

Response of benthic macroinvertebrates to gradients in hydrological connectivity: a comparison of temperate, subtropical, Mediterranean and semiarid river floodplains

BELINDA GALLARDO*, SYLVAIN DOLÉDEC[†], AMAEL PAILLEX^{‡,§}, DAVID B. ARSCOTT[¶], FRAN SHELDON^{**}, FLORENCIA ZILLI^{††}, SYLVIE MÉRIGOUX[†], EMMANUEL CASTELLA[‡] AND FRANCISCO A. COMÍN^{*}

^{*}Applied and Restoration Ecology Group, Pyrenean Institute of Ecology (IPE-CSIC), Zaragoza, Spain

[†]CNRS, UMR 5023, LEHNA, Biodiversité des Ecosystèmes Lotiques, Université Lyon 1, Villeurbanne, France

[‡]Laboratory of Ecology and Aquatic Biology, University of Geneva, Carouge, Switzerland

[§]Swiss Federal Institute of Aquatic Science and Technology, Dübendorf, Switzerland

[¶]Stroud Water Research Center, Avondale, PA, U.S.A.

^{**}Australian Rivers Institute, Griffith University, Nathan, Qld Australia

^{††}Instituto Nacional de Limnología (UNL-CONICET), Santa Fe, Argentina

SUMMARY

1. Despite a general recognition that benthic macroinvertebrates respond to changes in hydrological connectivity within floodplain ecosystems, no consensus about patterns in community structure and ecosystem processes across large scales and different climates has yet been established. Such knowledge is necessary since anthropogenic activities continue to alter the natural hydrogeomorphology of large floodplains, with most consequences for aquatic communities remaining unknown.

2. Using information from six large rivers located in four different climate regions (humid subtropical, maritime temperate, Mediterranean and dry semi-arid), we compared benthic macroinvertebrate responses along lateral gradients of hydrological connectivity. We tested hypotheses related to differences among climate regions and to similar hydrological constraints within any one climate. The large geographical scale covered by this study provides the first comprehensive comparison of aquatic community patterns across hydrological gradients under different climatic settings.

3. Multivariate ordinations demonstrated a higher overlap of trait community composition (50% variance explained by the first two axes) than taxonomic composition (15%) among floodplains, displaying high interclimate trait stability. The taxonomy-based ordination separated the subtropical floodplain, with an average 86% of non-insect taxa, from the insect-dominated temperate, Mediterranean and semi-arid floodplains (with >50% insect abundance). In the trait-based ordination, large body size (60% of organisms >4 cm) and long lifespan duration (80% of organisms) discriminated the subtropical from the other five studied floodplains.

4. Across a gradient of lateral connectivity, linear mixed effect (LME) models supported seven of 15 hypotheses, which suggests remarkably consistent macroinvertebrate patterns in floodplains regardless of the climate regime. Taxon and trait richness were positively related and peaked at sites of intermediate hydrological connectivity. Our predictions about the feeding guilds of macroinvertebrates (e.g. that shredders and scrapers would be more abundant in connected channels, and predators and deposit feeders at isolated sites) were more strongly supported by the data than those about life history (e.g. plurivoltinism and short lifespan would be better represented in connected channels). This difference was related to the influence of extended periods of hydrological disconnection as disturbance in addition to flooding.

5. Trait stability across hydrological connectivity provides a meaningful ecological context for the comparison of the macroinvertebrate benthos among climatic zones, where taxonomic composition differs strongly. In addition, trait similarities and dissimilarities found in this study suggest that large-scale biogeographical filters do operate on communities, resulting in different trait combinations in temperate and Mediterranean floodplains when compared to semi-arid and subtropical environments. The extent to which global macroecological factors (i.e. climate, dispersal history) and local biotic and abiotic factors (i.e. drought frequency, habitat structure, water chemistry) contribute to this difference requires further investigation.

Keywords: feeding habits, isolation, intermediate disturbance hypothesis, life history, River Habitat Templet

Introduction

Connectivity and isolation are fundamental concepts in ecology influencing the distribution of organisms within an ecosystem (e.g. Moilanen & Nieminen, 2002). Connectivity allows organisms to move from one area to another, increasing the resilience of ecosystems to disturbances, and supports key ecosystem processes, such as nutrient cycling and water retention (e.g. Moilanen & Nieminen, 2002). River floodplains comprise a complex mosaic of interconnected aquatic and terrestrial patches arranged along a gradient of lateral hydrological connectivity (Ward & Stanford, 1995). This gradient of connectivity extends from waterbodies with a high flood frequency close to the main channel (i.e. high hydrological connectivity), to those connected to the main channel only at high flows (i.e. intermediate hydrological connectivity), and isolated waterbodies that are only inundated under the most extreme floods (i.e. low hydrological connectivity) (e.g. Amoros & Roux, 1988). Since the first definition of the flood pulse concept in tropical environments (Junk, Bayley & Sparks, 1989), and its extension to temperate areas (Tockner, Malard & Ward, 2000), there has been wide recognition that the aquatic communities of floodplains respond to changes in hydrological connectivity in a predictable way (see the reviews of Petts & Amoros, 1993; Junk & Wantzen, 2004). Nevertheless, to our knowledge, no generalisations about benthic macroinvertebrate structure (including the representation of species traits) across large scales and different climates have been yet proposed. The lack of a general understanding of how the macroinvertebrate benthos responds across the hydrological gradient in floodplains may be partly due to a lack of comparable field observations from a range of rivers covering different climatic and hydrological conditions (such as in Minshall *et al.*, 1983).

In an attempt to provide a framework for comparing ecological processes and responses between different

river systems, a number of authors have undertaken river classifications from different regions (e.g. Poff & Ward, 1989; Kennard *et al.*, 2010). Broadly, these classifications have identified groups of systems that range from perennial rivers and streams, characterised by consistent base flow and predictable flood patterns (often from temperate regions) to intermittent rivers and streams with variable periods of no flow but seasonal (and therefore relatively predictable) floods. This latter case describes many Mediterranean and subtropical systems (e.g. Bonada, Dolédec & Statzner, 2007; Depetris, 2007). In contrast, unpredictable floods occur in many semi-arid systems from dry climates (e.g. Kennard *et al.*, 2010), with such rivers previously described as 'dryland' rivers (Walker, Sheldon & Puckridge, 1995). Such contrasts in climate and hydrology should result in variable spatiotemporal floodplain conditions yielding differences in the taxonomic structure of aquatic communities (e.g. Poff & Ward, 1990; Puckridge *et al.*, 1998). Because of biogeographical changes across broad regional scales (i.e. taxonomic composition in similar habitats differs), it can be difficult to get a clear picture of similarities or general patterns if relying on taxonomic comparisons alone. In contrast, the representation of species traits may reveal general patterns related to hydrological connectivity, since traits aggregate biological information shared among taxonomically different taxa (Heino, Schmera & Erős, 2013). Therefore, while large differences in taxonomic composition are to be expected in rivers from distinct climatic or biogeographical regions, there should be similarities in trait responses (e.g. Charvet *et al.*, 2000).

Although many authors have reported a significant response of benthic macroinvertebrates to a gradient of lateral connectivity, most of the available literature consists of local studies, focussed on temperate European rivers such as the Rhône (e.g. Castella *et al.*, 1984; Amoros & Bornette, 2002; Paillex, Castella & Carron,

2007), the Danube (e.g. Tockner *et al.*, 1999b; Ward, Tockner & Schiemer, 1999; Reckendorfer *et al.*, 2006) and the Rhine (e.g. Ward *et al.*, 1999). Fewer studies exist for Mediterranean (but see Bonada *et al.*, 2006; Gallardo *et al.*, 2008), semi-arid (but see Sheldon, Boulton & Puckridge, 2002; Sheldon & Thoms, 2006) or subtropical rivers (but see Marchese & Ezcurra De Drago, 1992; Arrington & Winemiller, 2006; Zilli, Montalto & Marchese, 2008). Although these studies suggest macroinvertebrate patterns across hydrological gradients are complex and depend on many interrelated factors, they allow us to formulate a number of *a priori* expectations, summarised in Table 1. For instance, the richness of Ephemeroptera, Plecoptera and Trichoptera (EPT) usually peaks in habitats with high hydrological connectivity, because of the requirements for a high concentration of dissolved oxygen and the limited thermal tolerance of many species (Usseglio-Polatera & Tachet, 1994). In contrast, richness of Coleoptera, Odonata and Heteroptera (COH) usually peaks at sites disconnected from the

main channel, characterised by low flooding frequency and high organic matter content (e.g. Arscott, Tockner & Ward, 2005; Bonada *et al.*, 2006; Skern, Zweimueller & Schiemer, 2010). Other groups of organisms are likely to peak at various levels of hydrological connectivity, depending on their habitat requirements. Furthermore, Tockner *et al.* (1999b), and later Arscott *et al.* (2005), demonstrated that different taxonomic groups show overlapping richness optima across a gradient of lateral connectivity in the Danube and Tagliamento rivers, respectively, with a maximum overall richness at intermediate connectivity, apparently supporting the intermediate disturbance hypothesis (Connell, 1978).

Because of the severe abiotic conditions, we might expect low trait richness and diversity under both high and low hydrological connectivity conditions, which are disturbed by frequent floods and anoxia, respectively. In comparison, the relative isolation of intermediately connected channels may foster biotic interactions and thus trait richness (Statzner, Dolédec & Hugueny, 2004).

Table 1 Expected response of macroinvertebrate metrics (taxonomic and trait) among floodplains in different climate regions (A) and within floodplains along a gradient of lateral hydrological connectivity (B)

Scale	Metrics	Type	Expectation	Reference
(A)	Taxonomic composition	Taxon	Differences among climatic regions	Poff and Ward (1990)
	Trait composition	Trait	Differences less pronounced than taxonomic composition	Charvet <i>et al.</i> (2000) Bonada <i>et al.</i> (2006)
(B)	EPT richness	Taxon	Peak in well-oxygenated habitats with a high hydrological connectivity because of the high dissolved oxygen requirements and lower thermal tolerance of associated species	Usseglio-Polatera and Tachet (1994)
	COH richness	Taxon	Peak at isolated sites because of life-history habits (large size, aerial respiration, predation) and habitat association (shoreline vegetation)	Bonada <i>et al.</i> (2006) Skern <i>et al.</i> (2010)
	Taxon richness and diversity	Taxon	Peak at intermediate hydrological connectivity where generalist and specialist species coexist, consistent with the intermediate disturbance hypothesis	Connell (1978) Tockner <i>et al.</i> (2000)
	Trait richness and diversity	Trait	Peak in intermediate and isolated sites where hydrological stability may foster biotic interaction	Statzner <i>et al.</i> (2004)
	Body size*	Trait	Small size (<0.5 cm) allows organisms to resist near-bed flow stress in connected sites	Townsend and Hildrew (1994) Statzner and Bêche (2010)
	Number of cycles/year*	Trait	Plurivoltinism (>1 cycle per year) allows resilience to frequent flood disturbance in highly connected sites	Townsend and Hildrew (1994) Sheldon <i>et al.</i> (2010)
	Life cycle duration*	Trait	Closely related to plurivoltinism, short lifespan confers resilience to frequent flood disturbance in highly connected sites	Townsend and Hildrew (1994)
	Resistance forms	Trait	Resistance forms such as cocoons, cells against desiccation or diapause allow resistance to desiccation in isolated sites	Townsend and Hildrew (1994)
	Feeding habits	Trait	Filter feeders, scrapers and shredders are adapted to exploit efficiently limited food resources in highly connected sites, including coarse particulate matter, attached algae and suspended particles Intermediate to isolated sites may favour large specialist predators and deposit feeders feeding on organic matter accumulations	Merritt, Benbow and Hudson (2002) Gallardo <i>et al.</i> (2009a) Statzner and Bêche (2010)

EPT, Ephemeroptera, Plecoptera and Trichoptera; COH, Coleoptera, Odonata and Heteroptera.

*Patterns in semi-arid rivers may be the opposite because of abiotic constraints related to prolonged periods of extended hydrological disconnection, that is, higher proportion of organisms with small body size, plurivoltinism and short lifespan under low hydrological connectivity.

According to the River Habitat Templet (RHT, Townsend & Hildrew, 1994), we should expect a higher proportion of small-bodied individuals, associated with plurivoltinism and short lifespan, in frequently disturbed habitats, as in the main river channel subject to frequent flooding. However, a highly variable flow regime and prolonged periods of hydrological fragmentation in intermittent rivers may reverse this pattern, with small short-lived, plurivoltine organisms dominating isolated floodplain waterbodies that eventually dry up (Sheldon *et al.*, 2010). In addition, gradual changes in the representation of feeding groups along a gradient of lateral connectivity can be anticipated, because of differences in the availability of various food sources. In particular, many shredders, scrapers and filter feeders have previously been shown to respond positively to high flow and may be better adapted to exploiting efficiently the limited food resources of habitats disturbed by frequent flooding, including coarse particulate matter, attached algae and suspended particles (Statzner & Bêche, 2010). Conversely, predators and deposit feeders responded positively to drought and reductions in discharge and therefore might be expected in disconnected habitats (Statzner & Bêche, 2010). Because different biological traits confer clear trade-offs (for instance, predators are generally large and univoltine, and small organisms are generally plurivoltine and short-lived), we should expect commonly associated traits to dominate under similar hydrological conditions.

Most of these predictions have been confirmed in temperate rivers, while significantly less information on the trait patterns of macroinvertebrates is available for other climatic regions, and studies comparing different regions are even rarer (but see Bonada *et al.*, 2007). These gaps in knowledge are important since anthropogenic activities continue to alter the natural hydrogeomorphology of large floodplains, with most of the consequences for aquatic communities still unknown (Wantzen *et al.*, 2008).

Using the available information from six large floodplain rivers, located in four different climate regions (humid subtropical, maritime temperate, Mediterranean and dry semi-arid), we compared patterns in benthic macroinvertebrates across hydrological connectivity gradients. We tested two sets of hypotheses: those associated with differences among climate regions and those testing a common response of macroinvertebrate communities to similar hydrological constraints (i.e. high, intermediate and low hydrological connectivity) within any one climate (see Table 1 for a summary of predictions). Ultimately, we aimed at a comprehensive comparison of aquatic community patterns across

hydrological gradients under different climate settings, thus increasing our understanding of river floodplain dynamics and interactions in a wide context.

Methods

Case study floodplains

We considered six different large rivers and their floodplains as representative of the humid subtropical (Paraná River, 'subtropical' hereafter), maritime temperate (Tagliamento and Rhône rivers, 'temperate'), Mediterranean (Ebro River) and dry semi-arid (Cooper Creek, Diamantina, Murray and Darling Rivers, 'semi-arid') climates (Fig. 1). The dominant climate of each system was determined according to the Köppen–Geiger climate classification and covered three major groups of climates: A- tropical, B-dry and C-mild temperate (http://en.wikipedia.org/wiki/Köppen_climate_classification; Peel, Finlayson & McMahon, 2007). The selection of river floodplains was based on the availability of comparable data with respect to the number and distribution of sampling sites (i.e. across floodplain connectivity gradients), sampling methodology and level of taxonomic resolution. While we are aware of the limited scope of the study, including one or two rivers per climatic region, we believe these six systems, arranged in a gradient from subtropical to semi-arid environments can provide useful insights into broader ecological patterns.

The humid subtropical Paraná River is characterised by high temperature (>15 °C) throughout the year and markedly seasonal rainfall, which drives the predictable river discharge: high during summer and low during winter and early spring (Depetris, 2007). The Paraná River has a 900-km-long floodplain, 30% of which is occupied by a large number of relatively shallow (<5 m depth) waterbodies of variable shape and size, permanent and ephemeral, directly or indirectly connected to the river channel (Drago, 1989). Only extraordinary flooding events related to the 'El Niño–Southern Oscillation' completely inundate floodplain habitats and connect waterbodies seldom affected by smaller events (Depetris *et al.*, 1996; Drago *et al.*, 2003).

Rivers from the maritime temperate climate are generally distinguished by a permanent discharge and relatively predictable floods, which reflect aseasonal rainfall, snow melt and low evapotranspiration with relatively infrequent droughts. Among these rivers, the Upper Rhône (from SW Switzerland to SE France) develops a great diversity of floodplain habitats caused by river

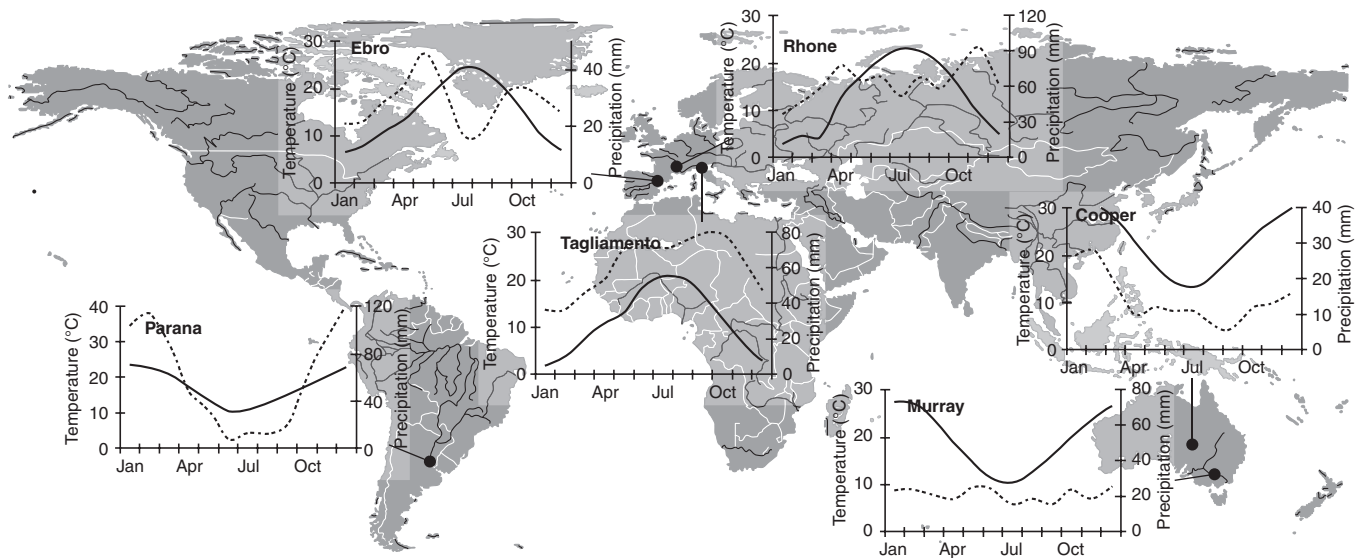


Fig. 1 Location of the six river floodplains included in this study: subtropical (Paraná), temperate (Tagliamento and Rhône), Mediterranean (Ebro) and semi-arid (Murray and Cooper). Ombrothermic diagrams (temperature: continuous line and rainfall: dashed line) are shown to illustrate the main climatic differences among regions.

dynamics, despite being affected by dams, water abstraction and lateral flood protection measures (Olivier *et al.*, 2009). Its hydrological regime is nivo-glacial, with annual floods normally occurring in spring, with snow melt and low flows in late autumn to winter (Olivier *et al.*, 2009). In contrast, the Tagliamento (NE Italy) is one of the last morphologically intact rivers draining the European Alps, characterised by a flashy pluvio-nival hydrological regime, with highest discharges during autumn and slightly lower magnitude floods occurring again in the spring, probably in relation to snow melt (Arscott *et al.*, 2005). Although it falls within the alpine to Mediterranean climate region (Peel *et al.*, 2007), Tockner *et al.* (2003) considered the Tagliamento River a reference ecosystem not only to the Alps but also to other large rivers from the temperate climate.

Mediterranean rivers are characterised by the seasonality and variability of rainfall and temperature, which results in highly variable discharges, torrential floods and severe droughts (Gasith & Resh, 1999; Bonada *et al.*, 2007). The Ebro River in NE Spain is an important river in the Mediterranean basin due to its very long main stem channel and its relatively high discharge. Flow regulation in the Ebro has resulted in partial fragmentation of the floodplain (Cabezas *et al.*, 2009a), although flooding still occurs between October and March, strongly structuring aquatic communities (Gallardo *et al.*, 2007, 2009b).

Dry semi-arid climates tend to be located in the tropics and subtropics, particularly around the fringes of subtropical deserts such as the Australian central

deserts region (Peel *et al.*, 2007). These climates have hot, sometimes extremely hot, summers and mild to warm winters that may result in desert landscape. Rivers draining such landscapes are typically characterised by the extreme variability in flow (Puckridge *et al.*, 1998) with considerable periods of time spent as isolated waterholes both within the main channel and across the floodplain (Bunn *et al.*, 2006). Combined with geomorphic complexity, this fragmentation provides a mosaic of hydrological connectivity both in space and time (Sheldon *et al.*, 2002), which makes them different from other rivers described above. The Cooper Creek and Diamantina River ('Cooper' hereafter as they were considered together) drain into the Lake Eyre Basin in central Australia. The combination of occasional monsoonal driven discharge, aridity and high evapotranspiration losses makes the Cooper one of the most variable rivers in the world (Puckridge *et al.*, 1998; Sheldon *et al.*, 2002). The Cooper is characterised by an extreme hydrological variability and a braided network of channels and tributaries, which are weakly affected by human activities (Knighton & Nanson, 1994; Bunn, Davies & Wining, 2003). In comparison, in the Murray–Darling system ('Murray' hereafter), water resource development has reduced the frequency and magnitude of small-to-medium flood events, thereby decreasing hydrological connectivity across the floodplain, whereas the presence of in-channel weirs has increased hydrological connectivity along the main channel waterholes (Walker & Thoms, 1993; Sheldon & Thoms, 2006).

According to the connectivity gradient described by Amoros and Roux (1988), the spatiotemporal stability of river systems increases from the main river channel, which is subjected to frequent floods, towards less frequently flooded waterbodies connected only rarely to the main channel. However, this general description is realised only if disconnected floodplain waterbodies maintain their water level and do not completely dry up. Because of the intermittent nature of semi-arid rivers, we might expect the patterns in macroinvertebrate life histories summarised in Table 1 to differ markedly from the other rivers investigated. In semi-arid landscapes, waterholes in the main river channel are actually the most hydrologically stable habitat, because of their persistence, whereas connection frequency and thus spatiotemporal stability of water level decrease in more isolated habitats. Consequently, life-history traits that confer the ability to cope with frequent flooding (e.g. small body size, plurivoltinism and short lifespan; Table 1) may also occur in organisms adapted to temporary habitats and, therefore, be more prominent in isolated waterholes of rivers in semi-arid landscapes.

Waterbodies sampled in the six river floodplains were divided into three homogeneous habitat types that could be easily arranged along a gradient of lateral connectivity to the river, ranging from high (i.e. the main river itself and secondary channels that are connected to it both up- and downstream), intermediate (i.e. waterbodies partially connected, usually at their downstream end), to low (i.e. isolated waterbodies with no up- or downstream connection) (Table 2). For all the studies considered, sampling was conducted in summer, when fragmentation of the system is highest, but the summer drought has not yet depleted aquatic communities. More information on sites selected in each river and methods used to sample macroinvertebrates is available in Table 2.

Macroinvertebrate sampling

Benthic macroinvertebrates were collected using a variety of methods (see Table 2, column *Benthic macroinvertebrates sampling*). Consequently, different sampling methodologies are likely to have yielded different estimates of macroinvertebrate abundance and richness (e.g. higher in Hess samples of the Tagliamento River, Kruskal–Wallis test, $P < 0.001$), although we could not separate the effect of sampling method and river. In this sense, methodological differences are likely to affect among floodplain analyses, for example clustering of rivers using the same method in ordination plots. All

taxonomic identifications were converted to the generic level, with a few exceptions such as the family level for the Chironomidae and order for the Oligochaeta (see Supporting Information, Table S1); these taxonomic groupings have been shown to be suitable for comparing the general structure of communities in terms of taxa and traits (Dolédéc, Statzner & Bournard, 1999; Gayraud *et al.*, 2003). As a result, a total of 228 taxa were included in subsequent analyses (Table S1). Total richness, Shannon diversity, and EPT (Ephemeroptera, Plecoptera and Trichoptera) and COH (Coleoptera, Odonata and Heteroptera) richness were calculated and compared among rivers (see *Data analysis* section).

A total of 11 benthic macroinvertebrate traits were extracted from Tachet *et al.* (2010) to calculate trait composition, richness and diversity (Table 3). These biological traits described different aspects of organismal biology including body size, reproductive technique, resistance forms and feeding habits. For 38 of 228 taxa not included in Tachet *et al.* (2010), scores were assigned based on average values derived from each taxonomic family, or the closest taxon (see Table S2 for uncoded taxa and families/taxa used as reference). This was the best option in the absence of individual trait information, although we acknowledge the subsequent loss of accuracy by this approximation, and the possibility of real scores being different from those used in this study. Traits were quantified using a 'fuzzy coding' technique (see Chevenet, Dolédéc & Chessel, 1994), a well-established method of coding that involves the assignment of an affinity score, from 0 to 3, of each taxon to each category for a given trait (see more about macroinvertebrate trait coding and analysis in Usseglio-Polatera *et al.*, 2000). This approach thus acknowledges trait variability, which often occurs among different life stages. We further described the trait composition of communities by multiplying the frequency of each category per trait by the relative log-transformed densities of species at a given site. The resulting trait-by-site array contained the relative abundance of each category per trait in each site. Finally, trait richness was calculated as the number of trait categories present in a site, and trait diversity as the Rao diversity coefficient, using the methodology developed by Champely and Chessel (2002), which incorporates both the relative abundance of species and a measure of the pairwise functional differences between species (Botta-Dukat, 2005).

Data analysis

Multivariate analyses (correspondence analysis, CA; fuzzy correspondence analysis, FCA) were used to

Table 2 River floodplains investigated in this study

Climate–River	N	High connectivity	Intermediate connectivity	Low connectivity	Sampling season	Benthic macroinvertebrate sampling
Subtropical Paraná	53	Site in a secondary channel (Mini river)	Two shallow wetlands with relatively high hydrological connection with the main channel	Two shallow lakes with low connection to the main channel	November 2005 to February 2006	Nine samples per wetland and three in the secondary channel. Macroinvertebrates sampled in unvegetated areas with an Ekman grab (0.0225 m ²) and sieved through a 200-µm mesh (Zilli & Marchese, 2011)
Temperate Tagliamento	42	Three sites along the main river channel and three secondary channels. Large gravel substratum	Three backwaters connected downstream only. Sand substratum	Six isolated wetlands near or far from the main channel. Sand/silt substratum	August 1998	Data obtained from lowland reaches IV, V and VI described in Arscott <i>et al.</i> (2005). Macroinvertebrates collected in unvegetated areas (gravel, sand and silt) in triplicate from each site with a Hess sampler (0.04 m ² ; 100-µm mesh size)
Temperate Rhône	28	Two sites in the main river channel and two secondary channels. Pebble dominated substratum	Six backwaters connected downstream only. Substrata dominated by pebble and gravel	Nine lentic isolated waterbodies, substratum dominated by silt	July 2003	Average values from quadruple quadrat samples 0.25 m ² per site, macroinvertebrates sampled in unvegetated habitats (pebble, gravel, silt) with a hand net, 500-µm mesh (Paillex <i>et al.</i> , 2007)
Mediterranean Ebro	43	Three sites along the main river channel and two secondary channels. Substratum dominated by pebble/gravel	Four backwaters connected downstream only. Gravel substratum	La Alfranca, Cartuja and Juslibol isolated oxbow lakes. Substratum dominated by sand/silt	August 2006	Triplicate samples per site collected from most abundant habitats (e.g. soft sediment, gravel, riparian vegetation). Macroinvertebrates sampled with a hand net (500-µm mesh size) covering a 0.25 m ² surface (Gallardo <i>et al.</i> , 2008, 2009a)
Semi-arid Cooper	20	Six permanent and semipermanent waterbodies along the main channel	Five temporary waterbodies	Nine ephemeral waterbodies	December 1991 Cooper, and November 1993 Diamantina rivers	Samples collected from most abundant microhabitats (e.g. large woody debris, aquatic vegetation and unvegetated areas) by sweeping a 500-µm mesh pond net over 5 m ² for 20 s (Sheldon <i>et al.</i> , 2002; Sheldon & Thoms, 2006)
Semi-arid Murray	20	Seven sites connected upstream and downstream, permanently flooded	Seven semipermanent (flooded >75% of the year) or temporal (flooded 50–75% of the year) sites connected up- or downstream only	Six ephemeral (flooded <10% year) isolated oxbow lakes	December 1990	

N = number of sampling points within each river. More information on the connectivity of sites and methods used to sample macroinvertebrates can be found in references cited in the *Benthic macroinvertebrate sampling* column.

assess taxonomic and trait differences among river floodplain systems. Because CA favours rare taxa (Hill, 1974), only those taxa contributing >5% of the macroinvertebrate community at a particular site were considered. As a result, only 60 of 228 taxa were kept in the analysis after this filter was applied, thus highlighting the high contribution of rare taxa to the fauna of these rivers. To minimise possible differences in abundance due to the sampling device used or the different time/area sampled, macroinvertebrate abundance was transformed to presence/absence data. The comparable number of taxa (60) and trait categories (62) considered in

the CA and FCA, respectively, facilitated testing our first assumption that the functional composition of climatically different rivers is less distinct than their taxonomic composition.

Linear mixed effect models (LME) were used to extract common patterns of benthic invertebrate communities across lateral connectivity gradients. This robust statistical technique is increasingly exploited for its capacity to avoid problems related to the lack of independence of ecological observations (Bolker *et al.*, 2009). River identity was included as a random factor, while hydrological connectivity (high, intermediate and low) was used as a fixed

Table 3 Biological traits and categories for benthic macroinvertebrates considered in this study (extracted from Tachet *et al.*, 2010).

Trait	Categories	Trait	Categories
Maximum size	<0.25 cm	Resistance form	Eggs, statoblasts
	0.25 < size ≤ 0.5 cm		Cocoons
	0.5 < size ≤ 1 cm		Cells against desiccation
	1 < size ≤ 2 cm		Diapause or dormancy
	2 < size ≤ 4 cm		None
	4 < size ≤ 8 cm		Flier
	>8 cm	Locomotion	Surface swimmer
Respiration	Tegument		Swimmer
	Gill		Burrower
	Plastron		Crawler
	Spiracle (aerial)		Interstitial
	Hydrostatic vesicle		Temporarily attached
Life cycle duration	<1 year (short lifespan)	Food	Permanently attached
	>1 year (long lifespan)		Fine sediments and microorganisms
Potential number of rep. cycles/yr	<1 (univoltine)		Detritus <1 mm
	1 (semivoltine)		Plant detritus ≥ 1 mm
	>1 (plurivoltine)		Living microphytes
Aquatic stage	Egg		Living macrophytes
	Larva		Dead animal > 1 mm
	Nymph		Living microinvertebrates
	Adult		Living macroinvertebrates
Reproduction	Ovoviviparity	Feeding habits	Vertebrates
	Isolated eggs, cemented clutches, cemented or fixed		Deposit feeders
	Asexual reproduction		Filter feeders
	Isolated eggs, free clutches, free vegetation clutches		Shredders
	Terrestrial clutches		Scrapers
Dispersal	Aquatic passive		Piercers
	Aquatic active		Predators
	Aerial passive		Parasites
	Aerial active		

effect. A total of 15 models were developed to test our initial predictions, summarised in Table 1. Kruskal–Wallis analyses of variance were performed by river to describe individual taxonomic and trait patterns.

Statistics and graphical outputs were computed with the libraries *ade4* (Chessel, Dufour & Thioulouse, 2004; Dray & Dufour, 2007; Dray, Dufour & Chessel, 2007), *vegan* (Oksanen *et al.*, 2007) and *nlme* (Pinheiro *et al.*, 2010); all of which were implemented in R CRAN (R Development Core Team, 2011).

Results

Benthic macroinvertebrate patterns among climate regions

According to multivariate ordinations, the taxonomic composition of the six subtropical, temperate, Mediterranean and semi-arid floodplains differed strongly, as might be expected considering their intrinsic climatic, geological, geomorphological and hydrological features

and their biogeographical differences. The first three axes of the correspondence analysis (CA) using the taxonomic composition data set accounted for 14.5% of total variability, illustrating considerable taxonomic heterogeneity across climate regions. However, our aim was not to demonstrate obvious biogeographical differences in macroinvertebrate composition, but rather to search for similarities across hydrological gradients.

The first and second CA axes separated the subtropical Paraná River on the left side of the plot from the other five rivers, particularly due to Bivalvia (e.g. *Pisidium* sp., *Musculium* sp.), Gastropoda (e.g. *Eupera* sp.) and Clitellata (e.g. *Erpobdella* sp., Oligochaeta) (Fig. 2). Furthermore, the Paraná River had an average of 86.2% of non-insect taxa, higher than values for temperate (38.8%), Mediterranean (38.7%) and semi-arid (42.0%) river floodplains (Kruskal–Wallis test, d.f. = 5, $\chi^2 = 71.05$, $P < 0.001$).

The first CA axis was positively related to the abundance of insects, which accounted for more than 50% of all individuals in the temperate, Mediterranean and

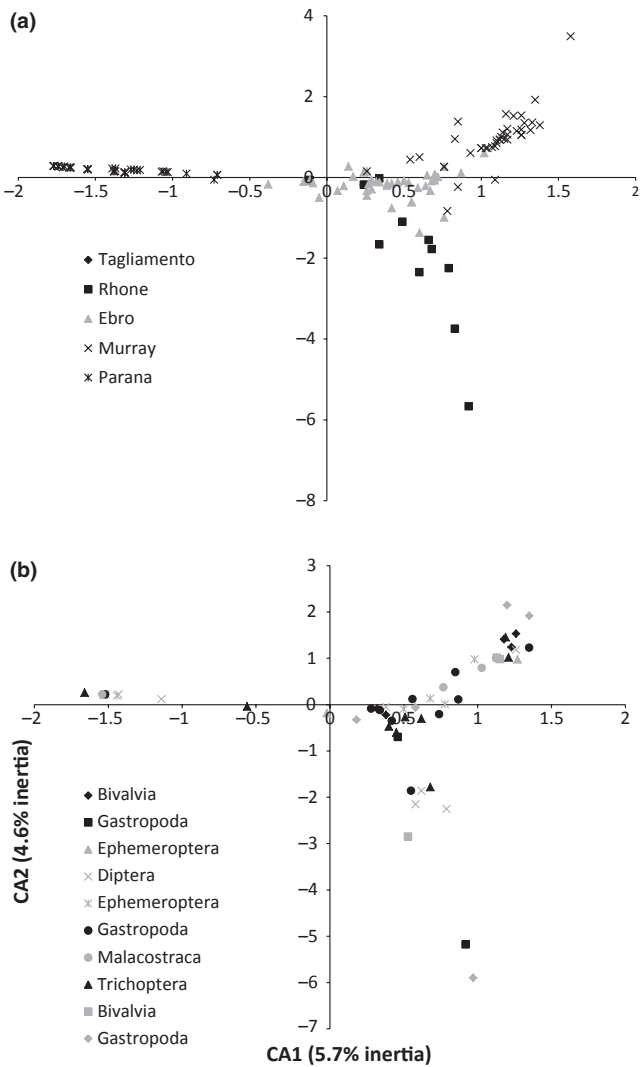


Fig. 2 Results of a correspondence analysis (CA) performed on taxonomic composition in the six river floodplains: (a) site scores. (b) Species scores grouped by taxonomic class/order.

semi-arid river floodplains, and included Odonata (e.g. *Ischnura* sp., *Coenagrion* sp.), Heteroptera (e.g. *Agraptocorixa* sp., *Enithares* sp.), Diptera (e.g. *Bezzia* sp., Culicinae), Ephemeroptera (e.g. *Clöeon* sp., *Caenis* sp.) and Trichoptera (e.g. *Triplectides* sp., *Oecetis* sp.) (Fig. 2). Certainly, Ephemeroptera and Plecoptera composed a greater percentage of the community in the temperate and Mediterranean river floodplains (average 10.9%) than in the subtropical (8.6%) and semi-arid (4.5%) systems located at lower latitudes (Kruskal–Wallis test, $\chi^2 = 77.68$, d.f. = 5, $P < 0.001$).

The second axis best discriminated the semi-arid Cooper and Murray rivers on the upper right side of the graphic, characterised by the presence of Coleoptera (e.g. *Hyderodes* sp., *Allodeus* sp.), Gastropoda (e.g. *Thiara*

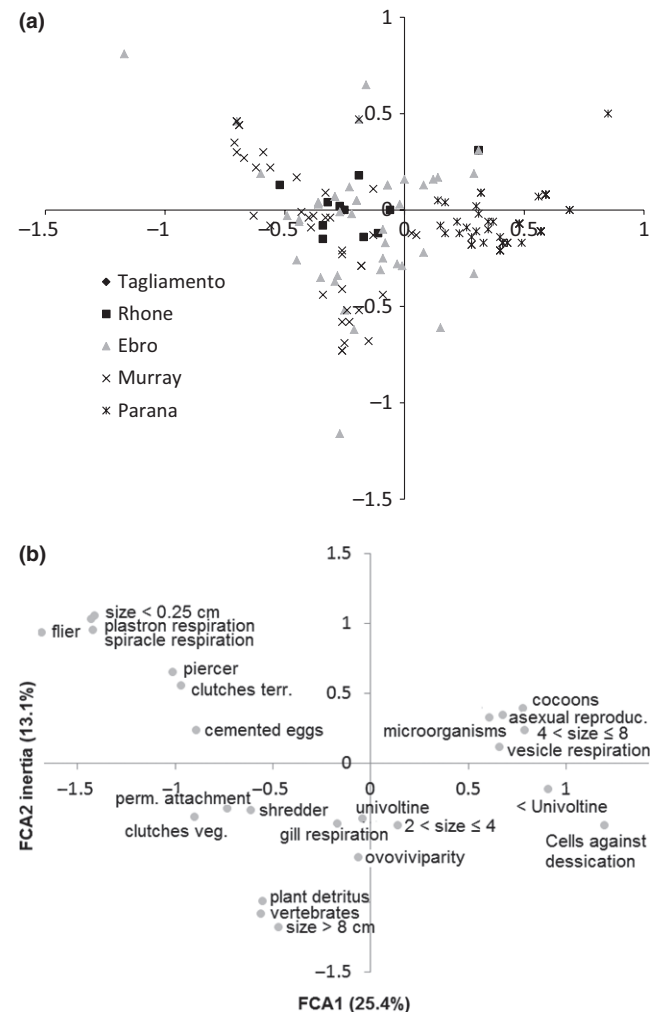


Fig. 3 Results of a fuzzy correspondence analysis (FCA) performed on trait composition in six river floodplains: (a) site scores. (b) Functional trait scores. See Table 3 for further information on trait categories.

sp.) and Malacostraca (e.g. *Paratya* sp., *Caridina* sp., *Cherax* sp.) (Fig. 2).

The first three axes of a fuzzy correspondence analysis (FCA) performed on trait composition explained 50.6% of the total variance, more than three times higher than the variance explained by the CA based on taxonomy. In contrast to the taxonomic CA, the six river floodplains were less distinct in the trait-based ordination, although the Paraná River was again separated from the others towards the right side of the plot (Fig. 3a).

Traits positively related to the first FCA axis, and thereby relating mainly to the Paraná, included resistant forms (e.g. ‘cells’ protecting against desiccation, cocoons), large body size (between 4 and 8 cm), long lifespan, asexual reproduction or deposition of free isolated eggs, tegument or aerial vesicle respiration,

and feeding on suspended material or organic deposits (Fig. 3b). The potential body size of benthic macroinvertebrates in the Paraná River floodplain – probably driven by dominance of bivalves and gastropods—was certainly larger (average 57.6% organisms >4 cm) than in the other five floodplains (from 0.3% in the Rhône to 38.0% in the Tagliamento). Moreover, an average of 80.9% of the organisms in the Paraná River had long lifespan compared with <40% in the temperate, Mediterranean and semi-arid river floodplains. Many of the taxa from the Paraná River were filter feeders (26.3%), deposit feeders (50.1%) and predators (19.2%). In contrast, shredders were less abundant there (1.4%), compared with the other river floodplains (ranging from 10.7% in the Rhône to 39.36% in the Murray; Table 4).

Trait categories that were positively related to the second FCA axis discriminated the two temperate rivers (upper part of the plot in Fig. 3a) and included organisms with spiracle or plastron respiration, short lifespan, terrestrial or vegetation clutches oviposition, intermediate to small body sizes (<1 cm), which were predominantly scrapers and piercers feeding on plant material (Fig. 3b).

The semi-arid and Mediterranean floodplains, taking mostly negative values on both the first and second FCA axes (i.e. the lower left corner of Fig. 3a), were characterised by taxa with ovoviviparous reproduction and intermediate to large body size (2 to 4 cm and >8 cm) (Fig. 3b). In these environments, shredders, scrapers and deposit feeders were the most abundant groups, accounting for 65–67% of the assemblage (Table 4).

Patterns in the benthos across lateral connectivity gradients

Although there was considerable diversity among systems, as revealed by the ordination techniques described above, linear mixed effects models (LME) allowed us to test our initial hypotheses about macroinvertebrate distributions across lateral connectivity gradients at the intercontinental scale. Seven of our 15 initial predictions were supported, which underlines the importance of hydrological connectivity for macroinvertebrate assemblage patterns in floodplains regardless of climate (Table 5).

As predicted, total macroinvertebrate richness peaked at intermediate hydrological connectivity (Fig. 4a), although models using taxonomic diversity were not significantly different among hydrological categories (Fig. 4b). The richness of EPT taxa peaked at the most connected floodplain sites (Fig. 4c), while differences across hydrological categories in the richness of COH taxa were not significant (Fig. 4d).

The frequency of particular trait categories across the connectivity gradient was uneven (Table 5). Small-bodied organisms were ubiquitous along the connectivity gradient (average 7–11% in all three categories; Fig. 5a), peaking at highly connected sites in the case of the Tagliamento River only (see Supporting Information Fig. S1a). Furthermore, plurivoltinism and short lifespan increased in isolated waterbodies in most rivers, in contrast to our initial hypotheses (Table 5; Fig. 5b–c).

The proportion of individuals with traits that confer resistance to desiccation (diapause, statoblasts and cocoons) were not significantly different across

Table 4 Mean (\pm SD) of taxonomic and trait attributes for the six floodplains investigated

Metrics	Type	Paraná	Tagliamento	Rhône	Ebro	Murray	Cooper
Taxonomic richness	Taxon	7.30 (\pm 2.37)	13.50 (\pm 6.53)	29.89 (\pm 9.30)	5.79 (\pm 2.52)	16.15 (\pm 4.11)	16.80 (\pm 5.69)
Taxonomic diversity	Taxon	1.39 (\pm 0.51)	0.96 (\pm 0.34)	1.63 (\pm 0.54)	0.96 (\pm 0.46)	1.46 (\pm 0.35)	1.56 (\pm 0.33)
EPT richness	Taxon	8.50 (\pm 13.03)	12.48 (\pm 21.18)	14.16 (\pm 19.15)	21.27 (\pm 37.50)	8.30 (\pm 9.89)	12.05 (\pm 20.86)
COH richness	Taxon	0.00 (\pm 0.00)	0.59 (\pm 1.04)	11.97 (\pm 16.56)	12.76 (\pm 29.63)	17.47 (\pm 30.51)	23.83 (\pm 28.23)
Trait richness	Trait	40.60 (\pm 5.57)	53.02 (\pm 3.40)	56.25 (\pm 1.76)	48.28 (\pm 4.98)	57.90 (\pm 2.13)	59.20 (\pm 1.79)
Trait diversity	Trait	58.84 (\pm 19.16)	41.30 (\pm 17.66)	48.05 (\pm 13.81)	44.10 (\pm 19.20)	47.41 (\pm 15.17)	57.51 (\pm 19.36)
Size <0.5 cm (%)	Trait	3.48 (\pm 3.75)	1.48 (\pm 1.74)	9.74 (\pm 9.48)	14.78 (\pm 26.18)	17.22 (\pm 21.41)	21.78 (\pm 19.10)
Short lifespan (%)	Trait	19.14 (\pm 17.37)	60.26 (\pm 36.33)	70.71 (\pm 12.47)	66.94 (\pm 28.74)	61.86 (\pm 23.54)	65.44 (\pm 24.97)
Plurivoltinism (%)	Trait	61.14 (\pm 18.33)	79.47 (\pm 16.03)	53.42 (\pm 5.86)	59.99 (\pm 25.92)	40.02 (\pm 21.42)	50.31 (\pm 24.33)
Resistance forms (%)	Trait	32.47 (\pm 13.24)	28.49 (\pm 11.25)	41.07 (\pm 16.80)	30.68 (\pm 23.04)	24.98 (\pm 21.27)	34.55 (\pm 16.90)
Deposit feeders (%)	Trait	50.14 (\pm 23.70)	54.24 (\pm 27.37)	16.31 (\pm 7.86)	30.38 (\pm 24.12)	11.83 (\pm 5.80)	20.89 (\pm 17.78)
Shredders (%)	Trait	1.35 (\pm 2.62)	10.72 (\pm 6.46)	23.40 (\pm 14.04)	29.86 (\pm 16.61)	39.36 (\pm 14.37)	28.79 (\pm 8.21)
Scrapers (%)	Trait	0.74 (\pm 1.53)	12.25 (\pm 12.23)	17.17 (\pm 11.35)	14.83 (\pm 10.12)	15.99 (\pm 9.06)	14.72 (\pm 12.21)
Filter feeders (%)	Trait	26.33 (\pm 22.23)	9.99 (\pm 8.18)	12.89 (\pm 10.29)	10.30 (\pm 10.87)	6.36 (\pm 2.98)	5.33 (\pm 3.90)
Predators (%)	Trait	19.23 (\pm 17.00)	8.75 (\pm 10.11)	9.20 (\pm 7.29)	7.67 (\pm 7.23)	18.11 (\pm 14.68)	16.84 (\pm 10.97)

Values are the mean of all the sites in each floodplain. Differences among rivers are all significant (Kruskal–Wallis test, d.f. = 5, $P < 0.01$).

Table 5 Results from the linear mixed effects models (LME) performed on 15 taxonomic and functional indicators using floodplain identity as random factor and hydrological connectivity (high/intermediate/low) as fixed factor

Metrics	Type	Corr	$F_{2,198}$	P-value	Trend expected	Trend observed	Accordance
Taxon richness	Taxon	0.84	7.15	0.001	Intermediate	Intermediate	YES
Taxon diversity	Taxon	0.53	1.23	n.s.	Intermediate	None	
EPT richness	Taxon	0.66	30.36	0.001	High	High	YES
COH richness	Taxon	0.80	2.34	0.099	Low	Low	YES
Trait richness	Trait	0.59	2.74	0.066	Intermediate to Low	Intermediate	YES
Trait diversity	Trait	0.37	0.01	n.s.	Intermediate to Low	None	
Size <0.5 cm	Trait	0.42	0.91	n.s.	High	None	
Short lifespan	Trait	0.64	0.09	0.091	High	Low	NO
Plurivoltinism	Trait	0.52	3.29	0.039	High	Low	NO
Resistance form	Trait	0.26	0.14	n.s.	Low	None	
Shredders	Trait	0.79	10.00	0.001	High	High	YES
Scrapers	Trait	0.61	9.52	0.001	High	High	YES
Filter feeders	Trait	0.57	11.07	0.001	High	Intermediate	NO
Deposit feeders	Trait	0.62	3.30	0.039	Low	Low	YES
Predators	Trait	0.42	2.03	n.s.	Low	None	

Corr: correlation between observed and fitted values. Marginally significant P -values (<0.1) are shown. n.s. not significant ($P > 0.1$). Trend observed: hydrological category where the metric shows a highest score. Accordance: support (YES) or rejection (NO) of expectations described in Table 1.

floodplains when considered together (Table 5; Fig. 5d), but they were more numerous at low connectivity sites in the subtropical Paraná and in the semi-arid Cooper

and Murray river floodplains (Fig. S1d). Diapause was the most common resistance trait (mean 19.3%) followed by statoblasts (mean 5.3%) and cocoons (mean 4.7%),

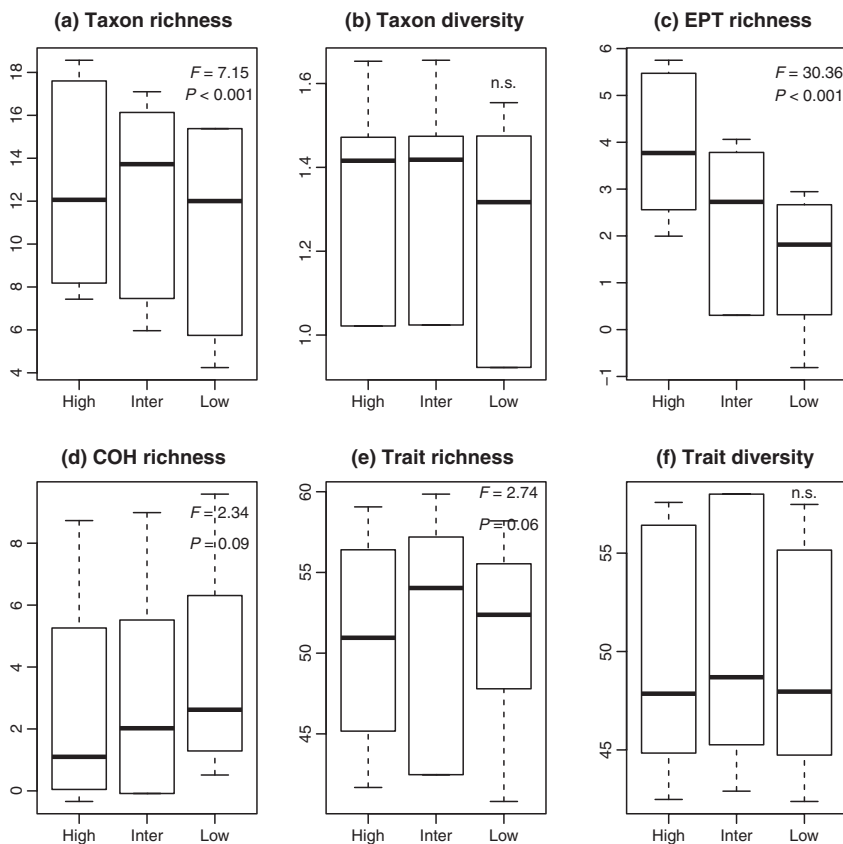


Fig. 4 Box plots of macroinvertebrate taxonomic metrics across lateral hydrological connectivity gradients (high, intermediate and low). Statistics given at the right-hand upper corner correspond to a linear mixed effects (LME) model using 'river identity' as random factor and 'hydrological connectivity' as fixed factor. Degrees of freedom of all models = 198, n.s. = non-significant model at $P > 0.1$. Marginally significant models ($0.1 > P > 0.05$) are shown for informative purposes.

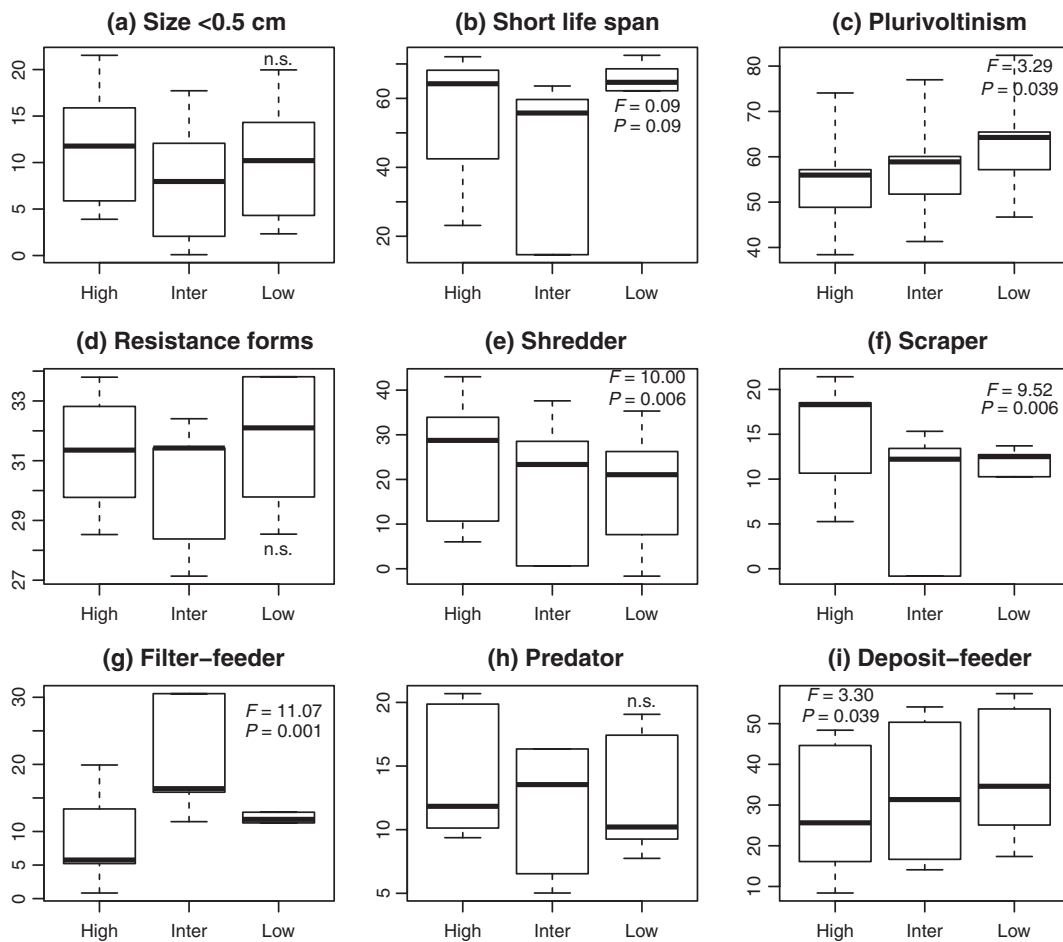


Fig. 5 Box plot of nine macroinvertebrate traits across hydrological connectivity gradients (high, intermediate and low). Statistics given at the right-hand upper corner correspond to a linear mixed effects (LME) model using 'river identity' as random factor and 'hydrological connectivity' as fixed factor. Degrees of freedom of all models = 198, n.s. = non-significant model at $P > 0.1$. Marginally significant models ($0.1 > P > 0.05$) are shown for informative purposes.

but the majority of taxa had no obvious trait related to desiccation (mean 68.0%).

Across a gradient of lateral hydrological connectivity, the frequencies of shredders and scrapers were significantly higher in connected sites (Fig. 5e–f); filter feeders were more frequent at intermediate levels of connectivity (Fig. 5g); and deposit feeders dominated isolated waterbodies (Fig. 5i).

Discussion

In this study, we compared the taxonomic and trait composition of benthic macroinvertebrate assemblages from a number of river floodplains under different climates and in different biogeographical areas. We adopted a macroecological approach to investigate the influence of hydrological connectivity in an effort to determine comparability of broad spatial patterns across climatic zones. Analyses revealed common taxonomic and trait changes

across climatically different floodplains, which may help disentangle complex responses in macroinvertebrate assemblages to different degrees of hydrological connectivity.

We assumed that trait variation would be more consistent than taxonomic patterns across large biogeographical scales because the trait filters across floodplain environments may be similar, whereas taxonomic composition depends on historical and evolutionary factors (Bonada *et al.*, 2006). Perhaps not surprisingly, overlap among the six river floodplains in multivariate analyses was greater for the trait-based than for the taxonomic analysis (Figs 2 & 3), suggesting greater similarity among climatically disparate river floodplains in biological traits than in taxonomic composition. These results agree with various studies reporting high trait stability in macroinvertebrate assemblages across Europe (Statzner *et al.*, 2001, 2004; Statzner & Bêche, 2010). They are also consistent with the findings of Bonada *et al.* (2007), who found

trait variability between temperate and Mediterranean rivers to be significantly less than taxonomic variability. We interpret this as trait stability across climatically different floodplains and suggest that it provides a meaningful ecological context for benthic macroinvertebrate comparison among climatic zones, when taxonomic composition differs strongly.

Interestingly, the taxonomically based ordination separated the subtropical Paraná floodplain, with an average 86% of non-insect taxa, from the insect-dominated temperate, Mediterranean and semi-arid floodplains (with >50% insect abundance). Other authors have found the main channel of the Paraná River to be highly dominated by non-insects, particularly the endemic Oligochaete *Narapa bonettoi*, due to instability of the sandy substratum, while bivalves and gastropods were more frequently observed in floodplain lakes (Marchese, Ezcurra De Drago & Drago, 2002). A significant change in aquatic insect diversity with latitude has been also observed before, as illustrated by the greater richness of Ephemeroptera and Plecoptera with increasing latitudes, related to their adaptation to cool waters (Pearson & Boyero, 2009).

Across lateral connectivity gradients, most of our taxonomic-specific hypotheses were supported when incorporating data from all six river floodplains. Total macroinvertebrate richness peaked at intermediate levels of hydrological connectivity, thus potentially supporting the intermediate disturbance hypothesis (Connell, 1978), assuming that the connectivity gradient partly equates to disturbance (Fig. 4a). As highlighted by Leigh and Sheldon (2009), although the response of richness to connectivity was initially described for temperate rivers (e.g. Tockner & Ward, 1999; Ward *et al.*, 1999; Arscott *et al.*, 2005), it has been found to be appropriate for describing biodiversity patterns in Mediterranean (e.g. Gallardo *et al.*, 2009b), semi-arid (e.g. Sheldon *et al.*, 2002; Marshall *et al.*, 2006; Leigh & Sheldon, 2009), subtropical and tropical systems (e.g. Thomaz, Bini & Bozelli, 2007; Zilli *et al.*, 2008; Leigh & Sheldon, 2009). As predicted, EPT richness peaked at the most connected floodplain sites (Fig. 4c), a pattern confirmed previously in temperate (e.g. Paillex *et al.*, 2009) and Mediterranean (e.g. Gallardo *et al.*, 2008) floodplains. Apart from macroinvertebrates, hydrological connectivity has been found to influence the richness of many other aquatic organisms, including aquatic plants (e.g. Amoros & Bornette, 1999), fish (e.g. Sheaves, Johnston & Abrantes, 2007), zooplankton (e.g. Frisch *et al.*, 2005; Gallardo *et al.*, 2009b) and phytoplankton (e.g. Van Den Brink, Van Katwijk & Van Der Velde, 1994; Gallardo

et al., 2009b), thereby underlying its prominent role on the distribution of organisms across the river floodplain habitats (Moilanen & Nieminen, 2002).

We also tested predictions of changes in trait categories across hydrological conditions, some of which were proposed by Townsend and Hildrew (1994) as part of the River Habitat Templet (RHT). We were aware, however, that adding the disturbance–connectivity relationship to the initial disturbance frequency prevailing in the RHT would involve complexity to our hypothesis testing. In accordance with the connectivity gradient described by Amoros and Roux (1988), we assumed that, in river floodplains, connected sites experience greater changes in habitat conditions related to flood disturbance (i.e. greater change in connectivity over time) and thus undergo larger temporal variability. In contrast, flooding frequency progressively decreases as we move from the main river channel towards isolated sites, where the temporal variability is relatively muted. As a result, maximum body size and longevity should decrease from low to highly connected sites and reproduction frequency increase (Townsend & Hildrew, 1994; Statzner & Bêche, 2010; Table 1). Similarly, body size, lifespan and reproduction preferences may be unconstrained in fragmented and isolated habitats. However, prolonged disconnection, as is often the case in many semi-arid systems, may impose intense abiotic constraints on macroinvertebrates, hence favouring small plurivoltine and short-lived organisms capable of using the habitat when available (Sheldon *et al.*, 2010). This agrees with results from the Cooper and Murray semi-arid rivers (Fig. S1a–c), where macroinvertebrate life-history patterns were the opposite to those of the more permanent Rhône and Tagliamento temperate rivers, as expected considering the intermittent nature of isolated waterbodies in semi-arid floodplain rivers (Sheldon *et al.*, 2010). To a lesser extent, the effect of fragmentation can be also noted in the Mediterranean Ebro and subtropical Paraná environments (Fig. S1a–c). Flooding and fragmentation are therefore extremes of the hydrological connectivity gradient limiting the range of life-history strategies of species that inhabit the river floodplain (Gallardo *et al.*, 2009a).

Despite of the lack of significant differences identified by our models, several studies have found spatial patterns in resistance to desiccation; for example, across the Paraná River, there were greater densities of oligochaetes (able to resist water loss through diapause or cysts) in marginal temporary fluvial wetlands (Montalto & Marchese, 2005). As another example, Reckendorfer *et al.* (2006) found higher densities of pulmonate molluscs,

which are better adapted to desiccation because they have aerial respiration and minimal water loss, in low connectivity sites with periodic anoxia and drought in the Danube River floodplain. Nonetheless, and consistent with our study, in their review of European and North American benthic macroinvertebrates, Statzner and Bêche (2010) found that the majority (>60%) of taxa had no obvious adaptations to desiccation.

Among the feeding habits, the frequencies of shredders and scrapers were significantly higher in connected sites (Fig. 5e,f), which may be related to the abundance of leaf litter transported by the river and attached algae providing food (Statzner & Bêche, 2010). Likewise, Gallardo *et al.* (2009a) reported a positive relationship between shredder occurrence and environmental variables associated with high connectivity, in particular chlorophyll-*a*. Interestingly, the proportion of shredders was low in the subtropical Paraná (Fig. S1e), where leaf decomposition is primarily driven by microbial action rather than by macroinvertebrates (Wantzen & Wagner, 2006). Actually, shredders prefer cool water and temperate zone riparian vegetation that produces more palatable and nutritious leaves compared with tropical environments (Yule *et al.*, 2009). In this regard, Zilli *et al.* (2008) pointed out that many of the shredder taxa present in northern rivers are absent from the Paraná, where they are mainly represented by chironomids and decapods. Large biogeographical differences among rivers, and the phylogenetics of the taxa involved, may therefore be partly responsible for the highly complex trait patterns observed in our study. Filter feeders were more frequent at intermediate connectivity (Fig. 5g), probably related to the availability of suspended and colloidal particles and lower shear stress currents compared with main channels (Cabezas *et al.*, 2009b). In contrast, deposit feeders were more abundant in disconnected waterbodies where organic matter tends to accumulate (Fig. 5i) (Tockner *et al.*, 1999a). Finally, predators are usually large generalist species and were thus expected to be most numerous in infrequently flooded environments (Paillex *et al.*, 2009), as was certainly true for the disconnected waterbodies of the temperate Rhône and Tagliamento and the Mediterranean Ebro river floodplains (Fig. S1i). This pattern was further confirmed in the subtropical Paraná and in the semi-arid Murray and Cooper rivers (Fig. S1i), where predators were more abundant and dominated connected sites. This was congruent with the patterns in potential body size (large) and life history (long lifespan, one reproductive cycle per year) described previously. The abundance of predators may again be related to the temporary nature of isolated habitats in the Cooper and

Murray rivers, compromising the survival of more long-lived or univoltine aquatic organisms; on the other hand, the permanence of highly connected channels presumably allows the colonisation of larger predators belonging, in the case of the Cooper and Murray rivers, to the Malacostraca (e.g. *Macrobrachium* sp.), Clitellata (e.g. *Erpobdella* sp.) and Insecta (e.g. *Enochrus* sp. larvae, *Austrogomphus* sp.).

Data considerations

The response of benthic macroinvertebrates to lateral connectivity can vary along a given river corridor. Those responses are linked primarily to hydrogeomorphological differences among floodplain reaches that influence habitat heterogeneity (physical, chemical and thermal; e.g. Arscott, Tockner & Ward, 2000) and inundation dynamics. In the Tagliamento River, Arscott *et al.* (2005) observed significant changes in benthic macroinvertebrate assemblages across a lateral gradient from headwaters to lowland stretches of the river, mainly associated with changes in the floodplain spatiotemporal heterogeneity and the scarcity of lentic habitats upstream. Although data in our study correspond to mid- and lowland reaches in all six river floodplains, differences among rivers in meandering and braiding patterns and floodplain heterogeneity may have influenced the responses observed. Hydrological connectivity modulates invertebrate patterns through multiple changes in their habitat (e.g. substratum and vegetation structure, water chemistry), food availability (e.g. transport and accumulation of organic matter and dissolved nutrients) and biotic interaction (e.g. transport of species through active and passive drift). We would probably have found clearer patterns in invertebrate functionality had we used these types of direct factors instead of a ranked estimate of hydrological connectivity (see examples using direct hydrological indicators in Sheldon & Thoms, 2006; Gallardo *et al.*, 2009a,b). As demonstrated by Statzner and Bêche (2010), the more directly a stressor acts on a particular trait, the less equivocal the interpretation of that trait response should be.

Apart from the effect of hydrological connectivity, human influence may greatly disrupt the response of macroinvertebrates to hydrological connectivity by reducing the frequency of large erosive floods that normally reset aquatic habitats, or by changing the seasonality of high and low flows. As an example, discharge in the Ebro River has decreased by 30% since the 1980s, embankments and dykes have counteracted floodplain interactions, and irrigation of the lowlands has resulted in an abnormally high groundwater table in summer (Cabezas *et al.*, 2009b).

Such hydrological disruptions are common to other large regulated rivers, dramatically affecting the spatiotemporal heterogeneity of the floodplain, and hence the functional response of macroinvertebrates.

Sampling methodology, the exact habitat sampled and in what season, taxonomic resolution and trait scoring may have also influenced our results. While we did observe some clustering of data by continent in ordination plots, it was difficult to separate the effect of sampling methodology from other large-scale differences among continents. Chironomidae and Oligochaeta are certainly important components of the riverine aquatic communities that are rarely identified to genus. In the Paraná River alone, more than 14 genera of Oligochaeta and 20 of Chironomidae were identified (Zilli & Marchese, 2011), while in the Cooper and Murray semi-arid rivers, Sheldon and Thoms (2006) reported at least 22 Chironomidae genera, which would have notably increased richness scores in this study. In addition to increasing total richness, identification of Oligochaeta and Chironomidae may provide information on the preferences of taxa to variable levels of hydrological connectivity. In this sense, Juget and Lafont (1994) reported very little agreement with their quantification of the Rhône River's habitat templet after identifying more than 50 species of Oligochaeta. Nonetheless, more accurate trait scores for non-temperate macroinvertebrates are still necessary. In this study, we assigned family average trait scores to those uncoded taxa in Tachet's (2010) classification (Table S2). In addition, real traits measured in the field can greatly vary from one region to another and may even deviate from potential traits represented in Tachet *et al.* (2010). Thus comparison among rivers from different climates would undoubtedly benefit from more accurate and comparable ecological information available for all species.

Perspectives

Macroinvertebrate taxonomic and trait variation in the temperate Rhône and Tagliamento and the Mediterranean Ebro rivers generally agreed with our *a priori* hypotheses and were in accordance with the trait profile reported by Statzner and Bêche (2010) for lotic macroinvertebrates in Europe and North America. Small differences – for instance, in respiration and reproduction types— can be explained by the inclusion of both lotic and lentic habitats in our study compared with the work of Statzner and Bêche (2010), who focussed only on lotic environments. In contrast, trait differences along connectivity gradients in the subtropical Paraná River and the semi-arid Cooper

and Murray rivers were either not significant or contrary to our expectations. Verberk, Van Noordwijk and Hildrew (2013) recently suggested that the low discriminatory power of current trait-based approaches might be partly explained by the functional equivalence of alternative suites of traits. Under this point of view, natural selection does not operate at the level of independent single traits, but on whole organisms carrying suites of interacting traits (Verberk *et al.*, 2013). It thus follows that large biogeographical and phylogenetic differences between the three northern temperate and Mediterranean rivers on the one side, and the three southern semi-arid and subtropical rivers on the other, led to alternative combinations of traits (as opposed to individual traits) as an adaptive response to the hydrological connectivity gradient prevailing in each floodplain. The extent to which global macroecological factors (i.e. climate, dispersal history) and local biotic and abiotic factors (i.e. drought frequency, habitat structure, water chemistry) contributed to this difference cannot be determined with the available data, which highlights the need for more international coordinated studies using comparable protocols for site selection, sampling and analysis.

In any case, trait similarities observed in our study suggest that large-scale filters still operate, resulting in apparently different trait combinations in temperate and Mediterranean river floodplains when compared to semi-arid and tropical environments. This emphasises the effect of climate, and especially the interplay of floods and droughts, as primary drivers of macroinvertebrate traits, and complexity that may have been underestimated in previous studies. Consequently, research based on traits should be prudent when using *a priori* hypotheses extracted from the literature, and consider the particular climatic and hydrogeomorphological determinants of the floodplain's spatiotemporal heterogeneity to develop ecologically meaningful predictions.

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References

- Amoros C. & Bornette G. (1999) Antagonistic and cumulative effects of connectivity: a predictive model based on aquatic vegetation in riverine wetlands. *Archiv für Hydrobiologie*, **115**, 311–327.
- Amoros C. & Bornette G. (2002) Connectivity and biocomplexity in waterbodies of riverine floodplains. *Freshwater Biology*, **47**, 761–776.
- Amoros C. & Roux A.L. (1988) Interaction between large water bodies within the floodplain of large rivers: function and development of connectivity. *Münstersche Geographische Arbeiten*, **29**, 125–130.
- Arrington D.A. & Winemiller K.O. (2006) Habitat affinity, the seasonal flood pulse, and community assembly in the littoral zone of a Neotropical floodplain river. *Journal of the North American Benthological Society*, **25**, 126–141.
- Arcsott D.B., Tockner K. & Ward J.V. (2000) Aquatic habitat diversity along the corridor of an Alpine floodplain river (Fiume Tagliamento, Italy). *Archiv für Hydrobiologie*, **149**, 679–704.
- Arcsott D.B., Tockner K. & Ward J.V. (2005) Lateral organization of aquatic invertebrates along the corridor of a braided floodplain river. *Journal of the North American Benthological Society*, **24**, 934–954.
- Bolker B.M., Brooks M.E., Clark C.J., Geange S.W., Poulsen J.R., Stevens M.H.H. *et al.* (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, **24**, 127–135.
- Bonada N., Dolédec S. & Statzner B. (2007) Taxonomic and biological trait differences of stream macroinvertebrate communities between mediterranean and temperate regions: implications for future climatic scenarios. *Global Change Biology*, **13**, 1658–1671.
- Bonada N., Rieradevall M., Prat N. & Resh V.H. (2006) Benthic macroinvertebrate assemblages and macrohabitat connectivity in Mediterranean-climate streams of northern California. *Journal of the North American Benthological Society*, **25**, 32–43.
- Botta-Dukat Z. (2005) Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science*, **16**, 533–540.
- Bunn S.E., Davies P.M. & Winning M. (2003) Sources of organic carbon supporting the food web of an arid zone floodplain river. *Freshwater Biology*, **48**, 619–635.
- Bunn S.E., Thoms M.C., Hamilton S.K. & Capon S.J. (2006) Flow variability in dryland rivers: boom, bust and the bits in between. *River Research and Applications*, **22**, 179–186.
- Cabezas A., Comín F.A., Beguería S. & Trabucchi M. (2009a) Hydrologic and landscape changes in the Middle Ebro River (NE Spain): implications for restoration and management. *Hydrology and Earth System Sciences*, **13**, 1–12.
- Cabezas A., Garcia M., Gallardo B., Gonzalez E., Gonzalez-Sanchis M. & Comin F.A. (2009b) The effect of anthropogenic disturbance on the hydrochemical characteristics of riparian wetlands at the Middle Ebro River (NE Spain). *Hydrobiologia*, **617**, 101–116.
- Castella E., Richardot-Coulet M., Roux C. & Richoux P. (1984) Macroinvertebrates as describers of morphological and hydrological types of aquatic ecosystems abandoned by the Rhône River. *Hydrobiologia*, **119**, 219–225.
- Champely S. & Chessel D. (2002) Measuring biological diversity using Euclidean metrics. *Environmental and Ecological Statistics*, **9**, 167–177.
- Charvet S., Statzner B., Usseglio-Polatera P. & Dumont B. (2000) Traits of benthic macroinvertebrates in semi-natural French streams: an initial application to biomonitoring in Europe. *Freshwater Biology*, **43**, 277–296.
- Chessel D., Dufour A.B. & Thioulouse J. (2004) The ade4 package. I: one-table methods. *R News*, **4**, 5–10.
- Chevenet F., Dolédec S. & Chessel D. (1994) A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology*, **31**, 295–309.
- Connell J.H. (1978) Diversity in tropical rain forests and coral reefs – high diversity of trees and corals is maintained only in a non-equilibrium state. *Science*, **199**, 1302–1310.
- Depetris P.J. (2007) The Parana River under extreme flooding: a hydrological and hydro-geochemical insight. *Interiencia*, **32**, 656–662.
- Depetris P.J., Kempe S., Latif M. & Mook W.G. (1996) ENSO-controlled flooding in the Parana River (1904–1991). *Naturwissenschaften*, **83**, 127–129.
- Dolédec S., Statzner B. & Bournard M. (1999) Species traits for future biomonitoring across ecoregions: patterns along a human-impacted river. *Freshwater Biology*, **42**, 737–758.
- Drago E.C. (1989) Morphological and hydrological characteristics of the floodplain ponds of the Middle Parana River, Argentina. *Revue d'Hydrobiologie Tropicale*, **22**, 183–190.
- Drago E.C., Ezcurra De Drago I., Oliveros O.B. & Paira A.R. (2003) Aquatic habitats, fish and invertebrate assemblages of the Middle Paraná River. *Amazoniana*, **17**, 291–341.
- Dray S. & Dufour A.B. (2007) The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software*, **22**, 1–20.

- Dray S., Dufour A.B. & Chessel D. (2007) The ade4 package – II: two-table and K-table methods. *R News*, **7**, 47–52.
- Frisch D., Libman B.S., D'surney S.J. & Threlkeld S.T. (2005) Diversity of floodplain copepods (Crustacea) modified by flooding: species richness, diapause strategies and population genetics. *Archiv für Hydrobiologie*, **162**, 1–17.
- Gallardo B., García M., Cabezas A., González E., Ciancarelli C., González M. *et al.* (2007) First approach to understanding riparian wetlands in the Middle Ebro River floodplain (NE, Spain): structural characteristics and functional dynamics. *Limnética*, **26**, 373–386.
- Gallardo B., García M., Cabezas A., González E., González M., Ciancarelli C. *et al.* (2008) Macroinvertebrate patterns along environmental gradients and hydrological connectivity within a regulated river-floodplain. *Aquatic Sciences*, **70**, 248–258.
- Gallardo B., Gascón S., García M. & Comín F.A. (2009a) Testing the response of the macroinvertebrate functional structure and biodiversity to flooding and confinement. *Journal of Limnology*, **68**, 315–326.
- Gallardo B., González-Sanchís M., Cabezas A., Gascón S. & Comín F.A. (2009b) Modelling the response of floodplain aquatic communities across the lateral hydrological gradient. *Marine and Freshwater Research*, **60**, 924–935.
- Gasith A. & Resh V.H. (1999) Streams in Mediterranean climate regions: abiotic influences and biotic responses to predictable seasonal events. *Annual Review of Ecology and Systematics*, **30**, 51–81.
- Gayraud S., Statzner B., Bady P., Haybach A., Schöll F., Usseglio-Polatera P. *et al.* (2003) Invertebrate traits for the biomonitoring of large European rivers: an initial assessment of alternative metrics. *Freshwater Biology*, **48**, 2045–2064.
- Heino J., Schmera D. & Erős T. (2013) A macroecological perspective of trait patterns in stream communities. *Freshwater Biology*, **58**, 1539–1555.
- Hill M.O. (1974) Correspondence Analysis – Neglected multivariate method. *Journal of the Royal Statistical Society Series C-Applied Statistics*, **23**, 340–354.
- Ivov J.M., Carrel G., Lamouroux N., Dole-Olivier M.J., Malard F., Bravard J.P. *et al.* (2009) The Rhône River Basin. In: *Rivers of Europe*. (Eds K. Tockner, C.T. Robinson & U. Uehlinger), pp. 247–296. Academic Press, Amsterdam.
- Juget J. & Lafont M. (1994) Theoretical habitat templates, species traits, and species richness – aquatic oligochaetes in the Upper Rhône River and its floodplain. *Freshwater Biology*, **31**, 327–340.
- Junk W.J., Bayley P.B. & Sparks R.E. (1989) The flood pulse concept in river-floodplain systems. *Canadian Special Publications of Fisheries and Aquatic Sciences*, **106**, 110–127.
- Junk W.J. & Wantzen K.M. (2004) The flood pulse concept: new aspects, approaches, and applications. An update. In: *Proceedings of the 2nd Large River Symposium (LARS)* (Eds R. Welcomme & T. Petr), pp. 117–149. Food and Agriculture Organization & Mekong River Commission.
- Kennard M.J., Pusey B.J., Olden J.D., Mackay S.J., Stein J.L. & Marsh N. (2010) Classification of natural flow regimes in Australia to support environmental flow management. *Freshwater Biology*, **55**, 171–193.
- Knighton A.D. & Nanson G.C. (1994) Waterholes and their significance in the anastomosing channel system of Cooper Creek, Australia. *Geomorphology*, **9**, 311–324.
- Leigh C. & Sheldon F. (2009) Hydrological connectivity drives patterns of macroinvertebrate biodiversity in floodplain rivers of the Australian wet /dry tropics. *Freshwater Biology*, **54**, 549–571.
- Marchese M. & Ezcurra De Drago I. (1992) Benthos of the lotic environments in the Middle Parana River system – transverse zonation. *Hydrobiologia*, **237**, 1–13.
- Marchese M., Ezcurra De Drago I. & Drago E.C. (2002) Benthic macroinvertebrates and physical habitat relationships in the Parana River flood-plain system. In: *The Ecohydrology of South American Rivers and Wetlands*. (Ed M.E. McClain), pp. 111–132. International Association of Hydrological Sciences (IAHS), Wallingford, UK.
- Marshall J.C., Sheldon F., Thoms M. & Choy S. (2006) The macroinvertebrate fauna of an Australian dryland river: spatial and temporal patterns and environmental relationships. *Marine and Freshwater Research*, **57**, 61–74.
- Merritt R.W., Benbow M.E. & Hudson P.L. (2002) Wetland macroinvertebrates of Prentiss Bay, Lake Huron, Michigan: diversity and functional group composition. *Great Lakes Entomologist*, **35**, 149–160.
- Minshall G.W., Vannote R.L., Cushing C.E., Sedell J.R., Bott T.L., Cummins K.W. *et al.* (1983) Interbiome comparison of stream ecosystem dynamics. *Ecological Monographs*, **53**, 1–25.
- Moilanen A. & Nieminen M. (2002) Simple connectivity measures in spatial ecology. *Ecology*, **83**, 1131–1145.
- Montalto L. & Marchese M. (2005) Cyst formation in Tubificidae (Naidinae) and Opisthocystidae (Annelida, Oligochaeta) as an adaptive strategy for drought tolerance in fluvial wetlands of the Parana River, Argentina. *Wetlands*, **25**, 488–494.
- Oksanen J., Kindt R., Legendre P., O'hara B. & Stevens M.H.H. (2007) *vegan*: Community ecology package. Available at: <http://cran.r-project.org/>.
- Paillex A., Castella E. & Carron G. (2007) Aquatic macroinvertebrate response along a gradient of lateral connectivity in river floodplain channels. *Journal of the North American Benthological Society*, **26**, 779–796.
- Paillex A., Dolédec S., Castella E. & Merigoux S. (2009) Large river floodplain restoration: predicting species richness and trait responses to the restoration of hydrological connectivity. *Journal of Applied Ecology*, **46**, 250–258.
- Pearson R.G. & Boyero L. (2009) Gradients in regional diversity of freshwater taxa. *Journal of the North American Benthological Society*, **28**, 504–514.

- Peel M.C., Finlayson B.L. & McMahon T.A. (2007) Updated world map of the Köppen–Geiger climate classification. *Hydrology and Earth System Sciences*, **11**, 1633–1644.
- Petts G. & Amoros C. (1993) *Fluvial Hydrosystems*. Chapman & Hall, London, UK.
- Pinheiro J., Bates D., Debroy S. & Sarkar D. & The R Development Core Team. (2010) nlme: Linear and nonlinear mixed effects models. R package version 3.1-97.
- Poff N.L. & Ward B. (1990) Physical Habitat Templet of lotic systems: recovery in the context of historical pattern of spatio temporal heterogeneity. *Environmental Management*, **14**, 629–645.
- Poff N.L. & Ward J.V. (1989) Implications of streamflow variability and predictability for lotic community structure – a regional-analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 1805–1818.
- Puckridge J.T., Sheldon F., Walker K.F. & Boulton A.J. (1998) Flow variability and the ecology of large rivers. *Marine and Freshwater Research*, **49**, 55–72.
- R Development Core Team. (2011) *R: A language and Environment for Statistical Computing*. R Foundation for Statistical Computing Vienna, Austria.
- Reckendorfer W., Baranyi C., Funk A. & Schiemer F. (2006) Floodplain restoration by reinforcing hydrological connectivity: expected effects on aquatic mollusc communities. *Journal of Applied Ecology*, **43**, 474–484.
- Sheaves M., Johnston R. & Abrantes K. (2007) Fish fauna of dry tropical and subtropical estuarine floodplain wetlands. *Marine and Freshwater Research*, **58**, 931–943.
- Sheldon F., Boulton A.J. & Puckridge J.T. (2002) Conservation value of variable connectivity: aquatic invertebrate assemblages of channel and floodplain habitats of a central Australian arid-zone river, Cooper Creek. *Biological Conservation*, **103**, 13–31.
- Sheldon F., Bunn S.E., Hughes J.M., Arthington A.H., Balcombe S.R. & Fellows C.S. (2010) Ecological roles and threats to aquatic refugia in arid landscapes: dryland river waterholes. *Marine and Freshwater Research*, **61**, 885–895.
- Sheldon F. & Thoms M.C. (2006) Relationships between flow variability and macroinvertebrate assemblage composition: data from four Australian dryland rivers. *River Research and Applications*, **22**, 219–238.
- Skern M., Zweimueller I. & Schiemer F. (2010) Aquatic Heteroptera as indicators for terrestrialisation of floodplain habitats. *Limnologia*, **40**, 241–250.
- Statzner B. & Bêche L.A. (2010) Can biological invertebrate traits resolve effects of multiple stressors on running water ecosystems? *Freshwater Biology*, **55**, 80–119.
- Statzner B., Bis B., Dolédec S. & Usseglio-Polatera P. (2001) Perspectives for biomonitoring at large spatial scales: a unified measure for the functional composition on invertebrate communities in European running waters. *Basic and Applied Ecology*, **2**, 73–85.
- Statzner B., Dolédec S. & Huguény B. (2004) Biological trait composition of European stream invertebrate communities: assessing the effects of various trait filter types. *Ecography*, **27**, 470–488.
- Tachet H., Richoux M., Bournaud M. & Usseglio-Polatera P. (2010) Invertebrés d'eau douce: Systématique, Biologie, Écologie, CNRS éditions. Paris, France.
- Thomaz S.M., Bini L.M. & Bozelli R.L. (2007) Floods increase similarity among aquatic habitats in river-floodplain systems. *Hydrobiologia*, **579**, 1–13.
- Tockner K., Malard F. & Ward J.V. (2000) An extension of the flood pulse concept. *Hydrological Processes*, **14**, 2861–2883.
- Tockner K., Pennetzdorfer D., Reiner N., Schiemer F. & Ward J.V. (1999a) Hydrological connectivity, and the exchange of organic matter and nutrients in a dynamic river-floodplain system (Danube, Austria). *Freshwater Biology*, **41**, 521–535.
- Tockner K., Schiemer F., Baumgartner C., Kum G., Weigand E., Zweimueller I. *et al.* (1999b) The Danube restoration project: species diversity patterns across connectivity gradients in the floodplain system. *Regulated Rivers-Research & Management*, **15**, 245–258.
- Tockner K. & Ward J.V. (1999) *Biodiversity Along Riparian Corridors*. Archiv für Hydrobiologie, pp. 293–310.
- Tockner K., Ward J.V., Arscott D.B., Edwards P.J., Kollmann J., Gurnell A.M. *et al.* (2003) The Tagliamento River: a model ecosystem of European importance. *Aquatic Sciences*, **65**, 239–253.
- Townsend C.R. & Hildrew A.G. (1994) Species traits in relation to a habitat templet for river systems. *Freshwater Biology*, **31**, 265–275.
- Usseglio-Polatera P., Bournaud M., Richoux P. & Tachet H. (2000) Biomonitoring through biological traits of benthic macroinvertebrates: how to use species trait databases? *Hydrobiologia*, **422**, 153–162.
- Usseglio-Polatera P. & Tachet H. (1994) Theoretical habitat templates, species traits, and species richness – Plecoptera and Ephemeroptera in the Upper Rhône River and its floodplain. *Freshwater Biology*, **31**, 357–375.
- Van Den Brink F.W.B., Van Katwijk M.M. & Van Der Velde G. (1994) Impact of hydrology on phytoplankton and zooplankton community composition in floodplain lakes along the Lower Rhine and Meuse. *Journal of Plankton Research*, **16**, 351–373.
- Verberk W.C.E.P., Van Noordwijk C.G.E. & Hildrew A.G. (2013) Delivering on a promise: integrating species traits to transform descriptive community ecology into a predictive science. *Freshwater Science*, **32**, 531–547.
- Walker K.F., Sheldon F. & Puckridge J.T. (1995) A perspective on dryland river ecosystems. *Regulated Rivers-Research & Management*, **11**, 85–104.
- Walker K.F. & Thoms M.C. (1993) Environmental-effects of flow regulation on the lower river Murray, Australia. *Regulated Rivers-Research & Management*, **8**, 103–119.
- Wantzen K.M., Rothhaupt K.O., Mortl M., Cantonati M., Laszlo G.T. & Fischer P. (2008) Ecological effects of

- water-level fluctuations in lakes: an urgent issue. *Hydrobiologia*, **613**, 1–4.
- Wantzen K.M. & Wagner R. (2006) Detritus processing by invertebrate shredders: a neotropical-temperate comparison. *Journal of the North American Benthological Society*, **25**, 216–232.
- Ward J.V. & Stanford J.A. (1995) Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. *Regulated Rivers-Research & Management*, **11**, 105–119.
- Ward J.V., Tockner K. & Schiemer F. (1999) Biodiversity of floodplain river ecosystems: Ecotones and connectivity. *Regulated Rivers-Research & Management*, **15**, 125–139.
- Yule C.M., Leong M.Y., Liew K.C., Ratnarajah L., Schmidt K., Wong H.M. *et al.* (2009) Shredders in Malaysia: abundance and richness are higher in cool upland tropical streams. *Journal of the North American Benthological Society*, **28**, 404–415.
- Zilli F.L. & Marchese M.R. (2011) Patterns in macroinvertebrate assemblages at different spatial scales. Implications of hydrological connectivity in a large floodplain river. *Hydrobiologia*, **663**, 245–257.
- Zilli F.L., Montalto L. & Marchese M.R. (2008) Benthic invertebrate assemblages and functional feeding groups in the Parana River floodplain (Argentina). *Limnologica*, **38**, 159–171.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Box plots of macroinvertebrate traits across a gradient of lateral hydrological connectivity (High, Intermediate and Low) in each of the six river floodplains investigated.

Table S1. Taxonomic list of macroinvertebrates and their presence (+) in the six large floodplain rivers investigated.

Table S2. Taxa not found in Tachet *et al.*'s (2010) trait classification, and the taxon used as reference for trait analysis.

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