plasticity of many of these taxa is remarkable. For example, desiccated cyanobacterial mats, collected from an intermittent Mediterranean stream, started to photosynthesize in the laboratory within 2 h after rewetting [55]. The extracellular enzymes associated to the cell wall allow an immediate use of dissolved organic matter [40]. The excretion of extracellular muccopolysaccharides by algae and cyanobacteria facilitates cellular water retention and therefore results in quicker rehydration. However, human-caused rapid or unpredicted drying does not provide sufficient time for the production of desiccation-resistant structures or physiological adjustments [56]. The ability to recover after drought also depends on the existence of reservoirs of propagules, stored in areas that did not dry out, or in the sediments, which facilitates recolonization processes [57].

When rivers begin to dry out, and consequently to fragment, the biota concentrates in the remaining pools leading to very high densities of invertebrates and fish [58]. Life in these pools is harsh because the accumulation of detritus increases nutrient concentrations that lead, together with the concurrent reduction of reaeration from the atmosphere, to decreased oxygen concentration. Leachates from decomposing leaves, which can be toxic to some organisms, accumulate in these ponds [59]. Fragmentation affects the entire trophic web. Algae growing on riffles disappear during the drying up process; grazers therefore decrease in numbers, while other feeding groups may benefit. Filter density may also be reduced because of the decrease of transported material [60], while collector-gatherers may increase in numbers in these pools. Predation pressure increases in pools. Acuña et al. [61] showed that the drying up of a Mediterranean stream caused an increase in macroinvertebrate density in isolated pools soon after flow ceased. Afterwards, when the pools shrank further, the invertebrate density rapidly decreased. In this Mediterranean stream, there was a difference in the macroinvertebrate community at the end of the summer dry phase (when flow resumed) compared to that present before drying began. High availability of food (detritus) for invertebrates during flow reduction in pools led to a considerable increase in invertebrate density and biomass. The taxa that increased significantly as flow decreased had low dissolved oxygen requirements (e.g. Lumbriculidae, Chironomideae), or were adults that

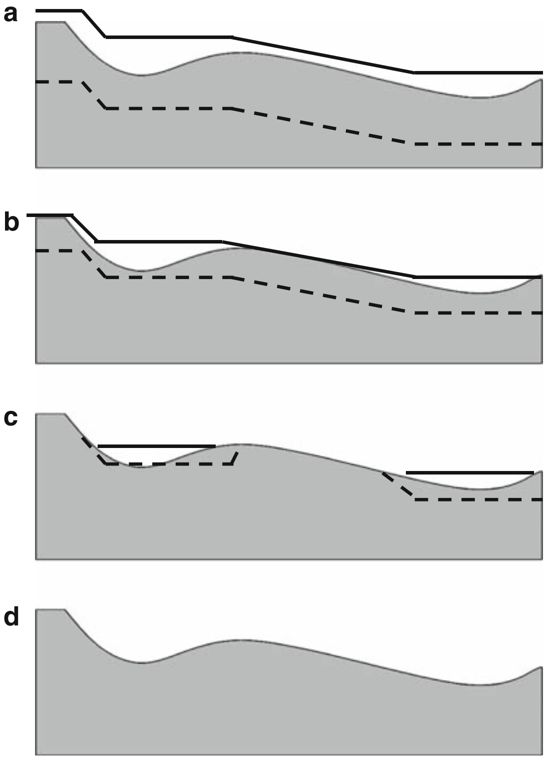

Fig. 5 Decrease of surface water and the effects on the longitudinal distribution of riverine habitats. During high flow (**a**) surface habitats, i.e. riffle (fast flowing sections) and pools (slow flowing sections), are available. Drying first affects the surface waters (**b**), causing fragmentation and the formation of remaining pools (**c**). During this phase the hyporheic compartment is also restricted to the pool habitats. Finally, both the superficial and hyporheic compartments dry completely up, and potential refuge for the aquatic biota disappear

breathe atmospheric oxygen directly (e.g. beetles). At the same time, taxa with high DO requirements (e.g. snails) were absent during this phase.

Droughts and floods have similar consequences on biota survival. Although floods may cause a complete resetting of the physical habitat, as well as the downstream drift of many individuals, the effects may be less persistent than those produced by droughts. As drying proceeds (Fig. 5), shallow surface habitats such as riffles disappear first, and a series of fragmented pools remain, together with a low water flow in the hyporheos [52]. This is called *superficial drought*. During a *subsurface drought* even the hyporheic zone can dry out [62], affecting the potential refuge of many organisms (see below). In an even more advanced step, *deep drought* implies that the phreatic layer can descend, which may cause early leaf abscission of riparian woody plants [63]. This extended decrease of the water table in the riparian zone may even impair riparian vegetation, trees being replaced by shrubs and later by herbs, with lower leaf litter input and allowing higher light penetration. In some areas of the Mediterranean where the phreatic level has decreased, riparian vegetation has disappeared, and with it has gone the function the riparian exerts as a nutrient buffer, as the refuge of species and a biological corridor [64]. This may have definite effects on moisture retention in the soil, as vegetation controls permeability near the surface. The riparian strips of headwaters and the main river sections play an essential role in the regulation of greenhouse gases (CO_2, N_2O) [65]. Riparian areas may protect against flood events and help in establishing biological corridors between polluted and unpolluted sections. In many areas of the Rivers Ter and Llobregat (NE Spain) the riparian area has been seriously damaged by overexploitation, groundwater extraction and subsequent phreatic decrease.

The fauna of seasonally intermittent streams have acquired, through evolution, a range of adaptations, such as specific life-history strategies, physiological mechanisms, and specific behaviours to search for refugia [66]. There are two major classes of refugium use strategies [67]. The most common type is refugium use within a given generation. It consists mostly of actively changing the habitat when the drought proceeds. Invertebrates may shelter below cobbles, among debris or macrophytes [66], and the most mobile seek refuge in the hyporheic (subsurface) sediment, as well as in the remaining pools [52]. This variability emphasizes the value of a well-preserved river habitat, which offers a greater variety of shelter [62] than physically disturbed reaches. A more specialized type of refugium-seeking occurs between generations, as happens when there are complex life cycles or changes in habitat use. This can be seen in some caddisflies, which lay terrestrial eggs [68], thus protecting their offspring from floods. Similarly, during droughts, some fish retreat to safe places like backwaters, or to permanent tributaries, and recolonize the stream with juveniles after the drought [56, 69].

However, other taxa do not show these adaptations, and may suffer from changing conditions. This may be seen in groups that are intolerant to desiccation or are relatively immobile (e.g. Unionid mussels; [70]). More difficulties in dispersal are faced by many groups of organisms [71], as they cannot circulate along intermittent watercourses. Water abstraction has been identified as one of the most detrimental factors for fish assemblages in Mediterranean watercourses. Fish can respond by changing their community composition, as well as their abundance, and condition [72]. The least exigent species survive these unstable conditions [73]. Droughts reduce the survival and reproduction rate of fish, and promote emigration towards other areas [58]. Some fish populations can even disappear when the frequency of drought is higher than in natural conditions.

Other consequences of decreasing water flow on biota are related to indirect effects on physical and chemical parameters (Table 2). Temperature may increase as a result of slow-moving, thinner water layers. Warmer waters and other stresses increase the possibility of fungal, viral and bacterial infections on fish. Certain invasive species can also take advantage of higher average temperatures and/or stabilized hydrological conditions. As an example, in the lower River Ebro (N Spain), reduced flow has favoured the proliferation of the mussel *Dreissena polymorpha*, the trematode *Phyllodistomum folium* that infects zebra mussels, and the Asian bivalve, *Corbicula fluminea*. Higher temperature reduces the solubility of gases in water, as in the case of oxygen. Lower oxygen may limit fish and invertebrate distribution. Temperature change and water flow changes can promote changes in the regional distribution of some taxa. Several insects [74] are sensitive to differences of only 3°C of mean summer temperature. Key life-history parameters of many species, such as egg dormancy and life cycle plasticity, may be affected by these temperature changes. Hence, increasing temperatures may support eurythermic species and generalists, resulting in less specialized communities. It is also true that the impacts of climate change might be reduced by catchment and floodplain land use; at least regionally, riparian forests may contribute to buffer future water temperature increases.

The extension of the dry period is also a critical factor. Dry periods longer than the generation times of the biota reduce the efficacy of potential adaptations. Larned et al. [75] observed that the total invertebrate richness decreased linearly while the invertebrate density decreased exponentially with increasing duration of the dry period. This is most possibly caused by dying or dispersal of the invertebrates, while few pre-adapted species remain. Drought may cause long-term effects. Although species are able to persist during droughts during their early stages, they may not recruit successfully during the next year. This lag effect in response to a drought [62] is most obviously for long-living biota (invertebrate and fish). Analogously, repeated episodes of drought can have cumulative effects on fish populations, which are not obvious at the reach scale but detectable at the watershed scale [76]. The amount and quality of fish refugia in a given summer would be dependent on the rain falling in the preceding years. Measurable changes in abundance are only apparent after several dry years with unusually high mortality or reduced recruitment [76].

4 Relevance of Water Interruption on Aquatic–Terrestrial Linkages

Rivers and their terrestrial realms are tightly linked by reciprocal flows of matter, energy and organisms [77]. The flow of material and energy is generally from the more productive to the less productive habitat. For example, a drought-induced decrease in in-stream productivity may reduce the energy flow from emerging aquatic insects into the adjacent riparian ecosystem, thereby affecting the composition and density of riparian predators. On the other hand, water stress may cause early leaf litter abscission, alter leaf litter quality (e.g. through photo degradation), and may lead to an accumulation of coarse particulate organic matter (CPOM; e.g. leaves) at the dry stream surface [78, 101]. Results from decomposition experiments along the Tagliamento River demonstrated that alterations of the inundation regime directly influenced decomposition processes [79]. After 30 days of exposure, the mean percentage of the remaining leaf litter (as AFDM) ranged between 51% (permanent wet) and 88% (permanent dry). Decomposition was significantly affected by the duration of inundation whereas frequency played a subordinate role in controlling leaf breakdown. Unexpectedly, leaf-shredding macro invertebrates played a lesser role for leaf breakdown except in the permanent wet treatment.

More generally, changing flow alters the relative proportion of input, storage, transfer, and transformation processes for organic matter and nutrients. Hence, the relative extent and the dynamics of the temporary channels within a catchment may control the capacity of a river network to produce, transform, and store nutrients and organic matter.

Dry river beds are considered temporal ecotones that shift between an aquatic and a terrestrial phase. While we are well aware of the aquatic life during the wet phase, there is a general lack of information on biodiversity patterns and ecosystem processes during the dry period and how wet and dry phases are linked to each other. We may expect that dry channels provide important habitats for terrestrial organisms [80]. However, they remain open if dry channels contain a unique fauna or just a subset of upstream communities. Further, do rivers that naturally fall dry contain a terrestrial fauna that differs from artificially dry channels? Finally, we may expect a strong functional linkage between aquatic and terrestrial organisms. Terrestrial organisms are expected to quickly react to available resources and exploit stranded aquatic organisms [81]. On the other hand, allochthonous detritus, despite a relatively high C:N ratio, provides a basal resource for intermittent stream food webs [82]. In Cooper Creek, Central Australia, fishes appeared to feed on potentially lower value resources such as detritus during the dry period, but were able to exploit the booming aquatic production during episodic flooding [83]. These boom and bust cycles are characteristic of arid and semi-arid river systems, whereas busts for the aquatic assemblages may be booms for the terrestrial assemblages. However, water management plans in many Mediterranean and dryland river systems may alter this sensitive balance between boom and bust periods, leading to the observed decline in ecosystem health.

5 Functional Alterations in River Ecosystems Associated with Water Scarcity and Temporality

Ecosystem functioning includes a variety of processes that involve the transference of matter and energy throughout the different compartments. Among these processes, the most relevant are nutrient turnover, decomposition and respiration of decaying organic matter, primary production, secondary production and respiration, and the resistance and resilience after disturbance. These processes are translated into visible entities for human societies [37], understood as goods and services. Among those, there is flood protection, improved water quality, food and timber production, maintenance of biodiversity, etc [84]. As structure and function within an ecosystem are tightly linked, it might be expected that a shift in the former implies a change in the latter.

River functioning (globally expressed as metabolism) does not often show unidirectional responses to stress, and therefore makes difficult the prediction of changes. Gross Primary Production (GPP) may be first enhanced because the decrease of water flow may result in shallower water depths and lead to more underwater light

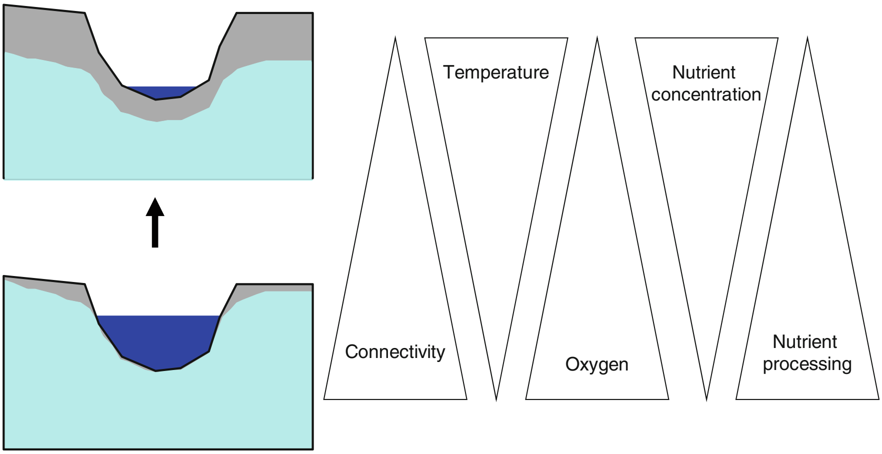

Fig. 6 Processes occurring along with drought in a river channel. Connectivity is lost, while water temperature and nutrient concentration increase in the remaining water. The efficiency of nutrient processing decreases, as well as it does the dissolved oxygen in the water and in the sediments

penetrating to the bottom. Altogether, higher nutrient concentrations and hydrological alteration may favour a shift towards autotrophy in aquatic ecosystems [85]. However there is a threshold of increase, as complete flow reduction may cause GPP to sharply decrease and finally stop during the drying phase [61].

The efficiency in many processes is expected to decrease, leading to undesired consequences (Fig. 6). The high nutrient content as well as the hydrological stability in the Llobregat River [86] favoured the massive growth of cyanobacteria during winter and early spring. These growths were associated with odours in the river caused by geosmin production. Respiration is also affected by lower flow and drought. Pinna and Basset [87] observed that the highest effects of summer drought on organic matter decomposition occurred in the headwater streams. The lesser effect detected in larger sections was mostly because the drought conditions were less intense there. Larned et al. [75] observed that the respiration rates in sediments declined rapidly with the onset of the dry period. Lower microbial biomass and sediment organic matter are found in ephemeral river sediments; there is therefore lower respiration than in wetter conditions. Claret and Boulton [88] suggested that there is threshold moisture for the sediment microbial activities, below which it might sharply decrease. In a forested Mediterranean stream, Acuña et al. [89] determined that the high accumulation of BOM during low flow caused extremely high ecosystem respiration (ER), though this depended on the intensity of the drought period in the stream which varied interannually.

Water fluctuations in Mediterranean rivers seriously affect fish production and droughts put important selective forces on fish communities [73] by reducing population density and species richness [58]. Fish also suffer from chemical and organic pollution affecting their physiological abilities [90].

Drought can increase the effect of other stressors such as pollutants, UV-impact, and thermal stress [27]. In the Llobregat River, for example, a wide range of human pharmaceuticals of high biological activity are present in low but ecologically relevant concentrations [91]. Their occurrence often coincides with low flow conditions and intensive water use, which increases their environmental risk. Multivariate analyses revealed a potential causal association between the concentration of some anti-inflammatories and β-blockers and the abundance and biomass of several benthic invertebrates (*Chironomus spp.* and *Tubifex tubifex*). Determining the relevance of the altered hydrological conditions on the multistress being suffered by organisms and ecosystems in polluted areas is an ultimate challenge.

Flooding is the predominant variable along large alluvial rivers, and as such triggers multiple functional processes. Floods not only increase the aquatic surface area but also reshape aquatic and terrestrial habitats, maintain its complexity, facilitate the dispersal of aquatic and terrestrial organisms, and provide key resources, thereby stimulating productivity and biodiversity. Recently, Bertoldi et al. [92] analysed oblique air-photos, sequentially taken at different water levels in a floodplain segment along the Tagliamento River (NE Italy). On the basis of these photos, various hydrological thresholds were identified, with lower water level thresholds nested within higher water levels. For example, an elimination of annual flood events may lead to an increase in vegetated areas, therefore altering the flow-inundation regime of the entire river-floodplain complex.

The predictions of the area-richness relationship indicate that a reduction in inundation area and duration will lead to a decrease in biodiversity, as well as in productivity [93–95]. A trait-based assessment might help to predict the species that will disappear as a consequence of flow alteration. We may speculate that the biota in Mediterranean rivers, adapted to naturally high seasonal and interannual flow variability, are less sensitive to flow reduction than biota in more temperate rivers. Evanno et al. [96] studied the effect of a severe drought on the genetics and species diversity of gastropods along the Ain River (France). They found that a natural disturbance leads to a decline in local (α) diversity and to an increase in regional (β) diversity, indicating that disturbances can lead to similar changes in genetics and community structure through the combined effects of selective and neutral processes. Thomaz et al. [97] observed that flooding increased species similarity among floodplain habitats.

There is a great need to identify and to quantify the multiple effects of duration, intensity, time, and frequency of surface flowing and drying, single and in concert, on both biodiversity and ecosystem processes. For example, the effect of inundation duration, following a rainfall pulse, controls process diversity in dry floodplains. Very short pulses, as typical for low order stream segments (or human altered ecosystems) release nutrients, which again increases in-stream productivity in adjacent permanent water bodies. Hence, the relative extent and the dynamics of the temporary channel network, as well as its spatial distribution within a catchment, may therefore influence the capacity of an entire river network to produce, transform, and store nutrients and organic matter as well as maintain its biodiversity.

6 Conclusions

Disturbances that increase water scarcity 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 the disturbance, the greater is the resemblance. 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 toautotrophy, even in relatively pristine rivers. Enforced hydrological stability or increased nutrient loading, among many other disturbances, may cause pronounced changes in system metabolism.

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 the estimation of the ecosystem services that they can sustain difficult. This will be especially relevant in arid and semi-arid areas and in those systems where water use is very intense. Decreasing flow leads to an increased exposure to UV, higher water temperature variation, further concentrations of nutrients and pollutants, and spreading of nonnative species, with cascading effects on aquatic and terrestrial biodiversity and ecosystem functioning. Further, we may anticipate a future global increase in pulsed events due to climate and land use changes; at the same time, major attempts are underway to reduce pulses by river regulation and impounding [27, 98]. Hence, a major challenge is to separate trend from event effects (e.g. gradual change in flow and temperature compared to pulsed events), and the timing and sequence of individual pulsed stressors (e.g. flood pulses, heat waves, disease outbreaks) that may shape ecosystem processes.

Acknowledgements This review has been funded through projects of the Spanish Ministry of Science and Technology (CGL2007-65549/BOS), the VIECO programme (009/RN08/011) of the Spanish Ministry of the Environment and Rural and Marine Affairs, the Banco Bilbao Vizcaya Argentaria Foundation project GLOBRIO, and by the EC project MODELKEY (Contract 511237-2).

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