# Riparian vegetation research in Mediterranean-climate regions: common patterns, ecological processes, and considerations for management

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Abstract Riparian corridors in Mediterranean-climate regions (med-regions) are resource-rich habitats within water-limited, larger landscapes. However, little is known about how their plant communities compare functionally and compositionally across med-regions. In recent decades, research on these ecosystems has expanded in both geographic scope and disciplinary depth. We reviewed 286 riparian-vegetation studies across the five med-regions, and identified common themes, including: (1) high levels of plant biodiversity, structural complexity, and cross-region species introductions; (2) strong physical controls on plant demographics and community structure; and (3)

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P. M. Rodríguez-González Centro de Estudos Florestais, Instituto Superior de Agronomia, Universidade Técnica de Lisboa, Tapada da Ajuda, 1349-017 Lisbon, Portugal e-mail: patri@isa.utl.pt ecosystems were the most represented among the studies reviewed, but Australia, South Africa, and Chile had the greatest proportional increases in articles published since 2000. All med-regions support distinct riparian flora, although many genera have invaded across regions. Plant species in all regions are adapted to multiple abiotic stressors, including dynamic flooding and sediment regimes, seasonal water shortage, and fire. The most severe human impacts are from land-use conversion to agriculture, streamflow regulation, nutrient enrichment, and climate change. Current knowledge gaps and subjects for future research include cumulative impacts to small, ephemeral streams and large, regulated rivers, as well as understudied ecosystems in North Africa, the western Mediterranean basin, and Chile.

intensive human impacts. European and Californian

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#### Introduction

Riparian corridors occupy a small proportion of the Mediterranean-climate regions (med-regions) throughout the world but are important far beyond the land area they occupy. As resource-rich "islands" in semi-arid, human-dominated landscapes, they provide ecosystem functions and services related to water quality, microclimate, structural habitat for wildlife and fish, an energy base for the food web, and bank stability, among others (Naiman et al., 2005).

Med-region riparian zones differ from their mesic temperate and tropical counterparts in several key ways. Regionally, they support a dense and productive closed-canopy forest ecosystem relative to the surrounding landscape, which is typically a matrix of xeric woodlands, shrub and grassland communities. Optimum conditions of sunlight, nutrients, and water support high productivity and forest canopy heterogeneity that is typically more complex than in adjacent and upland areas (Fig. 1; Barbour et al., 1993; Vaghti & Greco, 2007). Because of the local availability of water, biogeochemical fluxes and nutrient cycling rates are also generally greater in riparian zones than in the adjacent semi-arid landscape (Lewis et al., 2009).

Med-region riparian areas also support unique ecological communities. In a biome with high population pressure, agricultural conversion, and landscape fragmentation, they are hotspots of biodiversity (Aguiar & Ferreira, 2005; Underwood et al., 2009). Particularly in arid and semi-arid regions, riparian areas host high local plant diversity and a greater proportion of the biome's tree species than their counterparts in temperate or tropical regions. For example, in Southern Portugal, Santos (2010) found that 46% of the total woody plant community richness resulted from strictly riparian species, compared to 28% from sclerophyllous plants. Moreover, community richness was positively affected by the area of shrubs in the riparian zone and by the absence of human activities and grazing animals. Young-Mathews et al. (2010) found that woody riparian vegetation of the Sacramento River (California) supported greater plant diversity, nearly twice as much total carbon per hectare, and lower levels of soil nitrate and phosphorus compared to adjacent land managed for agricultural uses. Riparian zones in med-regions and other semi-arid environments also host a large proportion of the surrounding biome's wildlife species for some portion of their life history (Patten, 1998; Seavy et al., 2009a). Examples of high diversity include mammalian carnivores (Matos et al., 2009; Santos et al., 2010), birds (Leal et al., 2011), and beetles (da Silva et al., 2011).

Med-region riparian areas are extremely vulnerable to the cumulative, and universally increasing, pressures from land use, streamflow regulation and diversion, and climate change. Over the last two decades, there has been a large increase in the number and diversity of riparian research studies in medregions. Because the physical-ecological linkages are so strong and so similar among med-regions (Fig. 1), there is a high potential for application of analytical approaches and tools across the biome. However, most studies are focused locally, and inter-region studies are rare. As a result, there is a need to identify common findings across med-region riparian zones in terms of ecological linkages with physical processes, riparian composition and condition, and human threats to ecosystem integrity.

In this review, we highlight several salient themes that emerge from the last several decades of riparian research on woody plant communities in med-regions. Our primary focus is on woody plant communities because of the important role they play in providing physical habitat and regulating resource fluxes. Our review highlights several pertinent issues: (1) the distribution of med-region riparian research based on a bibliometric review of published articles; (2) a comparison of woody plant genera among the five medregions; (3) physical drivers and interactions with riparian vegetation that strongly influence distribution, composition, and life history of med-region woody riparian plants; (4) human impacts to these ecosystems; and (5) recent policy initiatives, classification and monitoring methods, and technical advances that have made the recent resurgence of med-region riparian research so extensive and fruitful. Finally, we identify key gaps in our understanding and future challenges for riparian science and management.





Fig. 1 Photograph montage of med-region riparian ecosystems: a Odelouca River during summer low flow, Algarve, Portugal (photograph by P. M. Rodríguez-González). b Oued Laou valley, Morocco (S. Dufour). c Piedra Blanca Creek 1 year

after fire, California (J. Bendix). **d** Gravel bar colonization along a dynamic reach of the Biobio river, Chile (B. Belletti). **e** Fynbos riparian zone, Cederberg Wilderness Area, S. Africa (J. M. Kalwij). **f** Canning River riparian zone near Perth, Australia (R. L. Pettit)

## Recent trends in med-region riparian research

Riparian research studies in med-regions have increased at a rapid pace in recent decades. In a biogeographic analysis of research on riparian vegetation and ecogeomorphic interactions (Bendix & Stella, in press), this biome had the greatest proportional increase of recent studies when compared to all other biomes, except dry tropical forest. In med-regions, 71% of articles in print since 1990 were published within the last 5 years, compared to 54% as a global average across all terrestrial biomes.

To better understand this recent trend, we undertook a more detailed analysis of the spatio-temporal

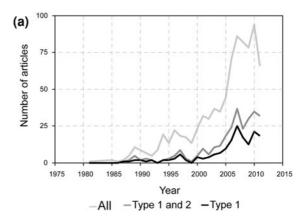


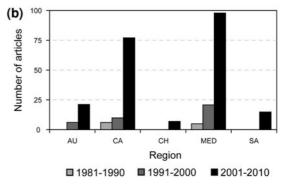
distribution of riparian research articles published amongst the five med-regions, expanding the scope to include all studies focused on vegetation, regardless of whether they also included physical processes. We performed a bibliometric analysis using results from the Scopus database, in which joint searches were performed on the word "riparian" and geographical terms, which included "Mediterranean" and individual med-region countries (e.g., "riparian" "Chile"). We searched for the co-occurrence of these terms in the title, abstract and/or keywords, and constrained our search to the period 1980-2011. The articles were then categorized manually into four degrees of relevance: (1) studies in which vegetation was the direct object of the research, or in which geomorphic drivers and vegetation exert one-way or reciprocal influences; (2) studies in which vegetation characteristics were a predictive factor or covariate for the object of the study, which was not vegetation; (3) studies in which the riparian area is either mentioned in passing, or is a relatively unimportant feature of the study; and (4) studies that are part of the geographic unit but not in the med-region. In all cases of groups 1 and 2, some aspect of vegetation was quantified (e.g., species richness, biomass, or areal extent), and we retained these studies for further analysis. We excluded those studies that took place in riparian areas without consideration of the vegetation characteristics (group 3), and those that were not conducted within the med-region portions of the countries searched (group 4). Criteria for the geographic boundaries of med-regions followed the biome maps generated by Olson et al. (2001).

Of the 861 articles returned from the series of database searches, 286 were focused on riparian vegetation distribution and ecology within med-region catchments (i.e., coded as groups 1 and 2). Within this group, the number of studies increased over the last three decades, and particularly since 2000 (Fig. 2a). Zaimes et al. (2011) document a similarly increasing trend in their review of riparian area studies in Greece, with 85% of 52 articles published after 2008. Among med-regions, the largest number of articles published since 1980 come from the Mediterranean basin (45%) and California (35%) and, within the former, 74% of the articles came from four countries: Spain, Italy, Portugal, and France. It is notable, however, that the number of articles from Australia, South Africa, and Chile has increased substantially since 2000 (Fig. 2b),

representing large proportional within-region increases over past decades.

In some cases, the recent surge in research has been indirectly promoted by regional management and policy initiatives. For example, riparian research in Mediterranean Europe has been greatly expanded under the EU's Water Framework Directive (WFD), which mandates a national assessment of health for all watercourses and a plan for improving those in poor condition (Munné & Prat, 2004; Sánchez-Montoya et al., 2009). Though the riparian plant resources are not specifically mandated in the WFD's focus on aquatic plants, fish, and benthic fauna, many member countries include some aspect of riparian assessment





**Fig. 2** Number of articles related to med-region riparian studies: **a** over time and **b** by region. *Lines series* in **a** refer to studies that were specifically focused on riparian plants (Type 1; n = 172), those that included vegetation as a part of a larger study on other organisms or processes (Type 2; n = 116), and the total number of studies returned by the original Scopus database search using the terms "riparian" and country/region keywords ("All"; n = 861). **b** The distribution of core studies (Types 1 and 2) by region and decade. *AU* Australia, *CA* California, *CH* Chile, *MED* Mediterranean basin, *SA* South Africa



in their protocols. Furthermore, Zaimes et al. (2011) link the increase in riparian studies in Greece to the establishment of another European policy, the Habitats Directive that established the Natura 2000 network.

Another clear result from our analysis is that, as with riparian studies in general, there is no primary publishing outlet for riparian vegetation studies in med-regions. The core studies in our analysis (n = 286) were published in 136 different journals  $(\bar{X} = 2.1 \text{ articles per journal})$  with more than 60% of journals containing a single article (n = 84 journals). The top twenty journals in terms of publishing frequency, which represent only 47.1% of the core articles, have an average 2010 Impact Factor of 2.19 (Table 1). A large proportion of this research is published in applied ecology journals (e.g., Restoration Ecology or Environmental Management) and less frequently in regional outlets (e.g., South African Journal of Botany) or hydrogeomorphological publications (e.g., ESPL or Geomorphology).

Table 1 Distribution of relevant riparian articles in med-regions among the top twenty journals by frequency and Impact Factor (2010 ISI Journal Citation Reports, Thompson Reuters)

	Journal name	Number	Frequency (%)	IF
1	Restoration Ecology	12	4.6	1.93
2	Environmental Management	11	4.2	1.50
3	Biological Conservation	10	3.8	3.49
4	Earth Surface Processes and Landforms	9	3.4	2.11
5	Forest Ecology and Management	9	3.4	1.99
6	South African Journal of Botany	9	3.4	1.11
7	River Research and Applications	9	3.4	1.82
8	Biological Invasions	6	2.3	3.47
9	Ecological Applications	6	2.3	4.28
10	Ecological Engineering	6	2.3	2.20
11	Hydrobiologia	6	2.3	1.96
12	Landscape Ecology	6	2.3	3.20
13	Wetlands	6	2.3	1.24
14	Aquatic Conservation: Marine and Freshwater Ecosystems	5	1.9	1.97
15	Landscape and Urban Planning	5	1.9	2.00
16	Plant Ecology	5	1.9	1.88
17	Ecosystems	4	1.5	3.68
18	Fresenius Environmental Bulletin	4	1.5	0.72
19	Geomorphology	4	1.5	2.35
20	Journal of Wildlife Management	4	1.5	1.56
		SUM	SUM	Weighted average
	Total	136	47.1	2.19

The IF-weighted average was calculated for the top twenty journals (i) using the following formula:  $(\sum (number\ articles_i/total\ articles) * IF_i)$ 

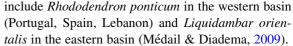
# Composition of woody riparian plant communities in med-regions

Comparison among regions

The riparian floras of all five med-regions have been described with various levels of thoroughness. For example, within the Mediterranean basin, extensive floristic or phytosociological studies have been conducted over the last 50 years in France (e.g., Archiloque et al., 1963; Gaudis-Montbrun, 1985; Varèse, 1994), Italy (e.g., Ballero, 1988; Manzi, 1988; Brullo & Spampinato, 1997), Spain (e.g., Díaz & Penas, 1987; García Fuentes et al., 1998; Fernández González & Molina, 1988; Amigo, 2005; Quesada et al., 2009), and Portugal (Vasconcelos, 1970; Costa et al., 1996; Rodríguez-González et al., 2003a; Duarte et al., 2004). In South Africa, Sieben & Reinecke (2008) describe a species template of fynbos riparian vegetation. From these and other studies, we compiled a list of the primary woody genera present in the five med-region

riparian zones in order to compare patterns of biodiversity and taxonomic origin between regions (Table 2; Appendix A in Supplementary material). Sources included descriptive flora and vegetation publications at different spatial scales (international and national articles, regional floras, theses, books, and reports), author's knowledge of their study regions, and personal communication of local botanists. From the descriptions available, we listed genera as present (P) or common (C) for each of the five medregions (Appendix A in Supplementary material), considering genera common if botanical sources indicated that their occurrence was widespread within a med-region's riparian ecosystems. We also indicated whether non-native species within the genus had dispersed widely within the region. Although we used authoritative sources for each region, the compilation is not exhaustive and necessitated a coarse-level classification as a result of the different degree of information available among and within regions. For example, within the Mediterranean basin, North Africa and the Middle East remain understudied compared to the European region.

A distinct regional flora has evolved within each of the five med-regions, though some common genera are considered native to several of these regions. These common genera include: *Populus* and *Salix* in Europe, California, and (for some Salix species) Chile; Baccharis in California and Chile; Coriaria in Europe and Chile; Muehlenbeckia in Australia and Chile; Erica, Ilex and Olea in South Africa and Europe; and Podocarpus and Maytenus in South Africa and Chile. Other med-region genera have species that invaded other med-regions outside their native ranges (e.g., Eucalyptus from Australia to the other four regions, *Tamarix* with native and non native species within the Northern Hemisphere regions, and Salix and Pinus in the Southern Hemisphere). Differences also exist within a given region; for example, Quézel & Médail (2003), in their synthesis for the entire Mediterranean basin, highlight the greater presence of Platanus, Juglans, Pterocarya, Liquidambar, and Periploca in the eastern part of the basin. The Mediterranean basin also harbors important plant glacial refugia that represent "phylogeographical hotspots", which are significant reservoirs of unique genetic diversity favorable to the evolutionary processes of Mediterranean plant species (Médail & Diadema, 2009). Examples of relict taxa within riparian communities



Despite differences in flora among regions, plant communities in these ecosystems are structurally similar, with a developed shrub layer, few dominant trees, and a patchy mosaic of herbaceous, shrubdominated, and closed-canopy ecotypes that are associated with distinct geomorphic landforms and/ or soil moisture regimes. Although it was formerly assumed that there had been a convergent evolution of traits among woody plants as a result of the unique seasonality of Mediterranean climate (med-climate) conditions (Cowling & Campbell, 1980), a recent study suggests that many common traits (e.g., sclerophyllous leaves) have come from Tertiary lineages, prior to the development of the current med-climate in these regions (Verdú et al., 2003). Thus, current trait similarities among the med-region taxa may be due to historical and phylogenetic constraints and not to evolutionary convergence (Verdú et al., 2003).

### Species invasions between regions

There has been a vast exchange of plant species among the five med-regions since the Age of Exploration (Aschmann, 1973; Fox, 1990). Various mechanisms have been described to explain how non-native species can invade and become established in plant communities, including evolutionary history, community structure, propagule pressure, disturbance, and stress (Alpert et al., 2000). Theoretically, med-region riparian ecosystems are highly invasion-prone because of disturbance-driven resource fluctuations (Davis et al., 2000), specifically the annual cycles of flooding, drought, and nutrient pulses that create new habitats for species colonization. In these cases, non-native species that exhibit a ruderal (i.e., disturbance-tolerant) life-history will be favored during colonization of bare and moist substrates; one example is the invasion of Arundo donax in California rivers (Quinn & Holt, 2008). However, there are native riparian species that are well adapted to these conditions as well, and species invasions in med-regions are more often aided by the alteration of natural disturbance regimes caused by flow regulation and bank improvements that reduce the geomorphic dynamism of the river channel (Stromberg et al., 2007). For example, shifts in flood timing on regulated rivers in the Southwestern U.S.



**Table 2** Number of dominant woody genera by family and region associated with riparian ecosystems in med-regions, based on a review of regional flora and other botanical/ecological sources

Family	Australia	California	Chile	Mediterranean basin	South Africa
Aceraceae		1			
Aextoxicaceae			1		
Anacardiaceae			1		
Apocynaceae				1	
Araliaceae				1	
Asteraceae	1	1	1		1
Betulaceae		1		1	
Bruniaceae					3
Caprifoliaceae		2		1	
Celastraceae			1		1
Chenopodiaceae		1			
Convolvulaceae				1	
Cornaceae		1			
Cunoniaceae					2
Ebenaceae					1
Elaeocarpaceae			1		
Ericaceae				1	
Escalloniaceae			1		
Fabaceae	2		1	2	
Fagaceae		1		1	
Grubbiaceae				_	1
Hippocastanaceae		1			_
Icacinaceae		•	1		
Juglandaceae		1	•		
Lardizabalaceae		•	1		
Lauraceae			2		
Liliaceae			2		1
Moraceae				1	•
Myrsinaceae				1	1
Myrtaceae	2	1	2	1	•
Oleaceae	2	1	2	1	1
Penaeaceae		1		1	1
Podocarpaceae			1		1
=	1		1		
Polygonaceae Proteaceae	1		1		2
Ranunculaceae			1	1	2
Rhamnaceae				1	
Rosaceae		2		4	1
Salicaceae	1	2	2	2	1
	1	2	2	2	1
Scrophulariaceae Smilacaceae				1	1
		1		1	
Tamaricaceae		1		1	
Thymelaeaceae				1	
Ulmaceae		1	1	1	
Vitaceae		1	1	1	
Winteraceae			1		

A more complete list of genera for each med-region is presented in Appendix A in Supplementary material along with indications as to their ecological status (common, present, and/or non-native)

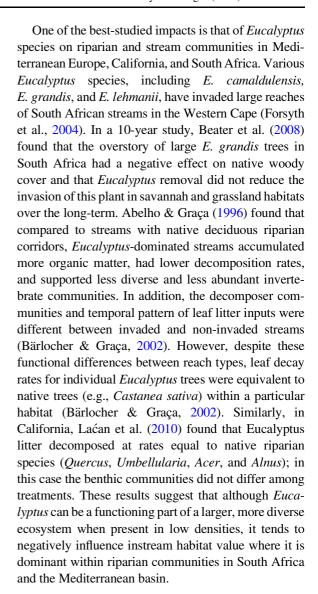


favor the reproductively opportunistic *Tamarix* over *Populus* and *Salix*, both of which have narrow germination windows (Stromberg et al., 2007). Recently *Tamarix* has been observed to invade wetland habitats in California's med-region (Whitcraft et al., 2007).

Invasive species often have a suite of adaptive traits that make them better competitors than natives, including better stress tolerance (e.g., greater salt tolerance in *Tamarix* compared to *Populus* [Di Tomaso, 1998]); multiple reproductive strategies (e.g., *Acacia* in Mediterranean basin, [Fox, 1990]), and increased productivity after disturbances (*Arundo donax* growth after fire in California [Quinn & Holt, 2008; Coffman et al., 2010]). Fox (1990) noted that fleshy fruit was a common feature among woody invaders in southern Australia, including species from the genera *Olea* (Mediterranean basin), *Chrysanthemoides* and *Lycium* (South Africa), and *Nicotiana* and *Destrum* (Chile). Bird dispersal of seeds is considered the primary vector of invasion in these examples.

In the Mediterranean basin, some of the most invasive species belong to the genera *Acacia*, *Arundo*, and *Eucalyptus* (Brunel & Tisson, 2005). In North America, by contrast, *Tamarix* has widely invaded aridland river ecosystems and shows important potential for further colonization in both riparian areas and in habitats that were not initially considered vulnerable to invasion (Whitcraft et al., 2007). Med-rivers of Chile have been strongly disturbed by human pressure (Amigo, personal communication) and the most common invasive genera there include *Rubus* and *Acacia*. In South Africa, *Arundo*, *Acacia*, and *Eucalyptus* have invaded river margins (Richardson et al., 2004; Nel et al., 2004).

The effects of invasive species can be observed at different levels from community composition to ecosystem functions and services. Cushman & Gaffney (2010) found that *Arundo* and *Vinca* have strongly negative effects on riparian plant community diversity, and advocated effective control and restoration efforts. For instream organisms, invasive riparian plants can alter trophic processes, decomposition rates, and ultimately community properties of invertebrates and fish. For example, insect shredder densities in streams in New South Wales, Australia, were significantly lower when a non-native invasive tree (*Cinnamomum camphora*) comprised >38% of the leaf litter, and growth rates for native caddisflies were depressed (Davies & Boulton, 2009).



#### Physical drivers and interactions

Plants in med-region riparian ecosystems are adapted to multiple physical drivers and stressors, including floods, droughts, and fire. Hydrological influences on riparian vegetation in med-regions are pronounced because of the extended dry season, but also because of an often flashy, streamflow regime. Bendix & Stella (in press) found that among recent riparian ecogeomorphology articles from med-regions, flood energy and sediment interactions with vegetation were the basis for 51% of studies, with an additional 21% considering multiple physical processes.



Overall, physical drivers in med-region riparian zones can be divided into five principal categories (Fig. 3): (1) flood magnitude and hydraulics; (2) flood timing; (3) streamflow and water table dynamics; (4) sediment dynamics and texture; and (5) fire. Some of these processes overlap in terms of how they affect species' life histories or community dynamics. For example, flood timing interacts with flood magnitude to control the availability of geomorphic surfaces available for colonization, and sediment texture and water table dynamics interact to provide soil moisture to plant roots (Dufour et al., 2007). Other critical influences involve feedbacks from biotic processes to the physical drivers listed above (Bendix & Cowell, 2010a).

#### Flood magnitude and flow hydraulics

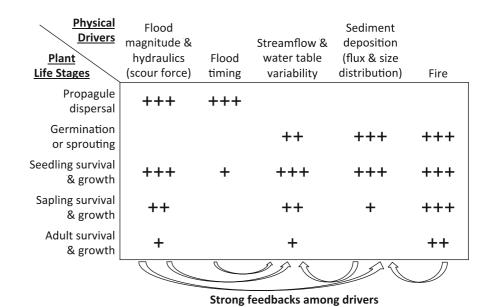
Floods affect plant communities by dispersing propagules, initiating recruitment of pioneer species on cleared, moist substrate, and killing vulnerable plants via hydraulic disturbance (Fig. 3; Bendix & Hupp, 2000). The energy associated with large floods damages plants through root scour and stem breakage (Hughes, 1997; Polzin & Rood, 2006), and the highmagnitude winter/spring floods typical in medregions, may cause significant plant mortality (Poesen & Hooke, 1997; Bendix, 1998). Many factors influence plant vulnerability, including plant size and flexibility, root and substrate characteristics, and

location relative to the distribution of energy within the streamflow (Bendix, 1999). Energy distribution is determined both by local geomorphic variables and by the vegetation itself, as feedbacks with plant density affect both hydraulic roughness (Bendix & Hupp, 2000) and the size and magnitude of scour patterns (Rominger et al., 2010). Seedlings are especially vulnerable because of their small size and limited root development, and the near-total failure of annual cohorts is a common occurrence (Sher et al., 2002; Stella, 2005).

At the landscape scale, vegetated area typically decreases after flood disturbance (Piégay & Bravard, 1997), then increases with colonization of the freshly deposited sediments, so that stand initiation and succession is linked to landform development (Michalkova et al. 2010; Corenblit et al., 2010; Stella et al., 2011). In rivers experiencing frequent high-energy flows, the resulting vegetation dynamics may not exhibit succession of plant communities, but rather a quasi-equilibrium state dominated by flood-adapted species (Bendix, 1998).

Flood magnitude is relevant not only in the context of disturbance, but also for hydrochory (i.e., dispersal by water). Hydrochory may involve transport of either seeds (Pettit & Froend, 2001) or clonal plant fragments (Douhovnikoff et al., 2005), and is most effective during overbank floods when propagules are dispersed across floodplains (Gurnell et al., 2006; Nilsson et al., 2010).

Fig. 3 Conceptual matrix of physical influences on woody riparian plants in med-regions. The number of symbols indicates the relative magnitude of the influence on each life stage. The arrows below indicate interactions between physical drivers that may mediate (i.e., reinforce or conversely lessen) effects on plants. See text for a full description of drivers, vegetation impacts, and feedbacks





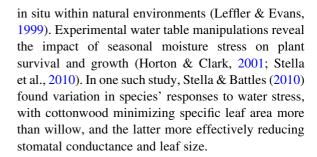
### Flood timing

In med-region riparian zones, seedling recruitment is limited by appropriate seedbed conditions and is often achieved by synchronization of seedfall with floods that scour and/or deposit moist substrate (Siegel & Brock, 1990; Pettit & Froend, 2001; Stella et al., 2006). The time window most critical for recruitment may reflect either the distinctive med-region precipitation regime (Pettit et al., 2001) or the spring runoff period for snowmelt-dominated rivers (Peterson et al., 2000; Stella et al., 2006). Because many Mediterranean species have seeds with short viability, seed dispersal is usually directly from parent plants rather than from seedbanks (Stella et al., 2006), and this can result in clustered establishment near parent trees (Pettit & Froend, 2001).

#### Streamflow and water table dynamics

In med-regions, seasonally fluctuating water tables and severe vapor–pressure deficits limit water availability for much of the growing season. Though riparian plants are generally well-adapted to disturbance (Lytle & Poff, 2004), many are intolerant of drought and rely on a phreatophytic root morphology, with deep roots permanently accessing groundwater or the stream (Karrenberg et al., 2002; Singer et al., 2012). Shallow-rooted plants, including seedlings and saplings, are particularly vulnerable to desiccation during water table recession, and this poses a major limitation on plant establishment (Fig. 3; Stella et al., 2010).

Despite their vulnerability to drought, riparian plants do demonstrate some adaptive traits. Rapid root extension and low shoot-to-root biomass ratios are common for riparian trees and potentially reduce stress related to seasonally-variable water tables (Kranjcec et al., 1998; Amlin & Rood, 2002). For example, in Western Australia, roots of Eucalyptus diversicolor can exceed 20 m (Hubble et al., 2010). Other morphological adaptations include reduction in leaf size (Stella & Battles, 2010) and specific leaf area (Busch & Smith, 1995), crown dieback (Scott et al., 1999), branch abscission (Rood et al., 2000), and reduced diameter growth (Stromberg & Patten, 1996). High water use efficiency is a common response of water-stressed plants and has been observed as enriched  $\delta$ 13C values in leaves and wood for riparian seedlings grown under experimental drought (Zhang et al., 2004; Stella & Battles, 2010) and for adult trees



#### Sediment dynamics

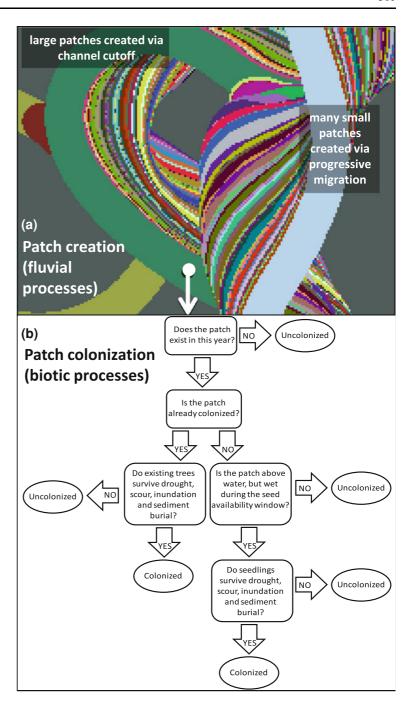
In med-region riparian settings, the varied roles of sediment dynamics include influences of bar and floodplain creation on vegetation colonization, plant mortality by burial, and textural controls on water availability (Fig. 3; Dufour et al., 2007; Hupp & Rinaldi, 2007; Bertoldi et al., 2009; Angiolini et al., 2011). On active alluvial rivers, channel migration regulates the spatio-temporal distribution of plant communities through formation of geomorphic surfaces that promote vegetation colonization (Fig. 4; Harper et al., 2011). Such surfaces include point bar deposits, mid-channel bars, and abandoned channels (Baker & Walford, 1995; Stella et al., 2011).

Sedimentation can also affect plants through mortality by burial. Many plant species can survive burial and resprout from epicormic buds (Bond & Midgley, 2001), but significant mortality may occur depending on the depth of sedimentation relative to plant size, season (dormant vs. active), and taxon-specific physiology. For example, *Tamarix* species show a greater vulnerability to burial than *Populus* (Levine & Stromberg, 2001) and *Salix* (Shafroth et al., 2010) under identical field conditions.

Sediment processes are also important because of the influence of sediment characteristics on soil resources (Francis & Gurnell, 2006). Soil texture controls capillarity and soil moisture availability, which influence plant germination, survival, and growth (McBride & Strahan, 1984; Hupp & Rinaldi, 2007). Soil texture is also related to nutrient availability. In floodplain forests along the Ibero-Atlantic coast, Rodríguez-González et al. (2010) found a complex interaction between texture, nutrients, and soil moisture. The nitrogen-fixing tree *Alnus glutinosa* grew fastest on coarse, well-drained soils regardless of nutrient availability, whereas *Salix atrocinerea*, in contrast, maintained maximal growth on fine, nutrient-



Fig. 4 Example of a process-based model of riparian cottonwood dynamics on the Sacramento River, CA (Harper et al., 2011). a The boundary conditions of the patchbased population model, which simulates the initial process of floodplain patch creation over 75 years from progressive channel migration (narrow multicolored polygons showing annual channel change) and channel cutoff and abandonment (large polygons). For each patch (white arrow leading to b), a submodel simulates cottonwood colonization using a decision matrix based on empirical relationships of germination, seedling establishment, and survival with seasonal and interannual flood characteristics. An overall population model tracks the age class of trees on each occupied patch and calculates aggregate output variables for the river corridor-wide population (Images courtesy of Fremier and the Ecological Society of America)



rich soils. *Alnus* only occurred where those soils were not fully saturated.

#### Fire

In med-regions, the impact of fire on riparian vegetation reflects the interplay between moist, fire-

resistant site conditions (Kobziar & McBride, 2006) and the tendency of severe fires to override variation in fuel characteristics (Keeley et al., 1999). Severe fires can dramatically affect riparian vegetation distribution and community dynamics (Davis et al., 1989; Vaz et al., 2011). In California, Bendix & Cowell (2010b) found that postfire composition was determined by



species' balance of mortality rate and resprouting rate, with alder (*Alnus rhombifolia*) losing its dominant position because of high mortality and low resprouting (Fig. 3). In that study, the fire's effects were spatially uniform across the valley floor, contrasting with the spatial variability of flood impacts. Moreover, the replacement of burnt mature stems by post-fire sprouts resulted in significant structural change, which affected habitat and stream shading, and decreased the stature contrast (trees versus shrubs) between riparian vegetation and the surrounding sclerophyllous shrubland.

Fire also affects competition between native and invasive species. Coffman et al. (2010) found that invasive *Arundo donax* in California was far more productive after fire than were native species. In medregion South African streams, invasive *Acacia* species regenerate through both seedling germination and prolific sprouting after fire (Pretorius et al., 2008; Reinecke et al., 2008), although their seedling germination rates can be suppressed somewhat by active reintroduction of indigenous species (Reinecke et al., 2008).

Feedbacks between physical drivers and vegetation

A growing literature is advancing our theoretical understanding of feedbacks between biological and geomorphic processes (e.g., Steiger et al., 2005; Stallins, 2006; Corenblit et al., 2011), and med-region riparian systems are strongly affected by such feedbacks (Fig. 3; Bendix & Cowell, 2010a). While vegetation responses to hydrogeomorphic influence have been outlined above, the vegetation feeds back to the geomorphic processes through its role in stabilizing banks and its contribution to hydraulic roughness (Bendix & Hupp, 2000; Gran & Paola, 2001; Gurnell & Petts, 2006, Malkinson & Wittenberg, 2007). These processes in turn affect the rate and spatial pattern of floodplain development, and influence recruitment success of seedling cohorts through seedbed availability, water table depth, and sediment texture (Figs. 3, 4).

One major agent of biogeomorphic feedbacks is large woody debris (LWD) in streams. Functional LWD (i.e., that in contact with the active channel) influences both flow characteristics and channel morphology, which affect both colonization by plants

and aquatic habitat (Gurnell et al., 2000a, b; Opperman, 2005). The complexity of these feedbacks adds to the contribution of fire to LWD supply, as shown by Vaz et al. (2011) in Portugal's Tagus River. The timing of wood inputs may be critical, and Keller & Tally (1982) have noted the potential role of LWD in buffering sediment transport following fire-induced sediment influxes from surrounding slopes. Bendix & Cowell (2010a) argued that both the temporal and the spatial distribution of wood inputs reflect the interplay of fire, post-fire flooding, and variation in the characteristics of burned species.

#### **Human impacts**

Human modifications of med-river corridors affect riparian vegetation directly and indirectly through land conversion and regulation of the hydrological regime. For example, in Greece only 10% of riparian corridors can be considered as near natural conditions (Zogaris et al., 2009; Chatzinikolaou et al., 2011). The riparian ecosystems in med-regions appear to be especially vulnerable because of cumulative impacts of these modifications, together with additive effects of climate change (Palmer et al., 2009; Seavy et al., 2009b, Perry et al., 2012).

Direct impacts of grazing, fire regime modification, cultivated agriculture and plantations, and urbanization may reduce riparian cover, influence floristic composition (Vasilopoulos et al., 2007; Dimitriou & Zacharias, 2010), and/or facilitate increased nonnative species frequency and cover (Meek et al., 2010). Land conversion and other activities are usually associated with reductions in riparian zone extent, community complexity, dispersal, and function (Katibah et al., 1984; González et al., 2010), although these impacts can be difficult to separate from other environmental variables. For example, near cities, humans may be responsible for introduction of cosmopolitan, ornamental, nitrophilous or cultivated species (Hruska et al., 2008). In rural areas where agricultural activity has decreased over the last century (e.g., piedmont reaches in south-eastern part of France), riparian woodlands have expanded into formerly grazed areas (Liébault & Piégay, 2002).

Indirectly, changes in hydrological regime and geomorphological processes strongly influence riparian vegetation. In med-region riparian zones, important



sources of change include (1) groundwater extraction and associated water table decline (Shafroth et al., 2000; Stromberg & Patten, 1996; Scott et al., 1999); (2) flow diversion and regulation, with effects on channel morphology, and riparian species extent, complexity, and function (Trush et al., 2000; Bombino et al., 2007); and (3) land uses changes in the watershed, and associated modification in sediment delivery and morphological processes (Piégay et al., 2004; Stella et al., in press). In Mediterranean and arid climates, modification of the water regime from dams, diversion, or land cover changes can also affect soil conditions, nutrient cycling (Sampaio et al., 2008; González et al., 2010), and/or salinity (Akeroyd et al., 1998; Callow & Smettem, 2007), with significant effects on ecosystem functions and vegetation patterns (Bejarano et al., 2011).

Levees and river embankments affect channel geometry through width reduction, steepened hydraulic gradients, and coarser grain sizes, leading to drier conditions on colonizable landforms. Thus, in channelized reaches, pioneer communities tend to be less diverse and dominated by drought-tolerant woody species (Dufour et al., 2007). River bed degradation can depress local water tables, resulting in decreased growth and survival of phreatophytic riparian trees, and modification of the floodplain environment to favor more xeric-adapted plants (Tabacchi et al., 1996; Bravard et al., 1997). Amplified channel incision and narrowing from human activities reduce both species richness at the reach scale and the proportion of pioneer riparian habitats (Hupp & Rinaldi, 2007). At the network scale, human modifications to channels may impact gene flow (Imbert & Lefevre, 2003). However, in specific cases, the reduction in channel mobility may increase the overall landscape diversity by facilitating expansion of woodland communities (Liébault & Piégay, 2002; Kondolf et al., 2007; Piégay et al., 2009) and human disturbances can increase the total species diversity and evenness (Kladis et al., 2011). Lastly, human-mediated invasion by nonnative species can result in altered competitive hierarchies both for establishing seedlings and for adult plants (Planty-Tabacchi et al., 1996; Aguiar et al., 2006; Stromberg et al., 2007; Mortenson & Weisberg, 2010; Santos, 2010).

Climate change resulting from increased anthropogenic greenhouse gas emissions is projected to have a particularly strong effect on med-regions (Parry et al., 2007). With an average temperature rise of 2°C or more

in the Mediterranean basin, decreased precipitation is projected, along with increased frequency and duration of the droughts and desertification. These trends have already been established in parts of the basin. In medrivers fed by snowmelt, reduced snowpack will alter the timing as well as the magnitude of flooding. A meta-study performed on the Mediterranean basin predicted an increased risk of inland flash floods from intensification of extreme events (Giorgi & Lionello, 2008). Greater fire frequencies under a warmer and drier climate are also likely in multiple med-regions, including the Mediterranean basin, South Africa, and California (Parry et al., 2007), with potential effects on riparian community composition and succession, vegetation structure, and carbon storage (Parry et al., 2007; Bendix & Cowell, 2010b).

Accompanying these ecosystem changes, the size of med-regions may change as well. In one analysis of three emissions scenarios using aggregated downscaled results from 23 general circulation models (Klausmeyer & Shaw, 2009), Chile's med-region is projected to increase from 29 to 53% over its current size by the end of the twenty-first century, whereas Australia would lose 23–51% of its current med-region area and South Africa may lose 65% of its fynbos biome. This will also result in severe contraction of many endemic species' ranges (Parry et al., 2007). Such contraction, combined with rates of human land conversion in these regions, with an average of 30% across regions, makes natural area protection important, particularly for Australia where the med-region may shrink dramatically (Klausmeyer & Shaw, 2009).

### Currently active and emerging research directions

The expansion of research since 2000 (Fig. 2) has accompanied, and often been driven by, advances in policy, management, and technology. Three main influences include (1) the development of riparian status indicators to address management and policy initiatives (e.g., European Water Framework Directive, CALFED Ecosystem Restoration Program in the San Francisco Bay-Delta region of California, and the Murray-Darling Basin Authority in Australia); (2) the propagation of remote sensing technology; and (3) the development of process-based predictive models of riparian community dynamics.



Riparian assessment and indices of ecological integrity

Plant-based river quality assessment methods have traditionally focused on the aquatic environment, and in particular the trophic state of macrophyte species, with numerous examples from temperate rivers. In Australia, the AUSRIVAS system is in common use (Halse et al., 2007), and in Europe, assessment systems include the Mean Trophic Rank system (MTR; Holmes et al., 1999) and the Macrophyte Biological Index for Rivers (IBMR; Haury et al., 2006). Some water-quality assessment approaches use riparian trees as bioindicators of trace metals (Madejón et al., 2004) or extremely acidic conditions (Rufo et al., 2011).

In contrast to these water quality metrics that use riparian plants as indicators, the direct assessment of the vegetated riparian zone's ecological integrity is a young field with little agreement as to appropriate approaches (Stromberg et al., 2006). In med-regions, the intrinsic spatio-temporal variability and its interplay with natural and human disturbances makes this field especially challenging, and a number of different approaches have been developed in the last decade to tackle this issue. For example, in Mediterranean Europe, early riparian vegetation assessment methods focused on richness and cover of native versus exotic species, as well as patch connectivity metrics (Espirito-Santo et al., 2000; Salinas et al., 2000).

The adoption of wide-ranging riparian monitoring and management mandates in med-regions has led to the development of a number of rapid assessment methods (RAMs) that could be applied extensively and simply within and amongst regions. For example, the European Water Framework Directive (WFD; 2000/60/EC) required development of new criteria to assess the ecological quality of riparian areas (González del Tánago & García de Jalón, 2006) as well as improve field assessment methods (Gutiérrez et al., 2001; Munné et al., 2003). These developments draw on the long history of aquatic ecosystem indicators (e.g., Karr, 1991; Pont et al., 2006), and the WFD guidelines allow the use of combined indices based on different biological elements such as fish and macroinvertebrates along with woody riparian vegetation (Navarro-Llácer et al., 2010). González del Tánago & García de Jalón (2006) developed a biotic quality index (RQI) based on longitudinal connectivity, woody riparian buffer width, native species composition and recruitment, and bank conditions. The qBR index (Munné et al., 2003), also developed in Spain, is based on riparian cover, structure, and channel alteration, and it has been adapted and applied in different med-region countries including Portugal (Rodríguez-González et al., 2003b), Greece (Zogaris et al., 2009; Chatzinikolaou et al., 2011), and Chile (Fernández et al., 2009; Palma et al., 2009). In Portugal, a multimetric approach was developed to assess the ecological integrity of rivers based on vegetation attributes including cover of alien and endemic species, and functional metrics associated with life cycle and reproduction (Ferreira et al., 2005a; Aguiar et al., 2009). Although this approach provided a reliable response to disturbance, classification was better at local rather than regional scales. Other assessment methods use vegetation relevé plots, consisting of a rapid inventory of species, their percent cover, and plot abiotic characteristics, to compare impacted sites with reference conditions (e.g., Sieben & Reinecke, 2008 in South Africa). Another approach is to use a scoring process that often includes component scores for riparian width and continuity, among other properties. For example, Carone et al. (2010) adapted the riparian, channel and environmental (RCE) inventory method, previously used by Petersen (1992) in the U.S., for Italian rivers. The RCE inventory method scores sixteen characteristics of the riparian zone, stream channel morphology, and the biological communities in both habitats to determine a combined index that can be used for prioritizing management actions.

Rapid assessment methods have been developed in other med-regions as well to support monitoring and management of riparian zones. For example in Australia, a rapid riparian assessment (RRA) tool has been developed to evaluate the condition of riparian zones based on buffer size and condition, geomorphic characteristics of the stream, and adjacent land-use (Taylor et al., 2005). Davies et al. (2000) developed the hierarchical habitat predictive modeling method, which uses gross catchment-level features to predict local-scale physical habitat characteristics that are measured at reference sites (Norris & Hawkins, 2000). Parsons et al. (2004) favored this approach in a comparison against three other methods of river habitat assessment currently used in Australia, and extended it to include attributes such as plant



community composition, degree of channel shading, and seedling regeneration success. These characteristics form the basis of the Australian government's recommendation for habitat assessment through its national, citizen-based, water monitoring program (Waterwatch Australia Steering Committee, 2004). In California, the California rapid assessment method (CRAM) has been developed to assess wetland and riparian ecological condition based on habitat connectivity, vegetation structure, hydrology, and biotic variables such as organic material accumulation and plant species composition (Sutula et al., 2006). This approach was designed as a cost effective tool for monitoring and managing all types of wetlands; however, its application in practice has been primarily within lentic wetlands.

# Proliferation of remote sensing and geospatial analyses

Another major influence on the recent growth in medregion riparian research has been the advance and proliferation of remote sensing and GIS tools (Dufour et al., 2012). Along med-rivers, geospatial methods have been used to map riparian vegetation and land covers at large scales in order to evaluate landscape connectivity and status (Piégay, 1996; Aguiar & Ferreira, 2005; Ivits et al., 2009; Tormos et al., 2011). At smaller scales, these tools have also been used to characterize riparian surfaces and canopy mortality (Dunford et al., 2009), changes in corridor pattern (Ferreira et al., 2005b), post-flood vegetation colonization (Hervouet et al., 2011), roughness generated by the vegetation (Forzieri et al., 2010), or other physical characteristics such as landform age (Bertoldi et al., 2011). Recent improvements in remote sensing and GIS technology allow finer descriptions with very high spatial resolution images that can be used to distinguish individuals and species (Hamada et al., 2007; Dunford et al., 2009). Often, these rely on lowaltitude aerial photography from planes, balloons, or unmanned aerial vehicles. In applied contexts, GIS and remote sensing have been used to detect invasive species (Hamada et al., 2007) and to provide information for river surveys at large scale in conjunction with field data collection in Italy (Carone et al., 2010), Spain (Magdaleno et al., 2010), California (Seavy et al., 2009a), and Australia (Johansen et al., 2010), among other areas.

Within the last decade, the proliferation of light detection and ranging (LiDAR) technology has improved researchers' abilities to analyze riparian canopy properties and associate structural attributes with fine-scale geomorphic features, avian habitat, and riparian zone connectivity (Seavy et al., 2009a; Benjankar et al., 2011; Johansen et al., 2010). Such tools also provide useful information to analyze species composition and distribution through spectral analysis (Fernandes et al., 2010), and to develop spatially explicit approaches to linking geomorphic and vegetation co-evolution (Girvetz & Greco, 2009; Stella et al., 2011; Harper et al., 2011) and large scale monitoring (Wiederkehr et al., 2010; Tormos et al., 2011).

#### Process-based vegetation models

The increased understanding of hydrogeomorphic drivers of riparian vegetation dynamics (e.g., Fig. 3; Swift et al., 2008; Stella et al., 2011) has facilitated the development of process-based and numerical models to predict vegetation change under altered future conditions of land use and climate (e.g., Harper et al., 2011; Benjankar et al., 2011; García-Arias et al., in press). Unlike probabilistic models of vegetation associations with landscape, abiotic, or other features, these models typically predict vegetation dynamics using mechanistic relationships and parameters based on empirical studies (Fig. 4). For example, the CASi-MiR-vegetation model, which was applied across a range of diverse European river systems (Rivaes et al., 2011, 2012), simulates vegetation change as an iterative process based on an initial vegetation map, floodplain topography, river hydrology, and spatially distributed physical drivers such as shear stress, flood duration, and height-over-base flow level (Benjankar et al., 2011). This spatially explicit approach allows for testing the impact of different management plans or restoration actions, such as implementing environmental flows. In California, Harper et al. (2011) developed a patch-based model of riparian floodplain colonization and forest dynamics (Fig. 4), which simulates interactions between model inputs of floodplain topography, annual discharge series, and empirderived ically relationships between demography and river hydrology (Stella et al., 2006, 2010; Stella & Battles, 2010). Both this model and CASiMiR-vegetation have been calibrated using field



data and are in various stages of model validation and/ or prediction of future conditions under changing climate and hydrology.

# Future research needs and management applications

Research gaps in med-region riparian ecosystems

Going forward, our ecological understanding of medregion riparian zones will be improved by more basic research in understudied ecosystems, classification systems that apply across ecoregions, and an understanding of how biophysical processes differ with spatial scale, especially for small, ephemeral streams (Zaimes et al., 2011) and for extremely large, regulated rivers subject to multiple human stressors (Stella et al., 2011). We recommend more research be initiated in the relatively understudied med-regions in the Southern Hemisphere, North Africa, and the western Mediterranean basin to complement the extensive studies conducted to date in Europe and California.

Second, we need to enlarge the scope of riparian studies beyond the site and reach to a true biogeographical perspective at the corridor, catchment, and regional scales. For this purpose, conceptual and practical tools (e.g., statistical and mechanistic models) need to be developed to scale up local processes to the larger landscape without oversimplifying the spatial variability in environmental drivers. This approach requires accurate and spatially distributed quantification of physical conditions, biotic functions, and ecosystem services in order to set management priorities and identify the most important sites to protect and restore. Thus, we need more general classification systems and a solid assessment framework that include indicators that work across systems and scales (Brierley & Fryirs, 2005; Piégay et al., 2009).

Third, we need to understand how physical stressors interact with increased water scarcity and climate variability that are occurring in most med-regions (Parry et al., 2007; Klausmeyer & Shaw, 2009). For example, we need to better understand how increased drought, fire, and resource variability under climate change will affect riparian species' life histories and population dynamics, if we are to improve our predictions of riparian community response (Perry et al., 2012). Our tools for achieving this will include novel applications of existing methods to riparian zones to understand ecohydrological processes governing vegetation function and distribution. For example, dendroecological methods are being increasingly used to infer influences on tree growth and survival in riparian zones (Dufour & Piégay, 2008; Rodríguez-González et al., 2010; Stella et al., in press) and can be coupled with stable isotope analysis that indicate changes in water stress, ecophysiological functioning (Horton & Clark, 2001; Leffler & Evans, 2001; Stella & Battles, 2010; Schifman et al., 2012), and shifts in source water use (Busch & Smith, 1995; Singer et al., 2012).

Applications to management of med-region riparian ecosystems

The increased understanding achieved over the last decade in riparian vegetation pattern and functioning provides a solid basis for rational resource management in med-river ecosystems (e.g., Downs et al., 2011). Approaches with strong precedent include releasing environmental flows to benefit riverine and riparian species (Hughes & Rood, 2003; Rood et al., 2005), as well as non-native species management (Reinecke et al., 2008). However, there are still gaps and deficiencies in the transfer from scientific findings to sound policies (Maruani & Amit-Cohen, 2009), notably because of the extensive time required to integrate research results into conservation and restoration strategies (Palmer et al., 2010). Both ecological and social consequences of restoration practices are not well understood yet, and the transfer of scientific knowledge to practitioners must be improved (Christian-Smith & Merenlender, 2010).

Because the five med-regions are geographically isolated and the majority of researchers work in a single primary region, increased exchange and comparisons among regions should benefit both their science and management (e.g., Chatzinikolaou et al., 2011). Programs that monitor restoration and management success can be more systematized to capitalize on ecosystem similarities between regions (e.g., see Reinecke et al., 2008 and Marais & Wannenburgh, 2008 for examples of non native species management programs in riparian corridors in South Africa).

In strongly modified systems, conservation, and restoration strategies need to enhance ecological



integrity of the ecosystems (e.g., relative to properties of reference sites), to quantify ecosystem services, and to recognize the human demands and plan for alternative scenarios (Tockner et al., 2003; Bombino et al., 2008; Bertoldi et al., 2009; Sánchez-Montoya et al., 2009; Dufour & Piégay, 2009; Dufour et al., 2011). This requires that we consider various human priorities (e.g., aesthetic, economic, cultural values) along with biophysical functions to address multiple management objectives (Piégay et al., 2005; Santos, 2010; Cottet et al., 2010). Assessment methods will need to consider the role of novel riparian habitats, for example those dominated by non-native species (e.g., Stromberg et al., 2007). Whereas future management should seek to reverse destructive patterns such as deliberate introductions of non-native species, our modern assessment tools need to acknowledge the ecosystem services that they do provide (Stromberg et al., 2007; Schlaepfer et al., 2011).

Finally, specific strategies for riverine and riparian management need to take into account future changes under non-equilibrium conditions (Palmer et al., 2009). Globally, human pressure will increase in med-regions (Underwood et al., 2009) and climate change is reducing the water supply in most of them (Klausmeyer & Shaw, 2009). Thus, research is needed on specific vulnerabilities and thresholds that can drive riparian systems into alternative undesirable states (e.g., Sher et al., 2000; Perry et al., 2012). On regulated rivers, environmental flows that mimic natural discharge regimes should capitalize on climatic stochasticity, making the most of wet years where high flows can be delivered without conflicting with regulation goals (Poff et al., 1997; Hughes & Rood, 2003; Rood et al., 2005; Stella et al., 2010). These sorts of opportunistic restoration strategies, in conjunction with realistic assessments of our operational limits, offer the best hope for water and land managers to limit further degradation and increase resilience of med-region riparian ecosystems that are under increasing demand for water, land, and functioning services.

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