

Mediterranean-climate streams and rivers: geographically separated but ecologically comparable freshwater systems

Núria Bonada · Vincent H. Resh

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Abstract Streams and rivers in mediterranean-climate regions (med-rivers in med-regions) are ecologically unique, with flow regimes reflecting precipitation patterns. Although timing of drying and flooding is predictable, seasonal and annual intensity of these events is not. Sequential flooding and drying, coupled with anthropogenic influences make these med-rivers among the most stressed riverine habitat worldwide. Med-rivers are hotspots for biodiversity in all med-regions. Species in med-rivers require different, often opposing adaptive mechanisms to survive drought and flood conditions or recover from them. Thus, meta-communities undergo seasonal differences, reflecting cycles of river fragmentation and connectivity, which also affect ecosystem functioning. River conservation and management is challenging, and trade-offs between environmental and human uses are complex,

especially under future climate change scenarios. This overview of a Special Issue on med-rivers synthesizes information presented in 21 articles covering the five med-regions worldwide: Mediterranean Basin, coastal California, central Chile, Cape region of South Africa, and southwest and southern Australia. Research programs to increase basic knowledge in less-developed med-regions should be prioritized to achieve increased abilities to better manage med-rivers.

Keywords Biodiversity · Disturbance · Droughts · Floods · Mediterranean regions · Seasonality

Preface

Streams and rivers in mediterranean-climate regions of the world (med-rivers) are ecologically unique and perhaps among the most vulnerable to environmental damage from human activities. Gasith & Resh (1999) presented the first review of these systems but, in the past 15 years, scores of research articles have appeared that have expanded on or challenged some of the concepts raised in that article. This Special Issue attempts to synthesize information available on med-river ecology since that publication. It includes 21 review articles by leading scientists conducting research in mediterranean-climate regions (med-regions) of the world, and covers both theoretical and applied aspects. In all articles in this Special Issue,

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N. Bonada (✉)
Grup de Recerca Freshwater Ecology and Management (FEM), Departament d'Ecologia, Facultat de Biologia, Universitat de Barcelona (UB), Diagonal 643, 08028 Barcelona, Catalonia, Spain
e-mail: bonada@ub.edu

V. H. Resh
Department of Environmental Science, Policy & Management, University of California, Berkeley, CA 94720-3114, USA

the authors are referring to a mediterranean-climate (med-climate) as a climatic type at the macroclimate scale (i.e., the climatic conditions that are a result of the interaction with large-scale processes) and only consider meso- and microclimate scale characteristics (i.e., the climatic conditions that are a result of changes in orography, altitude, orientation to the coast, and continental and oceanic influences) when considering within-region variability.

This Special Issue covers a wide variety of fundamental topics that have been widely studied in med-regions. These include hydrology, nutrient and organic matter dynamics (Bernal et al., 2013; Romani et al., 2013), food webs (Power et al., 2013), riparian vegetation structure and function (Stella et al., 2013), and seasonal and interannual biological changes (Hershkovitz & Gasith, 2013; Resh et al., 2013; Robson et al., 2013). Moreover, particular attention has been focused on natural and human-driven disturbances and ecosystem responses. Thus, this Special Issue includes articles on drought (Hershkovitz & Gasith, 2013; Robson et al., 2013), fire (Verkaik et al., 2013), land use influences (Cooper et al., 2013), chemical pollution (López-Doval et al., 2013), biological invasions (Marr et al., 2013), and climate change (Filipe et al., 2013). Management and conservation issues are also covered in several articles that review hydrological connectivity (Merelender & Matella, 2013), the assessment of ecological status (Dallas, 2013), water management (Grantham et al., 2013), and river restoration (Kondolf et al., 2013) in med-regions throughout the world.

The biological diversity of med-regions is an important issue because of these areas being “hot-spots” of biodiversity and the threats they face because of high human population density and the competition for water. Articles on this topic treat biodiversity by individual med-regions (Ball et al., 2013; Davies & Stewart, 2013; de Moor & Day, 2013; Tierno de Figueroa et al., 2013). All of these articles have a comparable structure that includes: (1) biogeographical aspects relevant for riverine organisms, (2) the current status of freshwater biodiversity knowledge, (3) detailed information on richness, endemism, and biological trait characteristics by taxonomic group, (4) conservation programs and practices conducted in each med-region, and (5) future challenges related to taxonomic knowledge and conservation issues.

Unfortunately but not unexpectedly, not all relevant topics could be covered in this compendium of articles. Litter decomposition, and plant or invertebrate invasions are examples. However, some information on these topics can be found embedded in several of the articles of this Special Issue. We hope that this compendium will encourage others to write reviews of these topics and perhaps expand on some of the topics that the articles in this review stress as needing a synthesis.

In this introductory chapter, we describe the climate, the physical environment, and the biological and ecosystem responses of med-rivers to a variety of abiotic characteristics. We also provide an overview on challenges for med-river conservation and management. All topics included here relate to the whole Special Issue and more details can be found in the respective chapters we refer to. Moreover, we believe that these articles may have application beyond med-regions. For example, many of the issues discussed and the conclusions reached in this chapter and throughout the whole Special Issue can also be applied to the monsoonal tropics, some oceanic islands, and other highly seasonal areas.

Introduction

The area surrounding the Mediterranean Sea is the origin of great cultures, the development of agriculture and resource utilization, and even the establishment of current religious beliefs. However, the climate that helped foster these developments can be also found in other areas of the world. This med-climate occurs in five different regions: the Mediterranean Basin (Med-Basin), coastal California, central Chile, the Cape region of South Africa, and the southwest and southern parts of Australia (Fig. 1). All these climatic regions lie between 32° and 40°N and S of the Equator, and are located in the south or west side of these continents (Aschmann, 1973a). Although there are strong geographical differences among these areas, they all conform to Aristotle’s and Goethe’s respective descriptions of the Mediterranean as “the only place on Earth suitable for civilized life” and “the land where orange trees are in bloom!”

The med-climate is typically defined by the high seasonality in the precipitation and temperature patterns that occur annually, with hot and dry

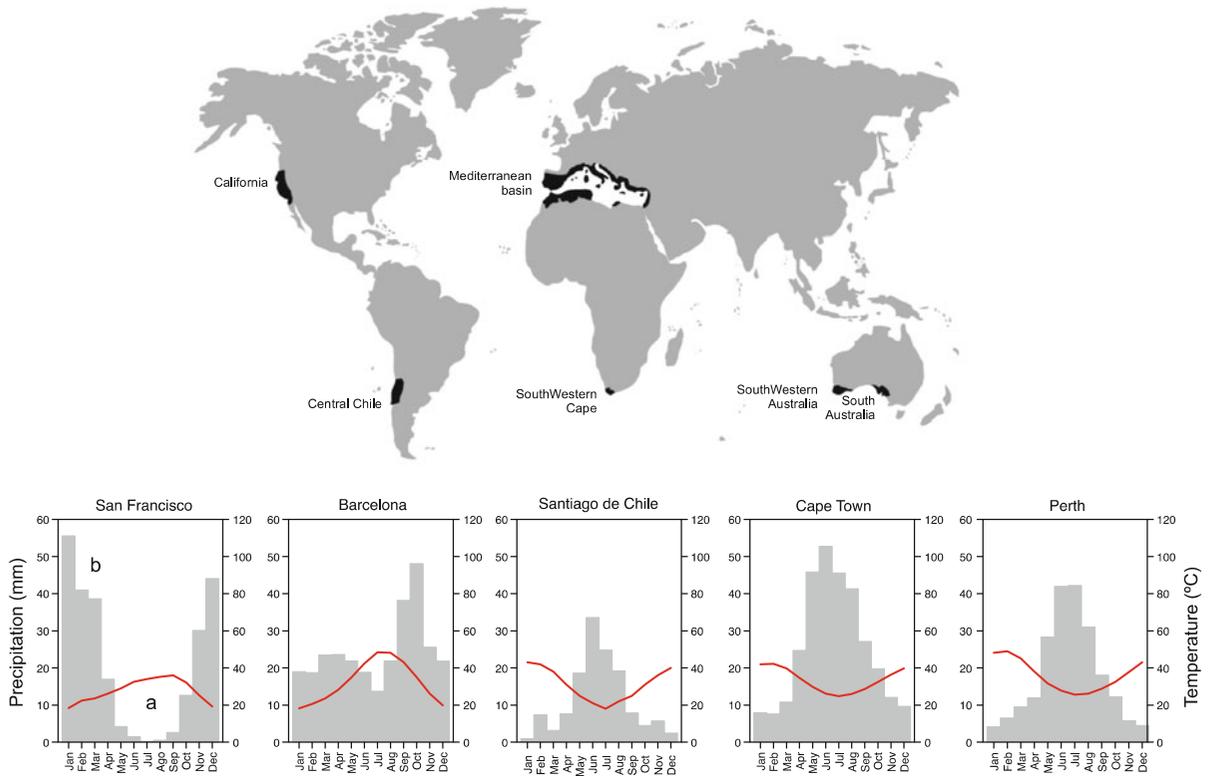


Fig. 1 Location of the five mediterranean-climate regions in the world with graphs showing monthly patterns of annual temperature and rainfall. For each graph, “a” indicates the water deficit period whereas “b” is the water surplus period. Climate data were obtained from www.worldclimate.com for all regions except for Chile, which was obtained from www.worldweatheronline.com. Med-Basin data were from the weather station located at the Barcelona International Airport (El Prat) at $\sim 41.42^{\circ}\text{N}$ 2.10°E and included temperature records from 1835 to 1987 and rainfall records from 1861 to 1987. Californian data were from the weather station located at the San Francisco International Airport (San Mateo County) at

$\sim 37.61^{\circ}\text{N}$ 122.38°W and included temperature records from 1961 to 1990 and rainfall records from 1948 to 1995. South African data were from a weather station in Cape Town at $\sim 33.90^{\circ}\text{S}$ 18.50°E and included temperature records from 1857 to 1992 and rainfall records from 1837 to 1989. Australian temperature data were from a weather station located at the Perth International Airport at about 31.90°S 116.00°E and included records from 1944 to 1992. Australian rainfall data were from a weather station located in Northam at about 31.65°S 116.60°E and included records from 1877 to 1988. Finally, Chilean data were from Santiago de Chile from an unknown weather station.

summers, and cool and wet winters predominating (Fig. 1). The annual precipitation of the med-climate areas worldwide ranges generally from 300 to 900 mm/year, with most rainfall occurring during winter months although in some med-regions spring and autumn rains often occur (Miller, 1983). Summer storms can be also frequent especially in the southern hemisphere, whereas in most northern hemisphere med-regions summers are completely free of rain (Cowling et al., 2005). Winter temperatures in med-regions are generally mild ($7\text{--}13^{\circ}\text{C}$) with infrequent frosts and snow, whereas summers are typically hot, with a mean temperature of $14\text{--}25^{\circ}\text{C}$ (Paskoff, 1973).

Interannual variability in precipitation is important in all med-regions, and the amount of precipitation defines dry, normal, and wet years. For example, in some areas in northern California (e.g., Sonoma Country), USA, precipitation has ranged from 238 to 1518 mm/year within a 7-years period (Bêche & Resh, 2007b). Overall, med-regions have been described as situated along a climatic gradient between temperate and desert climate regions (see Dallman, 1998). Moreover, even though we can describe generalities of the med-climate, climatic conditions can vary within specific areas of a med-region from mesic to xeric.

For each med-region, the geographical limits of the med-climate region depend on the climate classification system used. Many climate classifications exist and some have ancient origins. For example, Parmenides in the sixth century BC considered the five regions in the world as comprising three climate types: one that was torrid, two temperate, and two frigid (Sanderson, 1999). Even modern climatology has resulted in a myriad of classification systems (Köppen, 1936; Holdridge, 1947; Thornthwaite, 1948; Trewartha, 1968; Budyko, 1986; Prentice et al., 1992; Smith et al., 2002). The pioneering attempt and still the most commonly used modern climate classification is that of Köppen (1936), which was originally conceived to understand the vegetation boundaries present throughout the world. This classification considers values of temperature and precipitation regime based on monthly means of air temperature and rainfall totals, and classifies world climates in 30 typologies. Thus, according to Köppen, the med-climate would be included within the “dry-summer temperate” climate typology. This is the “Cs” type, with the temperature of the hottest month $>10^{\circ}\text{C}$, the coldest between -3 and 18°C , and precipitation of the driest summer month less than one-third of the amount in the wettest winter month. In addition, the subtypologies “hot summer” (“Csa” type, with temperature of the warmest month $>22^{\circ}\text{C}$) and “warm summer” (“Csb” type, with temperature of the warmest month $<22^{\circ}\text{C}$ and more than 4 months with $>10^{\circ}\text{C}$) would be included as med-climates in his classification (Khlebnikova, 2009). However, in following this classification, regions not typically considered mediterranean also would be included, such as areas in Mexico, Argentina, the northwest of Spain, or several of the Atlantic islands.

Other classifications, such as that originally proposed by Thornthwaite (1948), used the relationship between the potential evapotranspiration and the precipitation (i.e., water budget) in a region. This was an improvement of Köppen’s classification in that the water budget provides a better measure of water availability, but it has resulted in very complex and impractical maps with over 800 climate types. Further simplifications of the Thornthwaite method, such as that done by Feddema (2005) seem more appropriate and provide a much more restrictive distribution of med-regions than that of Köppen’s or Thornthwaite’s classifications.

Clearly, establishment of the temperature and precipitation limits of the med-climate is not an easy task and some authors also use a vegetation-based classification. For example, oftentimes authors refer to med-regions as areas where the climate favors a dominance of broad-leaved evergreen, sclerophyllous shrubs. However, this vegetation-based classification results in some misclassified areas because broad-leaved evergreen sclerophylls are also common in non-med-regions that receive maximum precipitation in summer, such as in Arizona, USA, or northern Pakistan (Blumler, 2005).

In the different chapters of this review series, we have considered the classification of Köppen and further simplifications to delineate med-climate areas.

The abiotic characteristics of the med-regions of the world

Below, we present a general overview of med-regions and refer to other chapters of this Special Issue for additional information and more detailed explanations. Additional information is presented in specific articles in the special issue and we refer to these below.

Mediterranean Basin

The med-region of this area consists of lands located around the Mediterranean Sea, excluding the most arid areas of Libya and Egypt but including most of the Moroccan and Portuguese Atlantic coast. It covers an area of about $1,100,000\text{ km}^2$ and is located at $31\text{--}45^{\circ}\text{N}$ (Grove & Rackham, 2001). The underlying geology is mainly composed of limestone with some sandstone, metamorphosed granites, and sedimentary deposits (Di Castri, 1981). The landscape is very heterogeneous and includes some high mountain areas, such as the Mediterranean Alps, the Betic Cordillera, and the Taurus, Atlas, and Kabylia Mountains. Lower hills and plains are very common on coastal areas and some tablelands are present in the interior regions (Fig. 2). The terrestrial vegetation is mainly dominated by evergreen trees and shrubs (usually referred to as “maquia” or “garrigue”), savannas, or dry steppe in the driest areas of the region. The most mountainous and wet regions have also several deciduous species (Grove & Rackham, 2001). For a more detailed

discussion of the med-region surrounding the Med-Basin, see Figueroa et al. (2013).

California

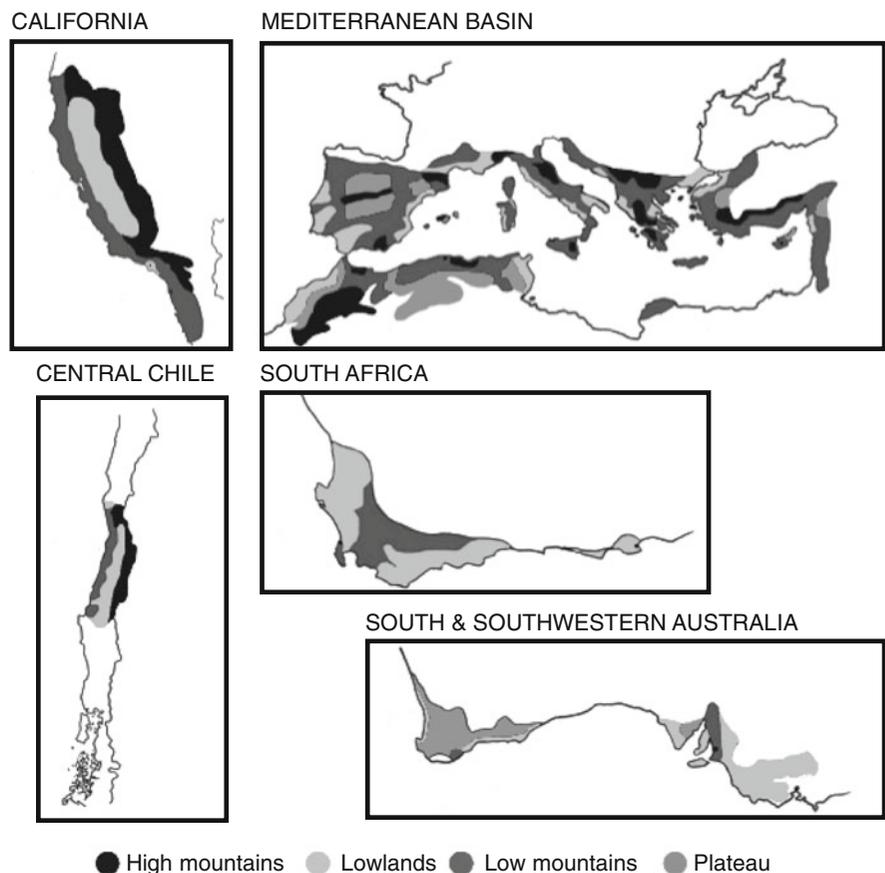
The med-region of the California extends to almost all coastal and inland California from southern Oregon and north of Mexico. It covers an area of about 250,000 km² and is located at 28–44°N (Grove & Rackham, 2001). The geology is mainly composed of metamorphosed granites and sedimentary deposits, with some small limestone areas (Grove & Rackham, 2001). The landscape includes coastal mountains, the western side of the high mountains of Sierra Nevada and a central plain (the Central Valley) that separates both mountain ranges (Fig. 2). Other high mountain ranges, such as the Klamath and Cascade mountains, are also included in the med-region area of California. The terrestrial vegetation is mainly dominated by evergreen trees and shrubs called “chaparral” and patches of redwood (*Sequoia sempervirens*) groves in

northern coastal California (Grove & Rackham, 2001). The most mountainous and wet regions also have several deciduous species of plants. For a more detailed discussion of the med-region of California, see Ball et al. (2013).

Chile

The med-region of Chile is located in the central part of the country, between regions IV and VIII of the country’s 15 administrative regions. It covers an area of about 70,000 km² and is located at 29–40°S (Grove & Rackham, 2001). The geology is mainly composed by metamorphosed granites and sediments, together with igneous batholith (Thrower & Bradbury, 1973). The landscape includes coastal ranges, a central valley, and the west side of the Andes Cordillera (Fig. 2). The terrestrial vegetation is constituted by evergreen trees and shrubs called “matorral” and woodlands with the deciduous *Nothofagus* sp. and the evergreen *Drimys winteri* (Hajek, 1991). For a more

Fig. 2 Landscape variability within each mediterranean-climate region in the world. Redrawn from Thrower & Bradbury (1973)



detailed discussion of the med-region of Chile, see Figueroa et al. (2013).

South Africa

The med-region of South Africa is located in the Western Cape area. It occupies an area of about 40,000 km² and is located at 32–35°S (Grove & Rackham, 2001). The geology mainly consists of volcanic and sedimentary rocks (sandstone and shale), which results in very acidic soils with very low nutrient concentrations (Thrower & Bradbury, 1973; Hoffman, 1999). The landscape consists of plains, and coastal and inland mountain ranges (e.g., Table Mountain and Franschoek, Drakenstein Mountains) (Fig. 2). The dominant vegetation consists of different types of assemblages of evergreen trees and shrubs called “fynbos” and “veld”. The fynbos is divided into the mountain and the coastal fynbos and includes evergreen shrubs and trees with many endemic species. The veld is divided into the Renosterveld and the Strandveld, and includes smaller evergreen shrubs located in the plain areas (Day et al., 1979). Besides the fynbos and the veld, “succulent karoo” (a biome with many succulent endemic plants) is found in the driest north-western areas whereas Afromontane forests are relicts in some coastal areas. For a more detailed discussion of the med-region of South Africa, see de Moor & Day (2013).

South and southwestern Australia

The med-region of Australia can be divided into a southwestern and a southern area, which are separated by 1000 km. It covers an area of about 350,000 km² and is located at 28–37°S (Grove & Rackham, 2001). The geology is mainly sandstone, granite, quartzite, and sedimentary deposits (Thrower & Bradbury, 1973). In the southwest, the landscape has a very low relief with coastal plains and a large inland plateau (the Darling Plateau), whereas in the south consists of plains and mountain ranges (the Flinders Ranges) (Conacher & Conacher, 1988) (Fig. 2). The terrestrial vegetation of the coastal areas is dominated by evergreen trees and shrubs called “heath” and “mallee,” whereas in the most inland areas the Jarrah and the Marri forests of *Eucalyptus* dominate (Dallman, 1998). For a more detailed discussion of the med-region of Australia, see Davies & Stewart (2013).

Biological characteristics of the flora and fauna of med-regions

The med-climate originated during the Pliocene to early Pleistocene (i.e., ~3.2 to ~2.3 mya). Therefore, med-regions have a very young climate-type geologically, and are of a far more recent origin than some of the faunal and floral biodiversity that they contain (Raven, 1973; Suc, 1984). It was previously assumed that the onset of the med-climate, and the similar Holocene climate history of all med-regions of the world (Roberts et al., 2001), resulted in similar selective forces that produced many of the common biological characteristics of the mediterranean fauna and flora we observe today (Mooney, 1982). However, recent studies on terrestrial plants have revealed that some convergent traits of med-regions, such as the evergreen-sclerophyllous vegetation, belong to pre-mediterranean lineages (Verdú et al., 2003). These findings suggest that ecological convergences among med-regions have probably been overestimated and that trait similarities may also be the result of historical and phylogenetical constraints.

Faunal and floral similarities among the med-regions of the world have long been recognized. Early explorers and naturalists arriving into the Cape region of Africa, central Chile, coastal and central California, and Western Australia in the mid-1700s noted a strong resemblance between plants of these regions with those of the Med-Basin (Di Castri, 1981). However, despite these apparent biological similarities, the biogeographical concept of a mediterranean-type biome was not established until a century after by Grisebach (1872), Drude (1980), and Schimper (1898). Today, most authors agree that the duration of the summer dry period and the persistence of typical low but not freezing winter temperatures seem to be the ecological factors that likely result in this biological similarity among med-regions (Aschmann, 1973a; Miller, 1983). In addition, the high stress from seasonal differences and the water deficit during the dry season implies that organisms must possess specific adaptations to cope with these conditions. Consequently, most of the affinities observed among these med-regions are related to physiological, morphological, or behavioral adaptations to avoid the severity of dry-season conditions (Table 1). For plants and animals living in flowing water systems, the effect of flooding is an additional selective stress (Hershkovitz & Gasith, 2013).

Table 1 List of biological trait characteristics from mediterranean plants, terrestrial arthropods, algae, riparian plants, and aquatic invertebrates

Organism	Biological traits
Terrestrial plants (Dallman, 1998)	<ul style="list-style-type: none"> Sclerophyll foliage Summer deciduous Geophytes important Annuals important Root growth adapted to drought Sprouting after fire Fire-enhanced seed germination
Terrestrial arthropods (Stamou, 1998)	<ul style="list-style-type: none"> Less permeable cuticle Higher water content Burrowing or sheltering strategies in summer Cryptobiosis Low metabolic rates Shorter life span Early maturity Parthenogenesis
Algae (Romaní et al., 2013)	<ul style="list-style-type: none"> Protective structures (carbonates, stromatolitic-like mats) Crust or mucilaginous formations Thick cell walls High extracellular polymeric substances Dormant zygospores Persisting rhizoids Photosynthetic inactivity Photooxidative protection and photoinhibition by carotenoids High colonization abilities
Riparian plants (Stella et al., 2013)	<ul style="list-style-type: none"> Shrub formation Closed-canopy species Low shoot-to-root biomass Rapid root extension Low leaf size and specific leaf area Crown dieback Branch abscission Reduced diameter growth
Aquatic invertebrates (Bonada et al., 2007a, b)	<ul style="list-style-type: none"> Small and large sizes Short life cycle duration Multivoltinism frequent Terrestrial egg-laying Asexual reproduction Resistance forms to drought Aerial respiration Flyers and swimmers Aerial active dissemination

All these traits show strategies designed to avoid and to recover rapidly from droughts

Because of the stress of the dry-season conditions, resilience and resistance are common attributes found among the med-region biota (Grubb & Hopkins, 1986; Hershkovitz & Gasith, 2013), with resilience being found more frequently than resistance (Fox & Fox, 1986). Functional similarities (i.e., adaptive biological traits) among med-regions have been widely recognized for a large variety of individual species and biological traits, as have the dynamics of recovery following disturbance (i.e., a measure of the resilience of these ecosystems, Carmel & Flather, 2004). This overall functional convergence of individual species, which is not as clear at community level (Blondel et al., 1984), suggests that ecological and evolutionary patterns and processes are deterministic, and are influenced by large-scale factors (e.g., the med-climate characteristics) rather than being dependent on historical contingencies (Pianka, 1975; Melville et al., 2006). Of course, small differences in biological traits between med-regions of the world exist because of local factors (Shmida, 1981).

Structural comparisons using floral and faunal communities, however, are more difficult because the historical and ecological contingencies of each med-region. For example, studies focused on plants (Cody & Mooney, 1978; Shmida, 1981; Coleman et al., 2003), lizards (Sage, 1973; Fuentes, 1976), birds (Cody, 1973; Herrera, 1995), terrestrial arthropods (Di Castri, 1973; Sage, 1973; Vitali-Di Castri, 1973; Majer & Greenslade, 1988; Stamou, 1998), and aquatic invertebrates (Banarescu, 1990; Bonada et al., 2008) have shown that taxa shared between med-regions either reflect patterns in place before the continents' breakup (i.e., much earlier than the origin of the climate type), from later land-connections between regions, or the result of long-distance dispersion. A clear example of the pre-continental breakup condition is the distribution of the ancient plant families Restionaceae and Proteaceae, which are almost exclusively found in South African and Australian med-regions (Deacon, 1983). In terms of later land-connections, the exchange of flora and fauna between Asia and North America through the formation of the Bering Land Bridge during glaciations is a clear example of shared taxa (Cook et al., 2005). Finally, long-term dispersal is evident in some mayfly families that originated in Africa but are now found in the Palearctic and Oriental regions, likely reflecting

past long-distance dispersion among continents (Edmunds, 1972).

In general, all med-regions are considered to be hotspots of biodiversity and have high rates of endemism (Myers et al., 2000; Smith & Darwall, 2006; Bonada et al., 2007a). The main reasons proposed for this high biodiversity are related to: (1) the high levels of landscape heterogeneity found in all med-regions compared to other biomes, and the consequent ecological mosaics that together comprise individual med-regions (Fig. 2) (Koniak & Noy-Meir, 2009); (2) the pronounced and predictable seasonality of the med-climate that results in a significant seasonal variability of biological communities (Bonada et al., 2007a); (3) the position of med-regions between two contrasting climates, that of the temperate climate and of the desert or xeric climates (Dallman, 1998); and (4) the Pleistocene glaciations in the northern hemisphere that resulted in many components of the biota using med-regions as refuge areas (Hewitt, 2004).

Although numerous national, regional, and international plans are being considered or actually initiated to preserve this high biodiversity of med-regions, all areas are currently at risk from a variety of factors, including habitat fragmentation, invasive species, pollution, and global change. For example, one of the most human-populated med-regions, the Med-Basin, hosts >25,000 plant species (>50% of them endemic) and is considered to be the fifth most vulnerable hotspot of the 25 existing areas worldwide (Malcolm et al., 2006; Cuttelod et al., 2008). Besides the enormous biodiversity of med-regions, conservation decisions are usually not easy to implement, especially in regions where complex biogeographical issues interfere with sociological and political ones, such as in the Med-Basin (Vogiatzakis et al., 2006).

Rivers in med-regions

In my country, the rain does not know how to rain

– Raimon, Valencian singer-songwriter

Abiotic characteristics

Med-rivers have flow regimes that reflect the precipitation patterns of the med-climate, and therefore

result in unique freshwater ecosystems from a hydrological and, consequently, biological point of view (Gasith & Resh, 1999). Because river flow is mainly governed by climate and patterns of precipitation, med-rivers are characterized by different levels of hydrological connectivity between seasons, with an expansion phase in the wet period (i.e., autumn–winter) and a contraction phase in the dry period (i.e., spring–summer) (Bernal et al., 2013). During the wet period, precipitation restores longitudinal, lateral- and vertical-flow connectivity; disconnected pools disappear, and the river functions again as a sequence of pools connected to riffles. In small and steep basins, this flow expansion occurs with a very short time lag because precipitation usually falls as intense storms that often lead to intense flash floods from late-summer to autumn (Camarasa-Belmonte & Segura-Beltrán, 2001; Llasat et al., 2010). During the dry period, the lack of precipitation and the high evapotranspiration rate of med-rivers result in a steadily reduction of the longitudinal-, lateral-, and vertical-flow connectivity. This reduction process can be very extreme in certain circumstances (Bonada et al., 2007b) and lead to a sequence of disconnected pools that may ultimately lack any surface water, leaving dry riverbeds. Streams that are large enough can maintain perennial flows in summer, and even some small streams can maintain flow by ground water (Vidal-Abarca, 1990; Bonada et al., 2007b). Therefore, by our definition, med-rivers are those with sequential seasonal flooding and drying periods, with increasing loss of habitat connectivity over an annual cycle that can result in temporary habitats especially during severe droughts.

Temporary rivers are not exclusive to med-regions; in fact, temporary rivers are very abundant in all climate regions in the world. For example, 59% of the total river length in United States and 39% in France is temporary (Nadeau & Rains, 2007; Snelder et al., 2013). However, when compared to temporary rivers in med-region, those in other climate regions are considered to be more unpredictable (i.e., only in extremely dry summers in most humid climates) or to last for longer periods (e.g., in desert, xeric, or polar climates) (Williams, 2006).

Although the timing of drying and flooding is very predictable in med-rivers, the intensity of these events is not. Some years have longer dry periods than others, or have a higher frequency of floods that reflect

another characteristic of med-rivers: their high inter-annual variability (Resh et al., 2013). This is particularly important in med-regions where El Niño and La Niña periods govern stream flows, such as in California or central Chile (Dettinger et al., 2000).

Med-rivers are also highly variable spatially, and consequently usually present a mosaic of flow conditions, even within a small section of stream. Thus, Gallart et al. (2012) proposed a classification of temporary rivers depending on the degree of flow connectivity. These authors subdivided temporary rivers in six different *aquatic states*, depending on the degree of longitudinal and vertical connectivity. The extremes of these states range from edaphic (without surface and subsurface water and dry hyporheic zone) to hyperrheic (the state during high flood conditions). These different states can occur simultaneously in the same river depending on the local conditions. Thus, reaches with riffles over a sand and gravel substrate have a higher probability to have a hyperrheic state than reaches with dominating pools over bedrock, where water will be retained for a longer time (Bonada et al., 2007b). Therefore, hydrological regimes in med-rivers are strongly determined by three dimensions: seasonal, interannual, and spatial.

As with designations of med-climate areas, the definition of med-rivers is thus much more simple than their delineation. While our definition can be applied generally to small- and intermediate-sized rivers, large rivers often cross non-mediterranean-climate areas or are large enough to display less seasonal variability in their discharge patterns. For example, the source of the Ebro River basin is located in a temperate climate region. However, further downstream it drains a med-climate region before it reaches the Mediterranean Sea. Thus, although the whole river does not fit into our specific definition of a med-river it is usually considered to be one from its overall characteristics (Cooper et al., 2013).

Med-rivers are not considered as a separate entity among the freshwater ecoregions proposed by the WWF (<http://www.feow.org>), which identify groups of freshwater systems having distinct freshwater species or communities. Thus, several of their ecoregions designations include med- and non-med-rivers, such as the “Cantabric coast-Languedoc” (WWF ecoregion number 403), which includes both a Spanish non-med-region and a French med-region. As with the climatic distinctions described above, this lack of a single med-

river entity is a problem of scale in that the WWF ecoregions are delineated at a mesoscale. Thus, the geographical limits of med-rivers are difficult to establish, especially if floristic and faunistic criteria are considered over hydrologic characteristics.

In all chapters of this special issue, authors refer to studies performed in med-rivers from different regions of the world. Below, we present a general overview of med-rivers characteristics of each particular med-region with notes on the abiotic features, such as hydrology, physico-chemistry features, predominant river typologies, and instream-habitat characteristics. For some med-regions, the lack of basic information on the rivers and/or the large variability on some of these features prevent generalizations, and thus are not presented.

Mediterranean Basin

Med-rivers of the Med-Basin are characterized by two annual peaks of flow, which occur in spring and autumn (Guidicelli et al., 1985). River beds have a wide variety of substrates, and bedrock is quite common in some areas, which result in the persistence of isolated pools in summer (Bonada et al., 2007b). Both siliceous and calcareous river basins occur, although the latter are much more frequent than the former. Many rivers supply the karstic aquifers present in the northern side of the Med-Basin. Natural saline rivers with high levels of sulfates and chloride are also found in some areas, such as in the most arid areas of south Spain, North Africa, and Sicily (Moreno et al., 2001; Gómez et al., 2005). Regions with coastal ranges have short and steeped-sloped rivers (Robles et al., 2002), whereas inland mountain regions harbor longer and wider rivers, some of which converge into big delta plains, such as the Po, the Rhône, and the Ebro.

Temporary rivers are part of the socio-cultural landscape. Thus, these temporary rivers have received popular names in almost all countries: *oueds* in north Africa, *arroyos* or *cañadas* in Spain, *ravins* in France, and *rambles*, *torrents*, *rieres* and *rierols* in the eastern part of the Iberian Peninsula and Balearic Islands (Vidal-Abarca, 1990). Some of these temporary rivers have been highly impacted by human activities. A popular example is the “Rambla de Barcelona,” a concrete covered street popular among the local population and tourists that was a hydrologically

active stream until 1477, when water was diverted outside of the medieval wall and then completely channelized through underwater pipes in 1900 (Casassas-Simó & Riba-Arderiu, 1992)!

California

Med-rivers in California are mainly characterized by a single annual flow peak in winter, although those with snowmelt influence (e.g., those draining Sierra Nevada mountains) may have a second flow peak in spring (Erman et al., 1988; Carter & Resh, 2005). Flow regimes are influenced by the El Niño/Southern Oscillation (ENSO) phenomenon, with higher flows than normal during El Niño years and lower flows during La Niña years, especially in the southern areas (Dettinger et al., 2000). River beds have a wide variety of substrates and bedrock is quite common in some southern California med-rivers (Cooper et al., 1986). Siliceous and calcareous river basins are present, although the calcareous geology is much more frequent and karstic rivers are common in the southern California (Mount, 1995). The state of California, together with Alaska, are those with many of the longer streams and rivers in United States (Barbour, 2003).

Med-rivers in the coastal area are short and steep-sloped, and drain medium altitude mountains, whereas rivers draining higher altitude inland mountains (e.g., those from Sierra Nevada) are larger, with most converging to the Sacramento-San Joaquin River Delta system (Mount, 1995; Carter & Resh, 2005). This river-delta system is currently considered to be one of the major ecological issues in the US. In California, most water is located in the northern part of the state but most of the population is in the large cities of the southern part (e.g., Los Angeles, San Diego). Furthermore, the Central Valley of California is the US “breadbasket,” supplying fruits, vegetables, and other agricultural products to the entire country. Consequently, a massive water diversion system was developed in the later part of the twentieth century to supply the human and agricultural needs of the central and southern parts of the state. The presence of endangered fish species in the northern rivers and the Delta, the declining quality of water available to Southern California, and the risk of levee failure from earthquakes (and constant disruption of water transfers) have underscored the urgency of dealing with these problems in a timely fashion.

Chile

Med-rivers in Chile are very similar to those found in California because the landscape configuration and geology of these two regions are similar. Thus, most river basins are orientated longitudinally from north to south, with headwaters in the Andes foothills and midstream reaches draining the Central Valley and the coastal ranges (Figueroa et al., 2013). In addition, several smaller and steep river basins are located in the coastal ranges. The annual flow peak occurs during the winter months and med-rivers are also influenced by the El Niño and La Niña episodes (Dettinger et al., 2000). River beds are also diverse in substrate and generally are either short and steep coastal rivers (called *quebradas*) or longer and wider inland rivers draining from the Andes (Thrower & Bradbury, 1973; Campos, 1985).

The med-region of Chile is the most fertile of the country and has 2/3 of the whole population in the country. Landscapes have been largely transformed to different crops that, together with livestock farming, forest plantations, industrial activities and the high population densities, have significantly modified the natural flows and the physico-chemical parameters of river ecosystems (Figueroa et al., 2013). In addition, a large percentage of the hydroelectric power generation of the country comes from the med-region. For example, the larger river basin in the area, the Biobío, which drains an area of 24,260 km² produces more than 50% of all the hydroelectric power consumed in the whole country (Goodwin et al., 2006). Water treatment and sustainable river management is still at the very early stages and the protection of freshwater species is limited (Grantham et al., 2013; Figueroa et al., 2013).

South Africa

Med-rivers of the Cape region have some unique characteristics and, similar to some other med-regions, there is a single annual flow peak in winter (e.g., see Flügel & Kienzle, 1989). Med-rivers draining from the Table Mountain are short and steeped, whereas others from inland mountains drain larger territories. Given the particular geology and soils characteristics of the Cape region, dissolved solids, nutrients, and conductivity are very low in headwaters but increase in downstream reaches (King et al., 1979; Midgley &

Schafer, 1992). Rivers located in areas with fynbos vegetation are of brown color and have very low pH because of the high amount of polyphenolic substances leached from dead vegetation, and the low calcium and magnesium concentrations in soils (de Moor & Day, 2013). In contrast, natural saline rivers are also present in some areas of the Berg and Breede river basins flowing over saline Malmesbury Shales (de Moor & Day, 2013). Most rivers have dense canopies and river beds have a diverse substrate, with large boulder dominating headwater reaches (Brown & Dallas, 1995; de Moor & Day, 2013). Very often, dense masses of Palmiet (*Prionium serratum*), an endemic reed of this med-region and of KwaZulu Natal, are present in the river edges.

Anthropogenic disturbances of south African med-rivers started relatively recently, with the arrival of the Dutch during the seventeenth century. Rivers draining the Table Mountain were channelized rapidly and landscape modifications have not stopped since then (de Moor & Day, 2013). The dominant and extensive wheat and grape production has considerably modified the physico-chemistry of rivers from the natural conditions, increasing the pH and the amount of nutrients. In addition, the inefficient performance of the Waste-Water Treatment Plants located in urban areas exacerbates the situation (de Moor & Day, 2013). All these disturbances reduce the habitat for native species in this med-region, the smallest in the world but the one harboring the highest level of endemic freshwater species (de Moor & Day, 2013).

South and southwestern Australia

Australian med-rivers also present a flow peak during the winter months and have waters with slightly lower pH compared to northern hemisphere med-rivers or Chilean ones (Bunn et al., 1986). Despite the low reliefs present in this med-region, streams and rivers arise from the highest areas (Davies & Stewart, 2013). Thus, rivers that occur in the plain, drain from the Darling Plateau in Southwestern Australia, and slightly steep-sloped rivers in South Australia drain from the Flinger Ranges. In this last med-region, many rivers flow into the Murray-Darling River Basin. This basin was the prime European settlement area in Australia, and developed into the fruit farms, vineyards, and grazing land that was the center of the Australian agricultural economy. It provides the

majority of water for irrigation and hydropower for the southeastern portion of the continent.

Because of the ancient origin of the continent, Australian med-river beds are mainly composed by highly eroded materials with gravels and sand being the most abundant substrates (Bunn, 1988). Moreover, these rivers have gone dry during recorded periods of Australia's history.

Biodiversity in med-rivers

This special issue includes chapters that analyze freshwater biodiversity of each med-region in detail and thus the specific characteristics of each of these regions are not presented here. Information for California can be found in Ball et al. (2013), for the Med-Basin in Tierno de Figueroa et al. (2013), for Chile in Figueroa et al. (2013), for South Africa in de Moor & Day (2013), and for Australia in Davies & Stewart (2013). Biodiversity of riparian vegetation is not specifically analyzed in the above-mentioned chapters but a summary for all med-regions can be found in Stella et al. (2013). All these chapters highlight that med-rivers have an enormous biodiversity with a high level of endemism. However, the current taxonomic knowledge is not homogeneous among groups and new species are still being described. Vertebrates, riparian plants, and macrophytes typically have been studied in greater detail than invertebrates and algae in all med-regions.

Adaptations for floods and droughts

The stress experienced by the fauna of med-rivers, especially that occurring in small streams, is among the most severe experienced by any lotic fauna. Sequential flooding and drying, anthropogenic impacts from high human population density, and the consequent competition between water needs for agriculture and domestic use, and the environment, make these systems the most diversely stressed of any riverine habitat in any climate type worldwide.

Because med-rivers throughout the world are subject to sequential and often severe periods of flooding and drying, the fauna present must adapt to unique stresses that require totally different adaptive mechanisms. For example, response to flooding may require strong morphological attachment features.

However, these would not be useful in drying conditions where desiccation mechanism would be favored. Because neither morphological nor behavioral adaptations are rarely if ever suitable for both types of stresses, tradeoffs and multiple types of adaptations are required (Hershkovitz & Gasith, 2013).

Adaptations of freshwater organisms to floods and droughts have been largely reported in the literature, and some specific examples have been presented for med-rivers (Table 1; Bonada et al., 2007a, b; Romaní et al., 2013). Survival during high floods and severe droughts is always a challenge for freshwater organisms. There are multiple strategies that organisms can adopt to cope with these disturbances and the ones selected for may be a function of the timing, predictability, and magnitude of these disturbances (Lytle & Poff, 2004). Lytle and Poff (2004) suggested that freshwater organisms can adapt to floods and droughts through particular life-history traits, behaviors, or morphological features. Although not specifically referring to med-rivers, they report that, in seasonal rivers, life-history traits synchronized with floods and droughts have been identified for fish, aquatic insects, and riparian plants. In contrast, in non-seasonal river types where flow disturbances are not predictable, bet-hedging strategies or specific behaviors to immediately cope with the disturbance (e.g., moving outside the river to find a temporary terrestrial refuge until the flood has receded) could have evolved. Thus, the evolution of morphological features could be more related to the frequency and magnitude of the flow disturbances than to their predictability (Lytle & Poff, 2004).

In med-rivers, life history, behavioral, or morphological adaptations to resist floods and droughts through endurance or avoidance have been observed for a wide variety of organisms (Hershkovitz & Gasith, 2013; Romaní et al., 2013; Stella et al., 2013). All these resistance strategies imply the organisms need to find refuges to shelter them during the disturbance (Robson et al., 2013). Endurance strategies refer to those that allow organisms to withstand flow disturbance. For example, some invertebrates find shelter in the hyporheic zone during a flood or survive as resistant forms in the dry river beds in summer (Franken et al., 2006; López-Rodríguez et al., 2009; Robson et al., 2011). Riparian vegetation in med-rivers can have a high flexibility and low shoot-to-root biomass, which avoid being pulled up by floods

and provides access to deeper water tables in summer (Stella et al., 2013). Alternatively, avoidance strategies allow organisms to escape from flow disturbance by actively or passively moving to a refuge (Hershkovitz & Gasith, 2013).

Avoidance strategies against drought are much more common in med-rivers than endurance ones, probably because med-river species are relicts from cooler times rather than the products of evolution under dryer climate conditions (Hershkovitz & Gasith, 2013; Robson et al., 2013). For example, riparian vegetation in med-rivers shows a wide variety of strategies to avoid summer drought, such as higher root biomass, small leaf sizes, or more frequent branch abscission, among others (Stella et al., 2013). Similarly, pool-dwelling aquatic insects have winged adults that can easily disperse to other pools as they dry out (Bonada et al., 2007a) or fish can actively migrate to perennial reaches in search of refuges as soon as the river begins to fragment (Aparicio & Sostoa, 1999; Magoulick & Kobza, 2003).

Besides the strategies that allow resistance to floods and droughts in med-rivers, resilience is also an important feature in med-rivers. Resilience (the ability to recover from a disturbance) and resistance (the ability to not succumb to a disturbance) are strongly related and usually confused, as many strategies that allow resistance facilitate further resilience (Bonada et al., 2007a; Hershkovitz & Gasith, 2013). For example, the presence of life-history stages or adaptations that are resistant to droughts enable rapid re-establishment of biota with the first autumn rains.

Community changes

The effect of the seasonal hydrological variability on biological communities in med-rivers has been well described (Gasith & Resh, 1999; Hershkovitz & Gasith, 2013; Resh et al., 2013; Robson et al., 2013). These studies emphasize the coupling of biological patterns and processes with the predictable timing of floods and droughts. However, many of these biological and ecosystem responses are not only the result of the predictable hydrological periods but also the result of changes in the number and type of available macrohabitats over the course of a year. Thus, the typical riffle-pool sequences that characterize many small med-rivers during the wet period become fragmented, resulting in a mosaic of pools during the

dry period before, and when, the river dries completely. Therefore, there is a seasonal community shift, with riffle-like taxa dominating the wet period and pool-like taxa domination the dry period (Bêche et al., 2006; Bonada et al., 2007b). Although several core taxa can persist throughout the year (Rieradevall et al., 1999), macroinvertebrate communities in the wet period are characterized by an assemblage of Ephemeroptera, Plecoptera, and Trichoptera that shift to Odonata, Coleoptera, and Heteroptera during the dry period (Bonada et al., 2007b). Richness and abundance also change seasonally. These latter orders tend to increase just after the river is fragmented into isolated pools but then decreased over time because of changes in the environmental conditions of the pools (Acuña et al., 2005). Local pool conditions and the time since the last connection of pools to riffles might serve as determinates of the community composition, richness, and abundance in pools (Bonada et al., 2006b).

Fish may show changes in community characteristics as well. Bêche et al. (2009), Marchetti & Moyle (2000), Bernardo et al. (2003), and others have generally found a pattern where fish abundance was lowest during drought years and highest during wet years. Likewise, fish communities may show marked seasonality in their abundance (Pires et al., 2000). In California, this may be attributed to differences in the timing of reproduction of native compared to non-native fishes (Moyle et al., 2003). In Portugal, Magalhaes et al. (2003) reported that the magnitude of wet-season floods also may affect resulting abundance.

Biological communities in med-rivers undergo seasonal differences in their metacommunity dynamics. During the wet period, communities form metacommunities with a hierarchical network, with downstream reaches being connected to headwaters through drift and upstream faunal movements (Brown & Swan, 2010). With habitat fragmentation during the dry period in med-rivers, however, the hierarchical structure of river ecosystems is broken and communities form metacommunities in pools connected randomly to other pools. During the dry-season, however, isolated pools act as islands. The composite metacommunity then is constrained by local environmental heterogeneity and connected by aerial dispersal (e.g., for insects). In contrast, although the few metacommunities studies done in rivers suggest that

hierarchical networks are governed by species sorting in headwaters and mass effects downstream (Brown & Swan, 2010), there is no information about controls during either the dry period or the transition between both periods.

Seasonal changes in community traits are also expected in med-rivers because species present have different strategies to cope with a particular stress or disturbance that temporally can vary in its influence. As expected in med-rivers, some community traits enable them to cope with or recover from floods and droughts (Bêche et al., 2006; Bêche & Resh, 2007a, b). However, research suggests that communities in med-rivers are characterized by a dominance of strategies that allows them to cope better with droughts at the annual scale, whereas rivers in temperate regions have community traits typically enabling them to cope better with perennial conditions (Bonada et al., 2007a).

Other secondary adaptations can be related to the resources available along the year. Thus, filter-feeders can be more important during the wet period, when floods mobilize inorganic and organic materials and move them downstream. Shredders follow the deposition of coarse organic material in riverbeds when floods recede. In contrast, during the dry period, pool conditions favor the presence of predators (Hershkovitz & Gasith, 2013), and the high temperature and insolation lead to a proliferation of algae that are consumed by scrapers (Power et al., 2013). Species interactions in med-rivers are thus dynamic and coupled to the hydrological characteristics. Pulsed floods reset food webs by bringing communities to initial successional states, but species interactions became more complex as med-rivers move from winter to spring (Power et al., 2013). Species interactions dominate over abiotic controls during the contraction phase and spatially are highly variable during the isolated-pool phase. Finally, in dry summer beds, aquatic food webs are replaced by terrestrial food webs until the first autumn rains connect river reaches and thus provide terrestrial subsidies to downstream permanent reaches that are used by fish and some aquatic invertebrates (Power et al., 2013).

In addition to these seasonal changes in community composition, long-term changes of biological communities of med-rivers are also significant (Resh et al., 2013). As with the seasonal community changes, dry years in med-rivers have communities dominated by

pool-like taxa and wet years by riffle-like taxa (Pace et al., 2013). Community changes during the dry period are also more accentuated during dry, low-rainfall years than during wet years (Acuña et al., 2005). Bêche et al. (2009), using 20-years of data from two California med-streams, found that the reduction in flow during a prolonged, multi-year drought resulted in increased abundance of in-stream and riparian vegetation, altering the stream habitat drastically. These physical changes resulted in a directional change in community composition and no clear recovery to pre-drought conditions occurred. Likewise, drought can shift biological communities with different species-trait composition (Lawrence et al., 2010). These continuing disturbances may result in irreversible regime shifts and a change from one stable community state to another (Bêche et al., 2009).

Ecosystem processes in med-rivers

Ecosystem function in med-rivers is highly modulated by the seasonality of flow. A remarkable phenomenon in med-rivers is the asynchrony between inputs of allochthonous resources arriving into rivers and the biological assimilation ability. This has been called the biogeochemical *heartbeat* (Bernal et al., 2013). At the beginning of the wet period, rainfall drains into river basins, increasing the longitudinal and lateral connectivity of rivers. This brings nutrients and allochthonous organic matter into rivers. The increase of stream flow and velocity reduce the contact between the water column and the benthos, where biological activity is mainly accomplished. Under these conditions, and independent of the level of resources available for the organisms present, most nutrients and organic matter is transported downstream via the high flows rather than being locally assimilated. Nutrient cycling is then characterized by a high nutrient export and long nutrient uptake lengths (Bernal et al., 2013).

Flash floods may have a major effect on nutrient cycling. These high-energy floods not only export nutrients downstream faster but also greatly disturb the biological communities responsible to process them (Bernal et al., 2002). In contrast, during the dry period following regular or flash floods, stream flow and velocity is reduced, increasing the contact with the benthos and facilitating nutrient retention. In addition,

the increase in water temperature and light conditions during the dry period increases autochthonous organic matter and accelerates microbial activity, promoting nutrient uptake (Romaní et al., 2013). Therefore, allochthonous and autochthonous organic matter inputs shift from the wet to the dry period in med-rivers, resulting in the differentiation of two periods of biofilm functioning (Romaní et al., 2013), and Dissolved Organic Matter (DOM) quality (Catalán et al., 2013), among other functional properties. However, in addition to autochthonous inputs being predominate during the dry period, allochthonous inputs can also increase in med-rivers as a consequence of water stress (von Schiller et al., 2011; Romaní et al., 2013).

Water stress during the dry period also diminishes the uptake and denitrification occurring in riparian forests, thereby reducing the ability of these forests to control nutrient inputs into rivers (Bernal et al., 2013). These situations are even more dramatic when rivers are fragmented into isolated pools during the dry period, and in these cases, nutrient dynamics might depend on the local characteristics of each pool (von Schiller et al., 2011; Bernal et al., 2013). Local pool conditions can also modify processing rates of organic matter, and ecosystem metabolism may even change from aerobic to anaerobic pathways if oxygen is limited (Romaní et al., 2013). Finally, nutrient dynamics present when rivers are completely dry should not be ignored in future studies, because the few existing studies have shown that riverbeds are still biogeochemically active, especially in fungal communities (Zoppini & Marxen, 2011), and the colonizing terrestrial plants could also promote nutrient mobilization. Wetted microhabitats (e.g., sediments) in dried riverbeds can also be refuges for heterotrophic biofilm communities that can rapidly respond to the organic matter inputs during the rewetting period (Romaní et al., 2013). Algae communities can also recover quickly, producing peaks of primary production just after the rewetting (Romaní & Sabater, 1997).

Disturbance in med-rivers

Med-rivers are subjected to many types of disturbances, both natural and human-induced. Seasonal floods and droughts themselves can be considered as natural disturbances, although in many cases their effects have been exacerbated by human activities,

such as water diversions and inputs (Gasith & Resh, 1999). Other natural disturbances include bush fires, many of these are also the result of human activities (Verkaik et al., 2013).

Organisms in med-rivers seem to have evolved strategies to resist or recover from these natural disturbances (Hershkovitz & Gasith, 2013). However, compared to terrestrial vegetation in med-regions, there are no apparent adaptive strategies to fire in med-river in-stream and riparian communities beyond a higher resilience ability (Stella et al., 2013; Verkaik et al., 2013). Like flooding and drying, fire is another predictable disturbance in med-regions, and mainly occurs in summer when med-rivers and riparian vegetation are dry (Verkaik et al., 2013). Likely, evolutionary consequences of drought disturbance have been much more important in terms of selective pressure to drying than to those traits acquired from fire.

Anthropogenic disturbances are numerous in med-rivers. Med-regions throughout the world have been affected for centuries, and in some cases millennia, to human activities. The type and extent of human impact differ among the med-regions of the world because of the different times of human colonization and densities of habitation (Aschmann, 1973b). The Med-Basin is by far the region that has received the longest human impact. Neolithic settlements were already present in the eastern regions of the Basin 10,000 years ago. Moreover, for example, the first water diversions for irrigation and human consumption, and non-native fish introductions, had already started at the beginning of Roman times (Copp et al., 2005; Cabrera & Arregui, 2010). Since then, landscape modifications, with their consequent effects on river ecosystems, have been continuous in the Med-Basin. The other med-regions received human impacts later, and these increased dramatically after the arrival and settlement of Europeans between the fifteen and eighteen centuries (Conacher & Sala, 1998).

Today, all med-regions suffer similar types of disturbances derived from agriculture and livestock, industrial practices, and human population growth and other accompanying activities. Changes in land use associated with human activities in med-rivers (and worldwide) have resulted in declines in discharge, changes in fluvial geomorphology, and increases in temperature and amount of light (Cooper et al., 2013). In addition, nutrients loads, pollutants, and salinity

have increased, and organic matter dynamics has been affected (Cooper et al., 2013). Land use changes have also increased habitat fragmentation and the associated human population growth have promoted human-induced fires and biological invasions (Merelender & Matella, 2013; Verkaik et al., 2013). All these human impacts have and continue to significantly impair aquatic biota, changing species biodiversity and composition, promoting faunal homogenization, and facilitating risk of species extinction.

Future climate change scenarios in med-regions predict an exacerbation of drought conditions and an increase of the occurrence of extreme events such as floods, heat waves, and wildfires (IPCC, 2007). Thus, for example, regional predictions for all med-regions indicate that warming will be larger than the global average, annual precipitation will decrease, and temperature will increase (Cayan et al., 2006; Christensen et al., 2007; Giorgi & Lionello, 2008; Giannakopoulos et al., 2009). Even though flashflood events are expected to occur more frequently in med-rivers, annual runoff is expected to decrease, and records since the 1950s agree with these forecasts (Milliman et al., 2008). Consequently, the decrease in river discharge likely will be more related to temperature increases than to precipitation decreases because of the high potential evapotranspiration of vegetation in med-regions (Tague et al., 2009). Forecasts of land use changes and increases in water demand will aggravate the present situation by reducing river discharge even further (Merelender & Matella, 2013). Species will face a trade-off between adaptation to new conditions or migration to new habitats, although the particular life-history traits of species in med-rivers might allow them to cope with climate changes up to a certain threshold (Filipe et al., 2013). In any event, med-rivers will experience shifts in community richness and composition, modifications of life-history traits, and, most likely will suffer local and regional extinctions (Filipe et al., 2013).

Besides the human-related disturbances mentioned above, new forms of disturbances are also appearing in med-regions and other areas of the world. Advances on analytical techniques have enabled the detection of new contaminants in water and sediments, such as xenobiotics or emerging organic pollutants (e.g., pharmaceuticals, personal-care products, hormones) (López-Doval et al., 2013). These contaminants are reported to have a wide variety of effects on organisms

that may eventually be found to have lethal or sublethal effects. For example, the presence of hormones in water and sediment samples caused endocrine disruption and intersexuality in freshwater fish in med-rivers (Petrovic et al., 2002; Lavado et al., 2004), and sympatholytics and non-steroidal anti-inflammatory drugs resulted in changes in biomass and growth of the midge larvae *Chironomus riparius* in laboratory experiments (López-Doval et al., 2012). These contaminants also have indirect effects on ecosystem functions. Thus, although nutrients generally increase leaf litter decomposition rates in med-rivers by stimulating microorganism activity (Menéndez et al., 2008), organic pollutants have been shown to have the opposite effect (Moreirinha et al., 2011). The seasonal variability in hydrology of med-rivers makes them more vulnerable to pollution and water extraction during the dry season (Cooper et al., 2013; López-Doval et al., 2013).

The aquatic fauna is declining more rapidly in med-regions than anywhere else in the world (Moyle & Leidy, 1992). Moreover, the ecological status is med-rivers is very poor in European-wide comparisons of streams (Prat & Munné, 2000). Med-regions also are more prone to be invaded by exotic species because natural disturbance often provides new chances for them to colonize after severe floods or droughts (Davis et al., 2000). Thus, taxonomic and functional similarity has significantly increased among med-regions because of species introductions. This has reduced the important biodiversity feature of med-rivers, which is their high levels of endemism (Marr et al., 2013). In terms of fish, for example, all med-regions have currently more introduced species than endemic species (Marr et al., 2010).

To avoid human disturbances, organisms in med-rivers may be able to find and use refuges as they do with natural disturbances (Robson et al., 2013). However, some disturbances may provide less evident refuges than others and many of them can last much longer than the life span of species. For example, available refuges to avoid salinization in a river may be scarcer than refuges to cope with hydrological disturbances. This is because salinization is a landscape-level disturbance whereas hydrological disturbances can occur locally (Robson et al., 2013). Recovery from human disturbances ultimately depends on the tolerance of species to a particular disturbance (i.e., endurance strategies), their ability to find refuges during the disturbance (i.e.,

avoidance strategies), and the presence of nearby non-disturbed habitats.

Conservation and management in med-rivers

River conservation and management in highly populated regions with high levels of biodiversity is a challenge, and clearly impose a difficult trade-off between environmental and human uses. Seasonal patterns of floods and droughts of med-rivers make this endeavor even more complex because management strategies should disentangle natural- from human-induced flow variation. Loss of habitat connectivity, for example, is part of the natural dynamics of med-rivers and contributes to their high biodiversity (Bonada et al., 2007a; Merelender & Matella, 2013). Habitat connectivity, however, is often disrupted, or made continuous, by human activities such as water abstraction or augmentation, respectively.

High water demand, together with water scarcity in med-regions, have resulted in numerous water management infrastructures, such as the building of large dams and reservoirs, or from systems enabling water transfers. These constructions have: modified habitat connectivity; changed natural flow regimes, water quality, and geomorphology; and facilitated the establishment of non-native species and created new species interactions (Cooper et al., 2013; Grantham et al., 2013; Kondolf et al., 2013; Merelender & Matella, 2013; Power et al., 2013; Robson et al., 2013; Stella et al., 2013). Alternatively, increasing habitat connectivity during the normal contraction phase in med-rivers also affects native species in med-rivers and may further promote non-native invasions (Merelender & Matella, 2013). Although the loss of natural- and human-induced habitat connectivity can apparently act as similar disturbances, differences in the timing, frequency, and duration of these disturbances may produce different effects. Thus, med-river species that have acquired traits to cope with the highly seasonal and predictable habitat connectivity losses might not be adapted to other disturbance regimes and can be seriously imperiled by them.

Management strategies should also be coupled with seasonal patterns of flow variation. Current water management approaches in med-regions do not account for these seasonal patterns, in that winter

peak flows have been reduced and low summer flows have been increased in several river basins (Grantham et al., 2013). Med-rivers that dry up in summer during dry years but flow during wet years impose an extra constraint on planning water allocations. Moreover, streams having summer low or no-flow conditions require specific reference conditions for biomonitoring programs in med-regions while, at the same time, low flow conditions enhance the effect of pollutants or organic matter on them (Dallas, 2013; López-Doval et al., 2013; Robson et al., 2013). Bioassessment approaches in med-rivers should account for this seasonal pattern, as methods used in one season may be inappropriate to another season (Feio et al., 2006). Similarly, bioassessment metrics should also consider interannual variability, and combination metrics and multivariate models seem to be better because their long-term accuracy (Mazor et al., 2009). Recently, several initiatives to assess the ecological status of temporary rivers in med-rivers have been developed (e.g., the MIRAGE toolbox, N. Prat pers. comm.). However, more efforts are needed in this regard, especially under the dramatic climate-change scenarios that are forecasted.

Bioassessment methods to assess the ecological status of med-rivers have been developed independently in each med-region and for different organisms types (Dallas, 2013; Stella et al., 2013). Because all med-regions face similar threats and constrains, collaborative efforts among stakeholders and policy makers may help to insure satisfactory management of water resources and to avoid repetition of the mistakes of the past. However, there are big gaps in sustainable water management strategies among and within med-regions, especially between developed and less-developed countries. In Chile, for example, the “Integration Era” of water management (characterized by a more sustainable water use) started recently when compared to those of other med-regions such as California or Spain (Grantham et al., 2013). Basic knowledge of med-river ecology in the less-developed countries is, however, scarce and direct implementation of strategies used in developed countries may not necessarily be appropriate.

Species conservation planning is another important issue to consider in med-region biodiversity hotspots. Med-regions are considered to have the most rapid loss of freshwater biodiversity (Moyle & Leidy, 1992). The International Union for Conservation of Nature (IUCN) provides lists of species that are vulnerable,

near-threatened, threatened, or endangered. Many species of macrophytes, molluscs, crustaceans, Odonata, amphibians, and fish in med-regions have been classified in the above categories (Ball et al., 2013; Tierno de Figueroa et al., 2013). However, other freshwater groups with many endemic species are overlooked (e.g., algae, fungi, most aquatic insect groups), likely because of the taxonomical difficulties to conduct identifications at the species level. In parallel, each med-region also has its own strategies to preserve native biodiversity by creating regional lists of vulnerable species or by protecting habitats. Just as important, species conservation approaches need to conserve refuges and maintain refuge connectivity to prevent biodiversity loss (Robson et al., 2013). Pro-active approaches that conserve habitats are required, especially in med-regions where there are still many taxonomic gaps and many species that may pass from being unknown to being lost. Conservation measures usually are the result of reactive rather than pro-active activities, despite this approach having higher economic costs (Drechsler et al., 2011).

Restoration in med-rivers is a challenge because of the highly dynamic flow regimes of these systems. Oftentimes, traditional restoration projects in med-rivers that have entailed the control of the flow regimes in attempts to make med-rivers more stable and esthetically pleasing from a societal point of view, have had disastrous results for natural communities (Kondolf et al., 2013). Allowing river channels of med-rivers to behave as highly dynamic ecosystems is probably the most effective restoration strategy to maintain the trade-off between environmental and human water uses (Kondolf et al., 2013). Future restoration strategies should also consider habitat connectivity and the creation of refuges to maintain med-river characteristics (Merelender & Matella, 2013; Robson et al., 2013). In addition, restoration projects should consider the multiple stressors currently impacting med-rivers. However, this is usually not the case, because the least costly to repair stressors and/or those that have the least political resistance often are those that are prioritized (Kondolf et al., 2013). In some cases, restoration of natural river channels is unimaginable because of the high societal and economical values now placed on what were formerly natural river systems. This is the case, for example, of the ephemeral med-river “Rambla de Barcelona” (see above), that has become a commercial

and tourist corridor with an extraordinary economic value, far greater than when it was an actual stream in the fifteenth century!

Finally, the pessimistic climate-change forecasts impose a constraint on future mitigation and conservation measures. Models on species distribution shifts may provide useful information on how and where these measures should be implemented. However, these models are still far from realistic because they usually overpredict species distributions. The incorporation of elements such as dispersal abilities, biotic interactions, long-term population or community variability, or complementary data on environmental requirements of species from laboratory experiments is necessary to provide more reliable results for management purposes (Filipe et al., 2013). The problem, in any case, is that climate change will favor species with higher temperature and pollution tolerance, and enable the establishment of new species introductions. This novel community composition will lead to homogenization, poorer ecological status, and, likely, to a redefinition of reference conditions and bioassessment methods that are appropriate for monitoring changes (Dallas, 2013). Surprisingly, even though scientific and management communities recognize the critical consequences of climate change, current policies are not designed to address climate-change issues (Johnson et al., 2001; Filipe et al., 2013).

Comparisons to temperate climate rivers

Med-regions have characteristics that fall between, and include aspects of, both temperate and desert climate regions (Romaní & Sabater, 1997; Dallman, 1998; Bernal et al., 2013). In particular, they behave more like streams in temperate regions during the wet period and more like those in desert regions during the dry period. At the same time, they show unique ecological patterns and responses produced by a well-defined and predictable seasonality on water availability (Hershkovitz & Gasith, 2013). Compared to research done in temperate rivers (temp-rivers), there are far fewer studies in desert climate rivers, and in most studies med-river characteristics have been compared to temperate ones. Based on the general literature and information in this Special Issue, we present a summary of the main differences between med- and temp-rivers (Table 2). All the

Table 2 Main differences in several ecological attributes between rivers in med-regions (M) and temperate climate regions (T), indicating in which river type each is dominant or more important

	M versus T	Comments	References
Physical and chemical parameters			
Seasonal fluctuation of physical and chemical variables	M > T		Sabater et al. (2008), Hershkovitz & Gasith (2013) and Verkaik et al. (2013)
Interannual fluctuation of physical and chemical variables	M > T		Resh et al. (2013)
Flood timing	M ≠ T	Autumn and winter in MED, spring in TEMP	Verkaik et al. (2013)
Large floods shape the geomorphic form of river channels	M > T		Kondolf et al. (2013)
Wet period hydrological connectivity	M = T		Bernal et al. (2013)
Dry period hydrological connectivity	M < T		Bernal et al. (2013)
Groundwater-to-stream hydrological flowpaths	M < T		Bernal et al. (2013)
Nutrient retention	M < T		Bernal et al. (2013)
Nutrient export	M > T		Bernal et al. (2013)
Riparian role on nutrient input regulation	M < T		Bernal et al. (2013)
Seasonal variability in nutrient uptake lengths	M > T		von Schiller et al. (2008)
Organic matter dynamics			
Inputs and retention of OM	M > T		Sabater et al. (2008)
Processing of DOM in dry periods	M < T		Romaní et al. (2013)
Processing of DOM in wet period	M = T		Romaní et al. (2013)
Recalcitrance of allochthonous OM	M > T		Romaní et al. (2013)
Seasonal pulse of allochthonous OM	M = T		Romaní et al. (2013)
Duration of allochthonous OM inputs	M > T		Romaní et al. (2013)
Summer allochthonous OM inputs	M > T		Romaní et al. (2013)
Biofilm communities			
Colonization rates by algae and bacteria	M > T		Romaní et al. (2013)
Bacterial/algal biomass	M > T		Romaní & Sabater, 2000
Polysaccharide decomposition capacity	M > T		Romaní & Sabater, 2000
Bacterial biomass and production	M < T	In rewetted sediments	Marxsen et al. (2010)
Bacterial diversity	M < T	In rewetted sediments	Marxsen et al. (2010)
Extracellular polymeric substances	M > T		Artigas et al. (2012)
Benthic organic matter storage	M > T		Alvarez & Pardo, 2006
Biomass of benthic primary producers	M > T	Measured as chlorophyll concentration	Sabater et al. (2008)
Seasonal variation in chlorophyll concentration	M > T		Sabater et al. (2008)

Table 2 continued

	M versus T	Comments	References
Macroinvertebrate, fish and riparian communities			
Regional diversity	M > T		Bonada et al. (2007a), Ferreira et al. (2007) and Stella et al. (2013)
Alpha diversity	M = T	but see Sabater et al. (2008) for M < T	Bonada et al. (2007a), Ferreira et al. (2007) and Stella et al. (2013)
Beta diversity	M > T		Bonada et al. (2007a), Ferreira et al. (2007) and Stella et al. (2013)
Rarity	M > T	In terms of abundance and occurrence	Filipe et al. (2013)
Endemicity	M > T		Filipe et al. (2013) and Marr et al. (2013)
Abundance	M < T	Slightly higher in T, no significant differences	Sabater et al. (2008)
Seasonal changes in taxa composition	M > T	More exacerbated in dry years	Hershkovitz & Gasith (2013) and Verkaik et al. (2013)
Seasonal changes in trophic structure	M > T		Sabater et al. (2008)
Grazers/shredders	M > T		Sabater et al. (2008)
Interannual changes in composition	M > T	More exacerbated in dry years	Resh et al. (2013)
Biological adaptations			
Flood adaptations	M = T		Bonada et al. (2007a)
Drought adaptations	M > T		Bonada et al. (2007a)
Resistance by endurance	M = T		Bonada et al. (2007a)
Resistance by avoidance	M > T		Bonada et al. (2007a)
Resilience	M = T		Bonada et al. (2007a)
Human-induced disturbances			
Human-induced changes to hydrology, geomorphology, and hydrochemistry	M = T	Similar but more extensive and intensive in MED	Cooper et al. (2013)
Community responses to land use changes	M = T	Similar but more extensive and intensive in MED	Cooper et al. (2013)
Immediate effects of fire on streams	M = T		Verkaik et al. (2013)
Mid- and long-term effects of fire on streams	M = T	But recovery is faster in MED	Verkaik et al. (2013)
Resilience to fire of biota	M > T		Verkaik et al. (2013)
Recovery of stream geomorphology and substrate after fire	M > T	Faster in MED	Verkaik et al. (2013)
Fire timing	M = T	In summer or autumn	Verkaik et al. (2013)
Time between fires and flood period	M ≠ T	1–6 months in MED, 9–10 in TEMP	Verkaik et al. (2013)
Role of vegetation condition for fire	M < T	Higher accumulation of debris and understory plants	Verkaik et al. (2013)
Catchment vegetation recovery after fire	M < T		Verkaik et al. (2013)

Table 2 continued

	M versus T	Comments	References
Erosion propensity after fire	M < T	Potentially lower because of the rapid recovery of vegetation	Verkaik et al. (2013)
Effects of prescribe fires versus wild fires	M = T		Verkaik et al. (2013)
Vulnerability to extinction by climate change	M > T		Verkaik et al. (2013)
Forecasted climate-change effects	M > T	Because the high levels of endemism but higher environmental tolerance and dispersal abilities in MED	Filipe et al. (2013)

topics included in that table highlight the particular characteristics of med-rivers and may help to develop parallel, future studies in desert regions to better elucidate the uniqueness of both med-rivers and temp-rivers.

Med-rivers differ from temp-rivers in several physico-chemical parameters, such as their hydrologic regime and nutrient dynamics. Organic matter dynamics also differs between these two climatic regions, especially for variables related to the contraction phase or the quality of the allochthonous inputs. In terms of their biofilm communities, many structural and functional parameters also differ between med- and temp-rivers. Diversity measures are usually higher in med- than in temp-rivers for several types of organisms, as are seasonal and interannual community changes. Given that human disturbances affecting river ecosystems are universal, med- and temp-rivers display fewer differences in this regard. However, the vulnerability of the biota seems to be greater in med-rivers despite their higher ability to cope with disturbances (Table 2).

Similarities and differences among med-rivers worldwide

Based on the description of med-rivers provided above, the few studies comparing med-river communities of the world (e.g., Bonada et al., 2008; Stella et al., 2013), and the information in this Special Issue, we prepared a summary that synthesizes the relative similarity among med-rivers in the world (Fig. 3).

This summary is based on general characteristics among the med-regions and does not consider variation within the different med-regions.

The pair-wise comparisons of med-rivers in regions worldwide indicate that no 2 med-regions are completely similar for all of the characteristics considered (Fig. 3). For example, the Med-Basin and the South Africa med-regions appear to be the most different in these characteristics, followed by the southern hemisphere med-regions. California and Chile are similar but this level is lower than that observed between California and the Med-Basin. Organic matter inputs and the level of impairment are similar among med-regions, with the latter indicating that human disturbances have similar effects worldwide. However, river typology and physico-chemistry show more differences between paired med-regions, which is likely related to non-climatic related features, such as regional geology and topography.

For biological communities, studies reveal that there are several taxa shared by two or more med-regions as a result of past historical connections and similar current climatic characteristics among med-regions (Bonada et al., 2008). Unless we consider invasive species, some of which can be found in all med-regions, these common taxa do not occur at the species level but rather at the genus or at higher taxonomic levels (Bonada et al., 2008; Stella et al., 2013). For riparian species, several genera are shared between med-regions and even between hemispheres, such as *Salix* for the Med-Basin, California, and Chile (Stella et al., 2013). California and the Med-Basin share more riparian genera, following by Australia and

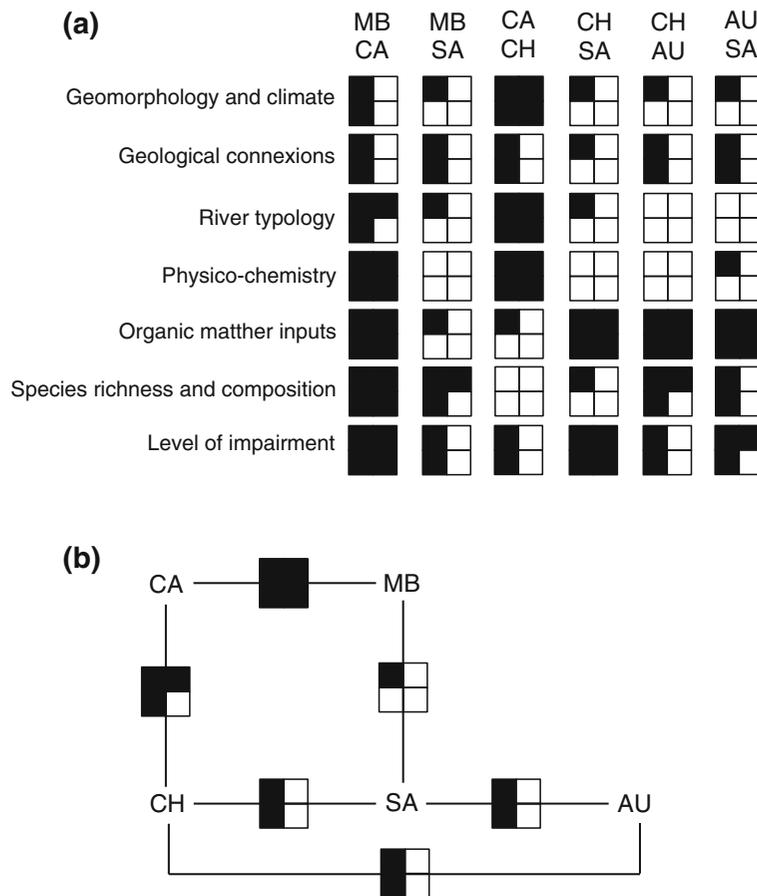


Fig. 3 Similarities among the five mediterranean-climate regions of the world (*MB* for the Mediterranean Basin, *CA* for California, *SA* for South Africa, *CH* for Chile, and *AU* for Southwestern and South Australia) based on information provided in the different chapters of this Special Issue and other references. Southern and Southwestern Australian med-regions are considered together because the few studies in South Australia. Each *large square* corresponds to 100% and it is divided in intervals of 25% units. The number of *black squares* between pairwise comparisons indicates the degree of

similarity. **a** Degree of similarity considering several topics related to rivers or organisms. See text for rationales. **b** Overall degree of similarity considering all topics. This design is based on that proposed by Di Castri (1981, 1991) for terrestrial ecosystems. Note that we have only considered pairwise comparisons of med-regions that are currently connected or have had past geological connections (i.e., connections between MB and CH, MB and AU or CA and SA or CA and AU are not considered although current human-induced connections, such as invasive species, have and continue to occur)

Chile (Stella et al., 2013). A similar global pattern is present for macroinvertebrates (Bonada et al., 2008), in that richness and composition of aquatic organisms in California are closer to the Med-Basin than to Chile. This pattern is evident despite the higher similarities in landscape geomorphology, river typology, and physico-chemical characteristics (Fig. 3), and contradicts what is known for terrestrial vegetation in these regions (Di Castri, 1981, 1991).

The level of impairment and the effects on natural communities also differ among med-regions. Non-native fish introductions, for example, are most

important in California but fish taxonomic and functional homogenization is highest in Chile and the Med-Basin (Marr et al., 2013). Land use patterns are also different among med-regions, mostly depending on difference in human population density (Cooper et al., 2013). Climate-change forecasts vary among med-regions, and expansions of med-regions are expected in the Med-Basin and the Chilean med-regions, whereas contractions are expected in the South Africa and Australia med-regions (Klausmeyer & Shaw, 2009). Likewise, spatial responses of aquatic biota to climate change also are expected to vary among med-

regions. Thus, for example, poleward migration to higher latitudes, one of the expected distributional shifts of species, will not be possible for species in the South African and Australian med-regions because freshwater habitats in the higher southern latitudes are non-existent (Dallas & Rivers-Moore, 2012).

Bioassessment approaches used in med-regions worldwide, also show many similarities (Dallas, 2013). Without considering Chile, where information and routine use of bioassessment methodologies are still in their early stages of development, benthic macroinvertebrates are the organisms most used in the other med-regions. Reference conditions are also identified and defined in a common way, and multivariate model approaches have been also developed (Dallas, 2013). Despite these similarities, not all med-regions include temporary rivers in their routine assessments, and there are also differences in how temporal variability is incorporated (Dallas, 2013). All these bioassessment approaches are being implemented in planning water policy although some countries, such as the European Med-Basin ones, are ahead of others. This is likely because of the influence of the nearby temperate European countries, where the application of biological indices to water quality monitoring have a very long history (Bonada et al., 2006a).

Conclusions

All articles included in this Special Issue have identified specific areas where knowledge is incomplete and where research efforts are needed. Together with Chile, North African and Middle Eastern countries are less studied than the other med-region countries. Basic ecological and biological information is still lacking for rivers in these countries, which also are slower in the implementation of sustainable river management policies and species conservation programs. In addition, there is a large contrast in the amount of information available on med-river ecology between northern and southern hemisphere med-regions, which is likely related to the larger number of researchers in northern med-regions. International research programs to fund research in med-regions worldwide and to promote exchange of researchers between these med-regions should be encouraged. Regional funding programs should also include funds

for long-term studies in med-regions to gather temporal information that might assist in understanding, predicting, and managing future impacts that occur in med-rivers.

Taxonomic studies must also remain a priority. Although most programs requesting research proposals in freshwater biodiversity assume that taxa currently can be identified with high certainty at the species level, this level of accuracy cannot be done in most med-regions of the world. Moreover, this assumption will never be realistically fulfilled unless further investments in taxonomy and identification of freshwater biota are allocated. Platforms, such as BioFresh (www.freshwaterbiodiversity.eu), that allow storage of freshwater biodiversity data from museums or researchers will help to increase our knowledge on biodiversity and species distribution in med-regions, and to design policies to preserve it.

After reviewing the last decade on med-river research, we can conclude that although we have significantly advanced our knowledge of med-rivers since Gasith & Resh's (1999) review, much research remains to be done. We hope that the entries in this Special Issue will help guide current and future researchers toward an understanding of how more sustainable river management can be accomplished in these highly diverse and ecologically vulnerable regions.

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