Freshwater Biology (2008) **53,** 772–788 doi:10.1111/j.1365-2427.2007.01940.x

Multi-scale assessment of macroinvertebrate richness and composition in Mediterranean-climate rivers

NÚRIA BONADA*, MARIA RIERADEVALL*, HELEN DALLAS†, JENNY DAVIS‡,
JENNY DAY†, RICARDO FIGUEROA§, VINCENT H. RESH¶ AND NARCÍS PRAT*
**Department of Ecology, University of Barcelona, Barcelona, Spain*
†Department of Zoology, University of Cape Town, Cape Town, South Africa
‡Aquatic Ecosystems Research Group, Murdoch University, Murdoch, Western Australia
§Aquatic Systems Research Unit, Environmental Science Center EULA-Chile, University of Concepcion, Concepción, Chile
¶Department of Environmental Science, Policy & Management, University of California, Berkeley, CA, U.S.A.

SUMMARY

1. Similar constraints in distant, but climatically comparable, regions may be expected to yield biotic assemblages with similar attributes. Environmental factors that constrain communities at smaller scales, however, may be different between climatically similar regions. Thus, patterns observed at large scales may differ from those detected at small scales, and international comparisons should be focussed at multiple scales.

2. Mediterranean-climate regions (MCRs) are characterized by remarkable seasonal variability in precipitation and temperature. Accordingly, rivers in these regions have seasonal and predictable floods and droughts, and temporary reaches are frequent. Present in six geographical regions of the world, MCRs have similar environmental constraints and are ideal for testing intercontinental similarities between macroinvertebrate communities.

3. We examined aquatic macroinvertebrate taxon richness and composition in MCRs at three scales: regional, reach and macrohabitat. At the regional scale, the Mediterranean Basin had the highest taxon richness at family level, and southwestern Australia the lowest. Taxonomic composition showed *c.* 85% similarity between the northern hemisphere MCRs of California and the Mediterranean Basin, which were followed in similarity by South Africa. The two Australian MCRs (South west and South) showed a similarity to each other of about 70% whereas the Chilean fauna was the most distinct.

4. At the reach scale, taxon richness was not significantly different between permanent and temporary reaches in any MCR, whereas taxonomic composition was significantly different among northern hemisphere MCRs. At the macrohabitat scale, taxon richness was not significantly different between lotic and lentic macrohabitats within any of the MCRs, but differences in macroinvertebrate communities were found between macrohabitats when considering regions.

5. Our results show that the strength of similarity between distant but climatically similar regions is scale-dependent, being highest at the macrohabitat scale. Although the similarities in richness and composition at the macrohabitat scale are presumed to be universal, the seasonal predictability of drought in MCRs is expected to result in characteristic macroinvertebrate responses at the reach scale. We suggest, however, that regional evolutionary history and environmental characteristics may override this general pattern of a similar response of MCRs at different scales. The Mediterranean Basin and

---

Correspondence: Núria Bonada, Department of Ecology, University of Barcelona, Diagonal 645, 08028 Barcelona, Spain.
E-mail: bonada@ub.edu

California, having similar historical and environmental condition, thus appeared as the most similar MCRs at all scales.

Keywords: local composition, macrohabitat scale, macroinvertebrate structure, Mediterranean regions, reach scale, regional composition, temporary rivers

Introduction

The distribution of organisms is determined by a set of environmental factors acting hierarchically from large to low scales (Poff, 1997), and climate is an obvious candidate as a large-scale factor. Intercontinental comparisons of community attributes have a long tradition in ecology and biogeography, and several authors have hypothesized that community attributes should be similar when comparing climatically similar regions (e.g. Paruelo *et al.*, 1998; Lobo & Davis, 1999; Dynesius *et al.*, 2004). In contrast, if there is little similarity in community attributes, it may be because differences in factors independent of climate (such as evolutionary history or regional environmental characteristics) prevail. Species richness and functional assemblages are community attributes that may be less affected by these non-climatic factors than is taxonomic composition (which is largely dependent on zoogeography), and most of the international comparisons have thus focused on these parameters (Lein, 1972; Cowling & Witkowski, 1994; Lamouroux, Poff & Argermeier, 2002). Information on biological traits is not available for all taxa throughout the world, however. Moreover, by focusing an analysis only on richness, we get only a partial view of the convergence between climatically similar regions. A complementary approach would be to analyse the responses of local taxonomic composition to factors that directly or indirectly relate to climatic characteristics at several local scales. If distant but climatically similar regions have similar multi-scale responses, then these climate-related factors are presumably strong enough to overcome regional differences in evolutionary history and environmental characteristics.

A number of authors have recommended intercontinental comparisons at several scales (Morris, 1987; Tonn *et al.*, 1990). Patterns observed at large scales can differ from those detected at low scales because environmental factors that constrain communities at lower scales, such as geological or soil characteristics, may differ between climatically similar regions. Thus, intercontinental similarities may be over- or underestimated if assessments are not focused at multiple scales. In practice, however, most studies that address intercontinental comparisons centre on only one scale.

Mediterranean-climate regions (MCRs) are ideal for testing intercontinental similarities because they are present in six distant regions of the world, distributed over five continents: the Mediterranean Basin, California, Chile, South Africa and southern and southwestern Australia. Because of seasonal variability in temperature and precipitation in MCRs, rivers in these regions are characterized by highly variable annual and interannual discharge regimes, with seasonal and predictable floods and droughts (Gasith & Resh, 1999). Such conditions make these systems different from those subject to supra-seasonal droughts (Lake, 2003). Thus, depending on local conditions, rivers in MCRs can have permanent and temporary reaches. During the dry period, as drought progresses, reaches gradually lose lotic sections and the remaining pools may become disconnected. These pools may dry up or they may persist until the following wet season when rainfall restores flow (Gasith & Resh, 1999; Lake, 2000). Thus, alterations in hydrological connectivity (from permanent to temporary) at the reach scale involve changes at the macrohabitat scale across seasons (e.g. macrohabitat availability changes from riffles and runs connected to pools, to pools connected to riffles and runs, and finally to isolated or disconnected pools).

The first intercontinental comparisons between MCRs focussed on botanical aspects, and revealed a strong similarity in morphology and structure of plants coping with summer drought (e.g. Mooney & Lloyd Dunn, 1970; Aschmann, 1973; Specht, 1979). Other studies on lizards, birds and terrestrial arthropods followed later (e.g. Fuentes, 1976; Cody & Mooney, 1978; Stamou, 1998) and showed similarities in community structure and functional characteristics.

Although intercontinental similarities between biomes, climates and continents have, however, been analysed using aquatic macroinvertebrates and fish (e.g. Lamouroux *et al.*, 2002; Vinson & Hawkins, 2003), none of these analyses exclusively examines similarities between MCRs.

In this study, we compared aquatic macroinvertebrate taxon richness and composition in MCRs of the world at three scales: region, defined as the area in each country subjected to a Mediterranean climate; reach, defined as a river section that can be permanent (i.e. flowing water throughout the year) or temporary (i.e. dry conditions in summer) and macrohabitat, defined as a combination of substratum and flow providing lotic (i.e. riffles and runs) and lentic (i.e. pools) conditions within a reach. At the regional scale, we analysed the pool of macroinvertebrate families throughout each MCR (i.e. regional richness and composition). Because global richness appears to be strongly related to climate (Francis & Currie, 2003), we should thus expect climatically similar regions to have similar regional richness. In addition, given that MCRs have undergone distinct geological processes, divergence in regional taxonomic composition should be higher between those with greater geological isolation, while those connected for a longer geological time should show greater similarities. For example, similarities might be expected between California and the Mediterranean Basin because of the connections between North America and Europe through the north Atlantic and Pacific routes (Banarescu, 1990) and between the southern MCRs because they all once formed part of Gondwanaland.

At the reach scale, we analysed taxon richness and composition in response to the temporary habitat by comparing permanent and temporary reaches of rivers in each MCR. At the macrohabitat scale, we studied taxon richness and composition in response to lotic and lentic conditions in rivers in each MCR. Temporary and lotic–lentic conditions are considered here as factors directly and indirectly related to climate respectively. Precipitation directly affects river discharge, whereas variability in seasonal discharge involves differences between lotic and lentic conditions (Bonada, Rieradevall & Prat, 2007b). Given the high biodiversity present in each MCR, the predictability of summer droughts (Gasith & Resh, 1999), and the fact that Mediterranean climate has persisted for at least 3.2 My (Suc, 1984), we should expect that the present taxa in MCRs are adapted to both temporary and lotic–lentic conditions. If so, taxon richness should be similar between permanent and temporary reaches, and between lotic and lentic macrohabitats, but taxonomic composition should differ. Thus, we hypothesized similar responses between MCRs in taxon richness and composition within reach and macrohabitat scales, independently of whether evolutionary history and environmental characteristics differ. Otherwise, more recent geological processes that have modified the evolutionary history of a MCR, or regional environmental factors that constrain organisms more than temporary or lotic–lentic conditions do, could prevail and similarities would not be found.

Methods

Regional richness and composition

The regional pool of families in each MCR (i.e. all families recorded in each region) was determined using all available data, including our own results as well as published and unpublished data compiled using faunal lists from all MCRs. The family level was used because: (i) at the large scale examined here there would be almost no similarities among MCRs if we used data at the genus level and (ii) MCR genera and species of several families are poorly known (e.g. Chironomidae).

Reach and macrohabitat field sampling

To compare MCRs at the reach and macrohabitat scales, in spring over the years 1999 to 2002 we sampled four MCRs: the Mediterranean Basin, California, South Africa and southwestern Australia. Data at reach and macrohabitat scales was not available for Chile.

We sampled a total of 73 unimpaired sites but, because the number of sites differed between MCRs (from nine sites in southwestern Australia to 42 in the Mediterranean Basin), we randomly selected nine sites from each MCR to achieve a more balanced analysis. Among these sites, some were permanent (P) and others were temporary reaches (T: i.e. the river-reach had dried the summer before sampling). There were 5P and 4T sites in the Mediterranean Basin and

South Africa, 7P and 2T sites in California and 6P and 3T sites in southwestern Australia. All reaches had clearly differentiated lotic (i.e. riffles and runs: R) and lentic (i.e. pools: L) macrohabitats, which were sampled separately. A more detailed description of the general environmental characteristics of each area sampled is found in Table 1.

Sites were sampled using the Protocol 2 developed by the GUADALMED project (see http://www.ecostrimed.net). Semi-quantitative samples were collected in R and L macrohabitats separately using a circular kick-net with 250 μm mesh net. We attempted to sample all habitats present (e.g. vegetation, boulders, sand and roots). Each sample was examined in the field and successive samples were taken until no more families were found. In the laboratory, samples were sorted, identified and counted at the family level. At each site, environmental data related to basin, instream habitat, riparian and water characteristics were recorded using maps, portable meters or by applying protocols described in Munné *et al.* (2003) and Pardo *et al.* (2004) (available in http://www.ecostrimed.net) (Table 2).

Table 1 Number of sites sampled and description of their general environmental characteristics*

MCR	General location of sampling sites	Basin characteristics	Riparian vegetation	Substratum composition	Water characteristics
MB	Iberian Mediterranean coast (along 1000 km)	Forested by deciduous and evergreen trees and shrubs	Evergreen and deciduous riparian vegetation falling in autumn	Highly variable	High pH, may have natural nutrient concentrations
CA	West side of Sierra Nevada and northern coastal region	Forested by deciduous and evergreen trees and shrubs	Evergreen and deciduous riparian vegetation falling in autumn	Highly variable	Neutral to high pH
SA	Table Mountain, Franschhoek and Drakenstein Mountains, Kogelberg State Forest Reserve	Forested by fynbos shrubs	Dominant evergreen riparian vegetation falling mostly in summer	Stony, bedrock. Few Lentic areas Importance of the instream vegetation	Acidic and oligotrophic
AU	Darling Plateau	Forested by trees and shrubs evergreen	Dominant evergreen riparian vegetation falling mostly in summer	Sandy	Slightly acidic and oligotrophic

MB, Mediterranean Basin; CA, California; SA, South Africa; AU, southwestern Australia.

*More information about environmental characteristics of sites can be found in: Robles *et al.* (2004) for Mediterranean Basin; Bailey (1995) for California; Dallas (2002) for South Africa and Storey *et al.* (1990) for southwestern Australia.

Data analyses

For regional composition, a cluster analysis using the Bray–Curtis similarity index was applied to the macroinvertebrate presence/absence matrix of all MCRs. This index is one of the most suitable for presence/absence data because it excludes double zeros and gives more weight to double presences (Legendre & Legendre, 1998). A description of several metrics (i.e. number of taxa and proportion of the main orders and classes per region) was made to assess the distribution of taxa between MCRs.

In order to examine climatic-independent factors that vary between MCRs, a principal components analysis (PCA analysis) was performed for sampled MCRs using the environmental data collected at each site. To be sure that the nine sites were representative of local richness in each MCR, and that we were not missing too much of the richness, taxon accumulation curves were calculated for each MCR (Erman & Erman, 1995). A sigmoidal curve was fitted of the form: accumulated taxa = $A/[1 + e^{-K(t-t50)}]$, where 'A' indicates the asymptote of the curve (total taxon richness per MCR), 'K' is the capture rate constant, 't' is the number of sampling sites and '$t50$' is the

Table 2 Variables measured and used in the analysis

Variable	Code	Description	Measured using
Basin morphology	Basin	Basin around the reach has a hilly or flat morphology	Visual examination
Peak of leaf litter	LeafPeak	Peak period of the leaf litter input	Lake *et al*., 1985
Longitudinal zonation	Zonat	Headwaters of midstream reaches	Stream order (1 : 250 000)
Riparian cover	RipCover	% of riparian area covered by trees and shrubs	Munné *et al*., 2003
Riparian margins	RipMargins	Slope of the right and left riparian margins	Munné *et al*., 2003
Shade	Shade	A score running from not shade to completely shaded	Pardo *et al*., 2004
pH	pH	Water pH	*In situ*; portable meter
Conductivity	Cond	Water conductivity (μS cm^{-1})	*In situ*; portable meter
Boulders and stones	Boulders	% of boulders and stones in sampling reach	Pardo *et al*., 2004
Pebbles and gravels	Pebbles	% of pebbles and gravels in sampling reach	Pardo *et al*., 2004
Sand	Sand	% of sand in sampling reach	Pardo *et al*., 2004
Silt and clay	Silt	% of silt and clay in sampling reach	Pardo *et al*., 2004
Leaf litter deposits	LeafLitter	% of leaf litter in the stream bed	Pardo *et al*., 2004
Filamentous algae	Plocon	% of filamentous algae in the stream bed	Pardo *et al*., 2004
Incrusted algae	Pecton	% of incrusted algae in the stream bed	Pardo *et al*., 2004
Macrophytes	Macrophytes	% of aquatic macrophytes in the stream bed	Pardo *et al*., 2004

'Code' corresponds to the codes used in Fig. 2.

number of sites at the inflection point of the curve (i.e. number of sites needed to collect 50% of total taxon richness).

Differences in taxon richness were analysed at the reach (between P and T) and macrohabitat (between R and L) scales in all MCRs, using a nested ANOVA. Residuals were checked for normality and homogeneity of variances using Shapiro–Wilk and Bartlett tests respectively. The nested design included three fixed factors in which macrohabitat was nested within reach, which was nested within MCR. Although nested ANOVA designs usually use random nested factors, fixed factors can be also be used (Quinn & Keough, 2002). When nested ANOVA was significant, *post hoc* pair-wise comparisons were performed using a Tukey's HSD test. The ratio EPT/EPTOCH (number of Ephemeroptera, Plecoptera and Trichoptera taxa in relation to number of Ephemeroptera, Plecoptera, Trichoptera, Odonata, Coleoptera and Heteroptera taxa) was plotted for the reach and macrohabitat scales and differences were also tested using a nested ANOVA and Tukey's HSD test. This ratio has been considered to be an index that characterizes temporary and lotic–lentic conditions in MCRs (Bonada *et al*., 2006, 2007b).

Differences in taxonomic composition were analysed using a two-way nested ANOSIM (Clarke, 1993), but with only two fixed factors (nested ANOSIM using more than two factors is not available in current statistical software) in which reach was nested within MCR, macrohabitat was nested within MCR and macrohabitat was nested within reach. ANOSIM is a method for testing multivariate differences among pre-defined groups and provides the statistic Global-R and a *P*-value obtained by permutations (100 runs). Global-R ranges from −1 to 1. It is 1 when all sites within groups are more similar to each other than to sites of other groups, and it is 0 when similarities among and within groups are, on average, the same. When a significant Global-R was found, *post hoc* pair-wise comparisons were performed using one-way ANOSIM. Furthermore, the Indicator Value method (INDVAL, Dufrêne & Legendre, 1997) was used to determine the most representative macroinvertebrate taxa of P and T reaches and R and L macrohabitats in each MCR. INDVAL is based on the relative frequency of taxa in the samples of one group and the mean abundance of taxa in the samples of that group compared with all groups. An indicator value (IV) was associated with each taxon, and only taxa with an IV > 25 (i.e. species present in >50% of the samples from one group and with a relative abundance in that group of >50%, Dufrêne & Legendre, 1997) were retained.

Finally, correspondence analysis (CA analysis) was performed on the reach and macrohabitat scales separately, and inertia was retained. Partial canonical correspondence analysis (pCCA analysis) was used to assess the relative effects of global environmental characteristics (using axis scores from the PCA-analysis to reduce the number of environmental factors) or characteristics of the region itself (MCR). These values were computed by entering each factor in the analysis as a variable and the rest as covariables. This removes the effects of the covariables and reports the variability solely explained by each factor (i.e. without interaction with other factors). These variabilities were referred to the inertia (Legendre & Legendre, 1998). PRIMER (version 5, Primer-E Ltd, Plymouth, U.K.), STATISTICA (1999, StatSoft, Tulsa, OK, U.S.A.) and the R FREEWARE (R Development Core Team, 2007) were used to perform all the statistical analyses.

Results

Environmental characteristics between MCRs

Principal components analysis revealed that, overall, MCRs clearly differed in their environmental conditions (Fig. 1). The Mediterranean Basin and California were most similar to each other with regard to the environmental conditions measured, and were associated with higher conductivities and pH values than the other two MCRs. MCRs also differed in instream vegetation and substratum composition, with southwestern Australian streams being dominated by filamentous algae (here called plocon), sand and silt, and South African rivers being associated with aquatic macrophytes and boulders. Other environmental factors, such as longitudinal zonation or shade over the stream, were not important for differentiating MCRs.

Multi-scale taxon richness

At the regional scale, MCRs contained 219 taxa, which included 216 families, two classes (Arachnida and Oligochaeta) and one subclass (Ostracoda) that could not be identified at the family level. Forty taxa were shared between the MCRs; the Diptera was the order with the most families in common. South Africa showed the highest number of unique taxa (13 families), followed by southern Australia and Chile, both with 11 taxa. The Mediterranean Basin had the highest regional taxon richness, whereas southwestern Australia and Chile had the lowest (Fig. 2a). Overall, and with the exception of Chile, Ephemeroptera and Plecoptera were richer in the northern than in the southern hemisphere (Fig. 2b), whereas non-insect taxa were proportionally more diverse in South Africa and Australia (Fig. 2b). Slight differences between MCRs were observed in the proportion of other orders (not shown).

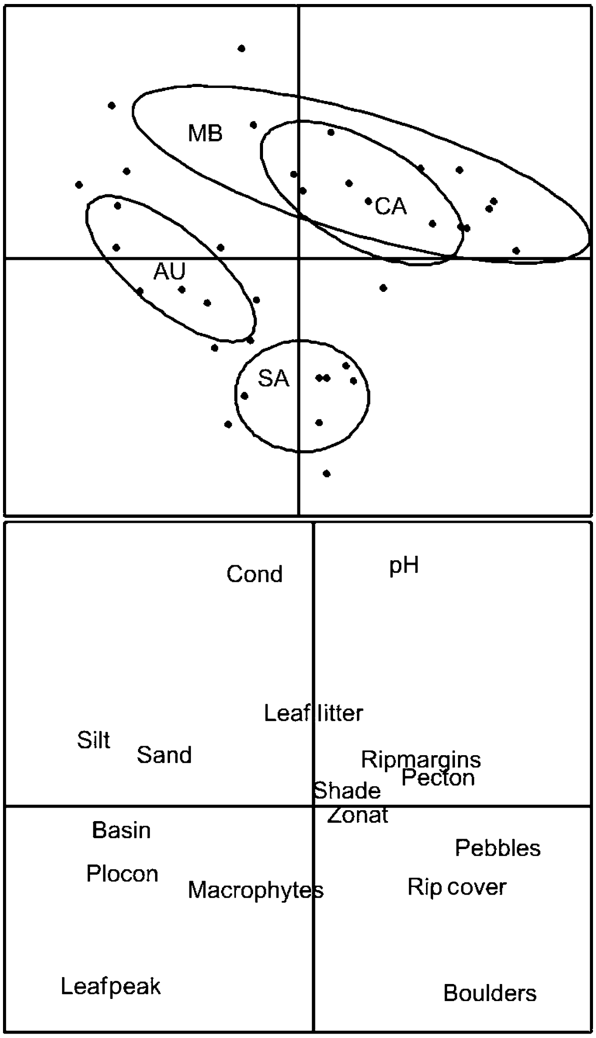

Fig. 1 Results of the principal components analysis using environmental data recorded in each sampled MCR. First and second axes explain 21.39% and 14.86% of the variance respectively. Meaning of the codes in the bottom plot is provided in Table 2. Ellipses envelop 70% of the sites of each MCR (MB, Mediterranean Basin; CA, California; SA, South Africa; AU, southwestern Australia).

Accumulation curves indicated that taxon richness increased faster in the Mediterranean Basin and California than in South Africa or southwestern Australia (Fig. 3). Although none of these curves reached a plateau, variability in richness was low considering that only nine sites were used and

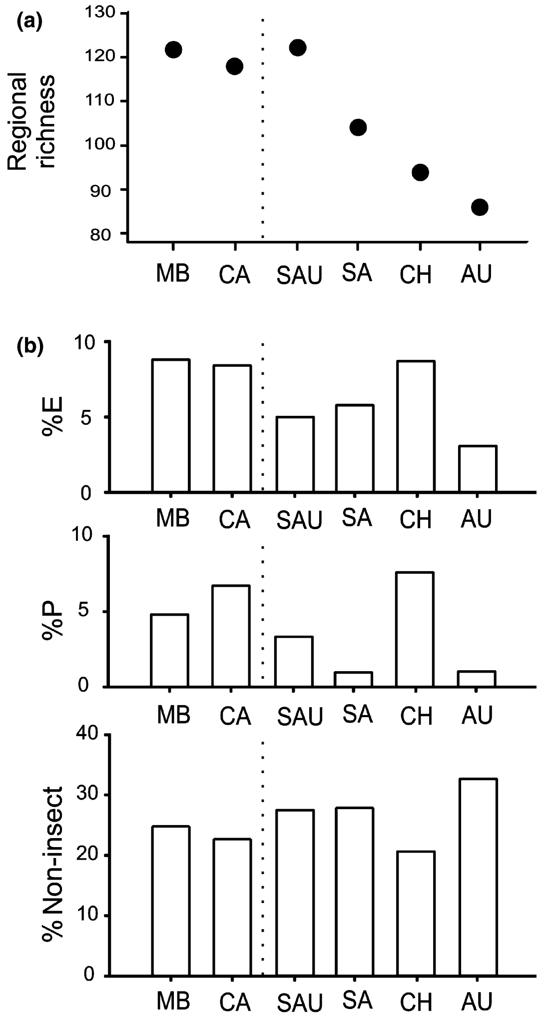

Fig. 2 (a) Regional taxon richness for all MCRs in the world. (b) Percentages of Ephemeroptera taxa (E), Plecoptera (P) and non-insect taxa of regional composition of all MCRs. Only the taxonomic orders displaying clear patterns among Mediterranean climate regions are shown. Dashed lines separate northern and southern hemisphere MCRs and regions are ordered decreasing in regional richness within hemispheres (MB, Mediterranean Basin; CA, California; SA, South Africa; AU, southwestern Australia; SAU, southern Australia; CH, Chile).

sigmoidal curves were significant with these relatively few number of sites (i.e. the proportion of explained variance was always higher than 0.90 and $P < 0.05$). This indicates that, at the scale of this study, nine sites encompass an appropriate representation of the richness in each MCR. On the other hand, accumulation curves also suggested that local taxon richness (i.e. richness per site) was much higher in the Mediterranean Basin and California, whereas southwestern Australia presented the lowest value. The same pattern was observed when considering P and T reaches (Fig. 4a) or R and L macrohabitats (Fig. 4b).

Taxon richness was significantly different between MCRs, but not between P and T reaches or between R and L macrohabitats within MCRs (Table 3, Fig. 4a,b). Pair-wise comparisons for the factor MCR showed that all pairs of MCRs, except the Mediterranean Basin and South Africa ($P = 0.974$), had significant differences in taxon richness (all $P < 0.02$). The ratio EPT/EPTOCH differed between P and T reaches within MCRs, and between R and L macrohabitats within reaches and MCRs, being higher in P and R than in T and L (Table 3, Fig. 4a,b). *Post hoc* pair-wise comparisons showed that EPT/EPTOCH was significantly different between P and T reaches in all MCRs ($P < 0.05$) except for southwestern Australia ($P = 0.641$). At the macrohabitat scale, this ratio differed significantly only for the Mediterranean Basin and California ($P < 0.03$).

Multi-scale taxonomic composition

Regional taxonomic composition was most similar between the Mediterranean Basin and California (Fig. 5a), with 85.12% Bray–Curtis similarity. The South African community was closer to those of the MCRs of the northern hemisphere than to the southern ones, with 66.67% similarity with the Mediterranean Basin, and 67.86% similarity with California. The two Australian MCRs (South west and South) were 70.47% similar to each other. Finally, Chile was the MCR with the most distinctive macroinvertebrate community, showing 59.00% similarity to that of South Africa, 59.81% to that of California and 61.54% and 59.63% similarity to those of southwestern and southern Australia respectively.

At the reach scale, taxonomic composition differed significantly between P and T within MCRs. One-way ANOSIM tests for pair-wise comparisons revealed that within-MCR differences were significant for the Mediterranean Basin and California, but not for South Africa or southwestern Australia (Table 3). At the macrohabitat scale, taxonomic composition also differed between R and L macrohabitats within reaches and MCRs, separately, but these differences were found in all pair-wise comparisons (Table 3). Overall, P reaches in all the regions were characterized by Ephemeroptera and Trichoptera, while T reaches were

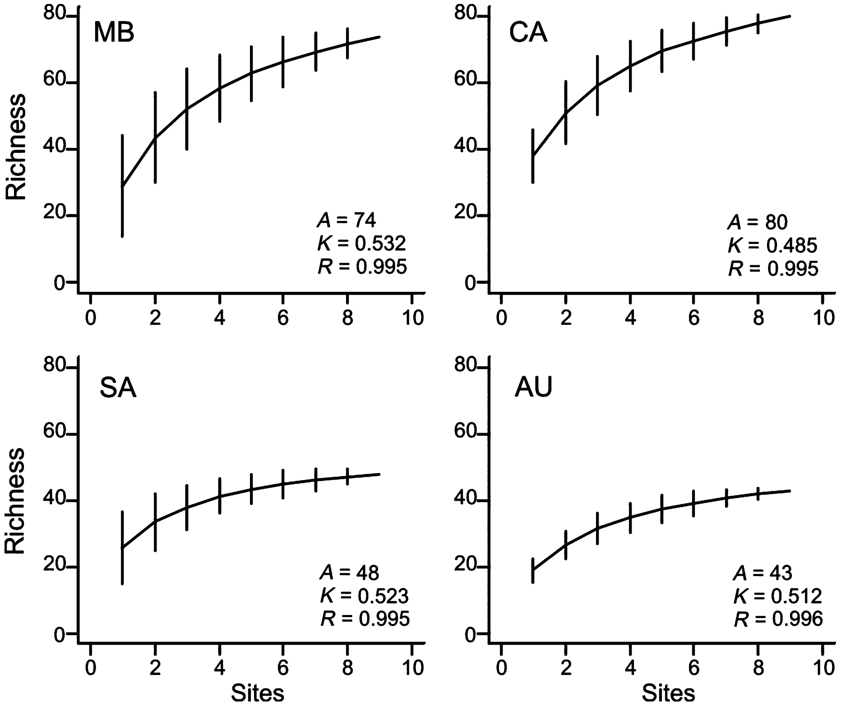

Fig. 3 Taxon accumulation curves in each MCR. The adjusted sigmoid curve, its *R* value and its characteristic parameters (*A*, *K*) are given. '*A*' indicates the asymptote of the curve (total species richness per MCR) and '*K*' is the capture rate constant (MB, Mediterranean Basin; CA, California; SA, South Africa; AU, southwestern Australia).

dominated by Mollusca, Crustacea, Odonata, Coleoptera and Heteroptera. The only plecopteran family found in the southwestern Australian MCR (i.e. Gripopterygidae) had higher IV in T than P reaches, whereas most plecopteran families in the Mediterranean Basin and California showed the opposite pattern (Table 4). Ephemeroptera, Plecoptera and Trichoptera were dominant in R macrohabitat for all the MCRs, whereas Heteroptera and most of the Odonata and Coleoptera were indicative of L macrohabitat (Table 5).

Although taxonomic composition differed significantly at reach and macrohabitat scales within the Mediterranean Basin and California, CA analysis revealed that at large scale, these regions were more similar in composition to each other than to other MCRs (Fig. 5b,c). By contrast, South Africa and southwestern Australia had very distinct composition, especially in regard to P and T reaches (Fig. 5b). At the reach and macrohabitat scales, taxonomic variability of CA was explained more by global environmental characteristics (pCCA: 11.1% and 7.4% for reach and macrohabitat scales, respectively) than by the region effect (6.4% and 4.4% for reach and macrohabitat scales respectively).

Discussion

Regional scale

With the exception of southern Australia, all MCRs have been considered hotspots for biodiversity, containing numerous plant and vertebrate species. Although this does not mean that these regions have similar numbers of species, large-scale studies on the relationship between regional richness and climate characteristics have suggested that similar climatic conditions should result in relatively similar levels of regional richness (Francis & Currie, 2003). Contrary to our hypothesis, we found that regional richness differed between MCRs. Richness was higher in northern hemisphere MCRs and southern Australia, and lower in southwestern Australia and Chile. This pattern could be explained by geological processes that affected each MCR. For example, glaciations in the northern hemisphere resulted in well-documented speciation in some areas (Hewitt, 2004), whereas the depauperate macroinvertebrate fauna of southwestern Australia is associated with a long drought period that occurred around 18 000 years BP, causing extinctions and isolating the fauna from that of southern Australia (DeDeckker, 1986). The same phenomenon would explain why few similarities in composition

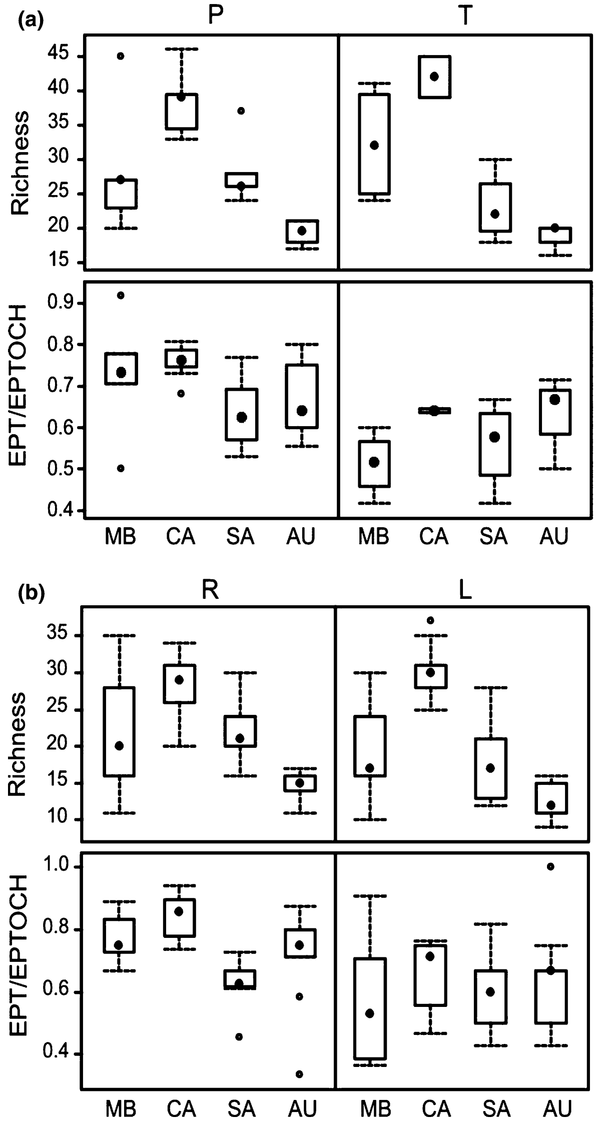

Fig. 4 (a) Local taxon richness between sampled MCRs, separated by permanent and temporary reaches. (b) Local taxon richness between sampled MCRs, separated by lotic (i.e. riffles and runs, R) and lentic (i.e. pools, L) macrohabitats. Each box-plot show medians (horizontal bars), 25th and 75th percentiles (boxes) (MB, Mediterranean Basin; CA, California; SA, South Africa; AU, southwestern Australia).

were found between the two Australian MCRs, despite their relative spatial proximity. On the other hand, the still limited knowledge of macroinvertebrate fauna in Chile (Figueroa *et al.*, 2007) and the insular condition of its MCR (located between the Andes, the Atacama Desert and the Pacific ocean: Armesto, Villagrán & Arroyo, 1997) could explain the low regional richness and the large degree of endemism in this MCR, despite the connections to the northern hemisphere (Di Castri, 1991).

As expected, overall regional taxonomic composition reflected past geological events, in agreement with results of previous studies with terrestrial plants (Deacon, 1983) or aquatic invertebrates (Banarescu, 1990). The faunas of historically more isolated MCRs have a more dissimilar composition than less isolated ones. For example, differences in macroinvertebrate composition between northern and southern hemisphere MCRs could be explained by the early break up of Laurasia and Gondwanaland during the Cretaceous (70–135 My BP). California and the Mediterranean Basin were highly convergent because of the connections through the North Pacific from early Cretaceous to post-glacial periods and through the North Atlantic until the Eocene (Banarescu, 1990). In contrast, macroinvertebrates in the southern hemisphere were more divergent, probably because of the early break up of Gondwanaland in the early Cretaceous. However, Africa was the first continent to split off from the rest of Gondwanaland and connections between the Neotropical and Austral areas were possible until the late Cretaceous (Brundin, 1965; Harrison, 1978), which could explain why Chile shares more macroinvertebrate families with Australia than with South Africa. Surprisingly, the South African MCR was closer to those of the northern hemisphere than to southern MCRs, indicating: (i) a possible active exchange of taxa between hemispheres (e.g. some Ephemeroptera that originated in Africa are now found in Holartic regions: Edmunds, 1972) and (ii) extinction of taxa shared with other southern hemisphere MCRs (e.g. some South African crustaceans were extinguished after a severe drought at the end of the Cretaceous: Bayly, 1993).

Current environmental conditions may also limit the presence of some taxa in some MCRs (Lobo & Davis, 1999). For example, Mollusca are under-represented in South Africa, possibly because of the highly acidic waters of the Cape Province (Brown, 1978; Harrison, 1978), while taxa characteristic of boulders and pebbles may be scarce in the old and eroded MCR of southwestern Australia. Similarity in environmental conditions between the Mediterranean Basin and California (Fig. 1) may result in a similar taxon richness and composition. Thus, it is often difficult to discern between the ecological and geological factors that explain current regional composition

Table 3 Results of the nested ANOVA and nested ANOSIM (1000 runs) for taxon richness, EPT/(EPTOCH) ratio and composition

Nested ANOVA			d.f.	SS	MS	*F*-value	*P*-value
Richness	Region	MCRs	3	2239.82	746.61	28.53	<0.001
	Reach	PT(MCRs)	4	139.70	34.93	1.33	0.268
	Macrohabitat	RL[PT(MCRs)]	8	200.10	25.01	0.95	0.479
		Residuals	56	1465.04	26.16	4.03	
EPT/(EPTOCH)	Region	MCRs	3	0.17	0.05	4.03	0.011
	Reach	PT(MCRs)	4	0.26	0.06	4.47	0.003
	Macrohabitat	RL[PT(MCRs)]	8	0.42	0.05	3.59	0.002
		Residuals	56	0.81	0.01		
Nested ANOSIM					Global-R		*P*-value
Composition	Region	MCRs			0.89		0.010
	Reach	PT(MCRs)			0.32		0.001
	Macrohabitat	RL(MCRs)			0.39		0.001
		RL(PT)			0.18		0.001
One-way ANOSIM					Global-R		*P*
	Reach	MB			0.33		0.034
		CA			0.92		0.026
		SA			0.32		0.082
		AU			0.18		0.229
	Macrohabitat	MB			0.32		0.002
		CA			0.52		<0.001
		SA			0.33		<0.001
		AU			0.39		<0.001

Results from *post hoc* pair-wise comparisons using one-way ANOSIM are also provided.
EPT/(EPTOCH), number of Ephemeroptera, Plecoptera and Trichoptera taxa in relation to number of Ephemeroptera, Plecoptera, Trichoptera, Odonata, Coleoptera and Heteroptera taxa; MCRs, Mediterranean climate regions; PT, permanent and temporary reaches; RL, lotic and lentic macrohabitats; MB, Mediterranean Basin; CA, California; SA, South Africa; AU, southwestern Australia.

(Endler, 1982). Both of these factor groups should be considered in interpreting the broad similarities in regional richness and composition in MCRs.

Reach and macrohabitat scales

The literature provides contrasting information when comparing taxon richness between P and T reaches. For example, while Wright *et al.* (1984) and Del Rosario & Resh (2000) found lower taxon richness in T than P reaches, Boulton & Suter (1986) and Miller & Golladay (1996) reported similar numbers of taxa. In addition, there is no agreement as to whether P and T reaches support taxonomically different or overlapping invertebrate composition, the above studies performed in the northern hemisphere showed both patterns, whereas those performed in the southern hemisphere found overlapping communities (Boulton & Lake, 1992). As hypothesized, we found similar taxon richness between P and T, but taxonomic composition was only significantly different in the northern hemisphere MCRs. In the southern hemisphere MCRs sampled, the lack of significant differences between P and T reaches could be explained by the lower regional richness in these MCRs (i.e. less probability of having a distinct P or T community), but also by other climatic-dependent factors. South African and southwestern Australian MCRs have a higher frequency of rainfall events in winter and summer and higher overall summer rainfall than northern hemisphere MCRs (Cowling *et al.*, 2005). Hydrological differences between P and T may therefore be less clear in these MCRs because these regional climatic peculiarities result in a greater overlap in taxonomic composition, a pattern that has been also considered for other non-Mediterranean South African and Australian rivers (Lake *et al.*, 1985; Wishart, 1998). On the other hand, southwestern Australia, in particular, experienced a past extinction of taxa adapted to permanent conditions (Bunn & Davies, 1990), which might also foster the macroinvertebrate overlap between P and T.

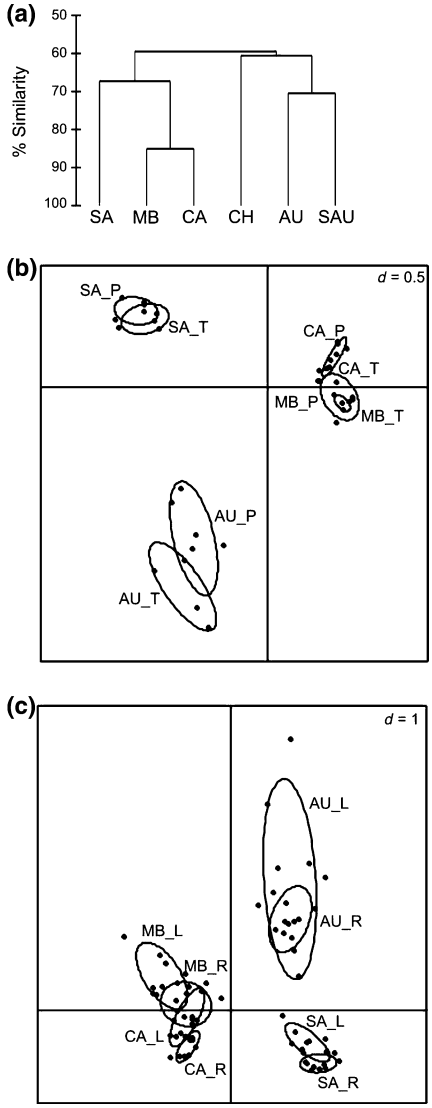

Fig. 5 (a) Dendrogram of regional taxonomic composition of all MCRs in the world using presence–absence data, Bray–Curtis similarity index and group average cluster mode. For each region, regional composition (at the family level) was obtained using personal communications and published and unpublished studies. (b) Results of the correspondence analysis using local composition of permanent (P) and temporary (T) reaches of each sampled MCR. First and second axes explain 13.71% and 10.57% of the variance respectively. (c) Results of the correspondence analysis using local composition of lentic (i.e. pools) and lotic (i.e. riffles and runs) macrohabitats of each sampled MCR. First and second axes explain 9.44% and 7.72% of the variance respectively. For (b) and (c), ellipses envelop 70% of the sites of each MCR (MB, Mediterranean Basin; CA, California; SA, South Africa; AU, southwestern Australia).

In terms of differences between macrohabitat conditions, our results for all MCRs support the hypothesis that similar taxon richness but different taxonomic composition occur between R and L macrohabitats, which is consistent with results of other studies (e.g. Scullion *et al.*, 1982; Logan & Brooker, 1983; McCulloch, 1986). Thus, the change of macroinvertebrates at the macrohabitat scale was more similar between MCRs than at the reach scale. Local factors, and above all stream velocity (the main factor differentiating R and L macrohabitats), constrain taxonomic composition more than larger-scale factors because of the direct effect on the environment where the organisms live (Sandin & Johnson, 2004).

The relationship between the richness of Ephemeroptera, Plecoptera and Trichoptera and Odonata, Coleoptera and Heteroptera, has been considered in northern hemisphere MCRs as a valuable index of temporary reaches and differences between macrohabitats (Bonada *et al.*, 2006, 2007b). When used in South Africa or southwestern Australia, however, the EPT/EPTOCH ratio did not show consistent differences at reach and macrohabitat scales. Southern hemisphere MCRs are depauperate in Ephemeroptera and Plecoptera because of their biogeographical histories (Fig. 2b, Banarescu, 1990). For example, Vinson & Hawkins (2003) found EPT to be richest between 10 and 40°N but did not find the equivalent in the southern hemisphere. In the regional composition of MCR invertebrate faunas, for example at family level, only one plecopteran (the Notonemouridae) is present in the South African MCR and one (the Griptopterygidae) in southwestern Australia, whereas six and seven are found in the Mediterranean Basin and California respectively. Similar patterns are observed regarding Ephemeroptera, with only six and three families in South Africa and southwestern Australia, respectively, and 11 and 10 in the Mediterranean Basin and California respectively.

Multi-scale similarities

One of the main results of our study is that the strength of similarity between distant but climatically similar regions is scale-dependent. Regional-scale comparisons appear to be strongly related to different evolutionary histories and environmental characteristics for both richness and composition. Lower scale comparisons, however, indicated some similar responses to temporary and lotic–lentic conditions, but there are more similarities at the macrohabitat scale.

Table 4 Results of the INDVAL analysis for permanent (P) and temporary (T) reaches in each Mediterranean climate region

Mediterranean Basin				California			
P	IV	T	IV	P	IV	T	IV
Hydropsychidae	77.27*	Hydrometridae	90.91*	Limnephilidae	100**	Culicidae	100**
Hydracarina	70.59	Lymnaeidae	89.74*	Nemouridae	85.71**	Stratiomyidae	100**
Polycentropodidae	70.59	Dytiscidae	86.21*	Perlidae	85.71**	Caenidae	93.33**
Heptageniidae	63.41	Ceratopogonidae	71.43	Ephemerellidae	85.11**	Brachycentridae	84.00
Calopterygidae	60.00	Notonectidae	62.50	Rhyacophilidae	85.11**	Corixidae	84.00
Chloroperlidae	60.00	Oribatidae	62.50	Ceratopogonidae	85.11**	Hydroptilidae	75.38**
Tabanidae	60.00	Leptophlebiidae	61.64	Sialidae	71.43	Physidae	73.68
Caenidae	55.70	Oligochaeta	59.63	Tipulidae	64.41**	Philopotamidae	60.00
Baetidae	55.28	Psychodidae	59.21	Empididae	63.16	Chloroperlidae	59.32
Limnephilidae	50.70	Gerridae	58.14	Peltoperlidae	57.14	Oligochaeta	59.04**
Corixidae	49.66	Ostracoda	55.85	Gerridae	53.33	Dixidae	58.33
Chironomidae	47.55	Chironomidae	52.45	Leptophlebiidae	52.05	Ostracoda	56.76
Perlidae	43.64	Cladocera	50.00	Simuliidae	51.49	Lepidostomatidae	55.56
Simuliidae	42.67	Culicidae	50.00	Baetidae	50.51	Hydracarina	55.06
Tipulidae	42.35	Dugesiidae	50.00	Dytiscidae	50.42	Elmidae	52.50
Elmidae	40.00	Elmidae	50.00	Chironomidae	50.00	Hydropsychidae	52.50
Erpobdellidae	40.00	Hydrophilidae	50.00	Elmidae	47.50	Heptageniidae	52.24
Glossosomatidae	40.00	Libellulidae	50.00	Hydropsychidae	47.50	Belostomatidae	50.00
Sericostomatidae	40.00	Planorbidae	50.00	Hydracarina	44.94	Chironomidae	50.00
Ephemerellidae	37.65	Sphaeriidae	50.00	Asellidae	42.86	Coenagrionidae	50.00
Empididae	36.92	Limnephilidae	49.30	Calamoceratidae	42.86	Copepoda	50.00
Hydroptilidae	36.92	Simuliidae	46.67	Odontoceridae	42.86	Ephydridae	50.00
Gerridae	33.49	Baetidae	44.72	Perlodidae	42.86	Haliplidae	50.00
Ancylidae	32.73	Hydrobiidae	41.67	Sphaeriidae	42.86	Hydraenidae	50.00
Oligochaeta	32.29	Nemouridae	41.67	Cordulegasteridae	42.86	Naucoridae	50.00
Perlodidae	30.00	Ephemerellidae	39.71	Oligochaeta	40.96	Sciomyzidae	50.00
Athericidae	28.24	Caenidae	33.23	Heptageniidae	40.94	Tabanidae	50.00
		Psychomyiidae	32.61	Chloroperlidae	40.68	Baetidae	49.49
		Stratiomyidae	32.61	Ostracoda	37.07	Simuliidae	48.51
		Gammaridae	25.86	Psychodidae	33.61	Leptophlebiidae	47.95
		Aeshnidae	25.00	Lepidostomatidae	31.75	Polycentropodidae	46.67
		Bythinellidae	25.00	Polycentropodidae	30.48	Gerridae	46.67
		Coenagrionidae	25.00	Psephenidae	30.48	Psychomyiidae	43.75**
		Dixidae	25.00	Dixidae	29.76	Tricorythidae	43.75**
		Hebridae	25.00	Corydalidae	28.57	Dytiscidae	41.18
		Perlodidae	25.00	Glossosomatidae	26.37	Gomphidae	38.89
		Physidae	25.00	Oribatidae	26.37	Hydrophilidae	38.89
		Platycnemididae	25.00	Uenoidae	26.37	Lestidae	38.89
						Planorbidae	38.89
						Sericostomatidae	36.21
						Tipulidae	35.59
						Dugesiidae	33.87
						Pteronarcyidae	31.82
						Siphlonuridae	31.82
						Glossosomatidae	26.92
						Aeshnidae	26.92
						Cambaridae	26.92
						Leptoceridae	26.92
						Oribatidae	26.92
						Uenoidae	26.92

Table 4 (*Continued*)

South Africa				Southwestern Australia			
P	IV	T	IV	P	IV	T	IV
Petrothrincidae	80.00*	Paramelitidae	78.95*	Hydropsychidae	68.42*	Griptopterygidae	61.54
Barbarochtonidae	80.00**	Oligochaeta	53.96	Baetidae	66.67	Hydrachnidae	53.33
Tipulidae	73.68**	Hydracarina	52.63	Leptophlebiidae	61.54*	Oligochaeta	50.00
Glossosomatidae	71.11	Leptophlebiidae	51.72	Simuliidae	55.56	Chironomidae	50.00
Blepharoceridae	69.19	Hydraenidae	49.30	Aeshnidae	53.03	Leptoceridae	50.00
Leptoceridae	69.14**	Chironomidae	48.39	Ceratopogonidae	52.38	Perthiidae	48.48
Ecnomidae	67.88	Simuliidae	47.45	Oligochaeta	50.00	Ceratopogonidae	47.62
Corydalidae	60.00	Elmidae	45.45	Chironomidae	50.00	Dytiscidae	44.44
Notonemouridae	56.69	Helodidae	45.45	Hydroptilidae	50.00	Ostracoda	44.44
Baetidae	55.88	Teloganodidae	45.45	Leptoceridae	50.00	Simuliidae	44.44
Elmidae	54.55	Baetidae	44.12	Athericidae	50.00	Leptophlebiidae	38.46
Helodidae	54.55	Notonemouridae	43.31	Corduliidae	50.00	Psychodidae	38.10
Teloganodidae	54.55	Dytiscidae	39.47	Hydrobiosidae	50.00	Tipulidae	38.10
Simuliidae	52.55	Ostracoda	38.27	Empididae	44.44	Coenagrionidae	33.33**
Hydropsychidae	51.89	Ceratopogonidae	37.50	Gomphidae	44.44	Gyrinidae	33.33**
Chironomidae	51.51**	Psychodidae	35.71	Parastacidae	44.44	Oxidae	33.33**
Hydraenidae	50.70	Dugesiidae	31.25	Caenidae	38.89	Stratiomyidae	33.33**
Ceratopogonidae	50.00	Empididae	27.78	Griptopterygidae	38.46	Ancylidae	26.67
Leptophlebiidae	48.28	Hirudinea	25.00	Hyriidae	33.33	Oribatidae	26.67
Hydracarina	47.37	Hydrosalpingidae	25.00				
Oligochaeta	46.04	Libellulidae	25.00				
Veliidae	42.35	Pisuliidae	25.00				
Hydroptilidae	40.00						
Coenagrionidae	40.00						
Ostracoda	39.18						
Empididae	35.56						
Philopotamidae	32.73						
Cladocera	30.48						
Limnichidae	28.24						

Only taxa with an indicator value higher or equal to 25 (IV) are presented.
*$P < 0.05$; **$P < 0.01$ by Monte Carlo permutation test (9999 runs).

The Mediterranean Basin and California appeared as the MCRs with the closest similarities from regional to macrohabitat scales. Our results suggest that this results from their similar evolutionary histories and environmental conditions (Fig. 1). In addition, when considering all MCRs at a large scale, taxonomic composition of the faunas of rivers in the Mediterranean Basin and California was very similar (Fig. 5b,c), and environmental characteristics explained part of the macroinvertebrate variability. In contrast, the need for a multi-scale approach in international comparisons is more apparent with regard to southern hemisphere MCRs because, when considering both richness and composition, similarities to northern MCRs were observed only at specific scales. Richness was similar at the reach and macrohabitat scales but not at a regional scale, whereas responses in composition were similar only at macrohabitat scale.

Because our study focused only on MCRs, one might speculate as to whether these similarities in richness and composition at different scales are universal or are limited to MCRs. Distinct hydraulic requirements between R and L macrohabitats are universal (Statzner, Gore & Resh, 1988) and we should thus expect similar responses to this factor, independent of the region considered. Indeed, similar levels of taxon richness but different taxonomic composition have been found in non-Mediterranean countries (Scullion *et al*., 1982; McCulloch, 1986).

In contrast, despite being relatively common in many parts of the world, temporary conditions differ in intensity, frequency and predictability among regions (Williams, 2006). In contrast to other climate regions, droughts in MCRs are seasonal and predictable (Gasith & Resh, 1999; Lake, 2003). Furthermore, because natural discharge predictability determines the adaptability

Table 5 Results of the INDVAL analysis for lotic (i.e. riffles and runs, R) and lentic (i.e. pools, L) macrohabitats in each Mediterranean climate region

Mediterranean Basin				California			
R	IV	L	IV	R	IV	L	IV
Simuliidae	75.55**	Gerridae	88.89**	Hydropsychidae	92.59**	Gerridae	93.75**
Hydropsychidae	74.24**	Baetidae	52.17	Simuliidae	86.84**	Dytiscidae	76.19**
Elmidae	66.66*	Polycentropodidae	50.33	Tipulidae	70.97**	Leptophlebiidae	63.16*
Empididae	55.55**	Chironomidae	47.46	Rhyacophilidae	69.14*	Ceratopogonidae	59.26
Perlidae	55.55**	Hydrometridae	45.45	Chloroperlidae	68.00*	Ostracoda	58.33
Ephemerellidae	54.73	Notonectidae	44.44**	Perlidae	67.43*	Sialidae	55.56**
Chironomidae	52.54	Leptophlebiidae	41.67	Heptageniidae	60.22	Lepidostomatidae	52.78
Ceratopogonidae	51.85	Caenidae	41.48	Ephemerellidae	57.35	Chironomidae	50
Heptageniidae	46.18	Limnephilidae	40	Elmidae	55.56	Limnephilidae	49.49
Hydroptilidae	44.44	Dytiscidae	39.68	Baetidae	55.17**	Hydracarina	47.92
Hydracarina	44.44	Oligochaeta	38.89	Oligochaeta	54.55	Baetidae	44.83
Perlodidae	41.67	Ancylidae	34.72	Nemouridae	54.32	Elmidae	44.44
Oligochaeta	38.89	Lymnaeidae	28.28	Hydracarina	52.08	Oribatidae	44.44
Baetidae	37.2	Heptageniidae	27.08	Philopotamidae	50.51*	Oligochaeta	40.4
Caenidae	36.3	Corixidae	25	Chironomidae	50	Physidae	38.1
Psychodidae	34.57			Empididae	48.48	Corixidae	37.04
Tabanidae	33.33			Polycentropodidae	48.48	Dixidae	36.67
Erpobdellidae	29.63			Peltoperlidae	38.1	Cordulegasteridae	33.33
Ostracoda	27.35			Hydroptilidae	38.01	Gomphidae	33.33
Limnephilidae	26.67			Dugesiidae	35.56	Sphaeriidae	33.33**
Gammaridae	26.26			Glossosomatidae	34.72	Calamoceratidae	33.33**
Leptophlebiidae	25			Uenoidae	34.57	Empididae	30.3
Rhyacophilidae	25			Psephenidae	27.78	Sericostomatidae	29.17
Tipulidae	25			Psychodidae	25.4	Psephenidae	27.78
				Perlodidae	25	Leptoceridae	26.67
				Dixidae	25	Nemouridae	25.93

South Africa				Southwestern Australia			
R	IV	L	IV	R	IV	L	IV
Hydraenidae	79.99**	Ostracoda	61.11*	Simuliidae	90.32**	Leptoceridae	59.26
Simuliidae	77.49**	Oligochaeta	55.36	Hydropsychidae	88.89**	Chironomidae	49.12
Notonemouridae	72.49**	Chironomidae	47.76	Ceratopogonidae	62.5	Ostracoda	47.62
Teloganodidae	64.10**	Hydracarina	45.98	Griptopterygidae	60.44	Dytiscidae	35.56*
Baetidae	59.62	Elmidae	38.1	Oligochaeta	60.32	Corduliidae	35.35
Leptophlebiidae	59.52*	Leptoceridae	36.46	Leptophlebiidae	54.48	Gomphidae	29.63
Helodidae	58.14	Leptophlebiidae	35.98	Chironomidae	50.88	Ceratopogonidae	29.17
Elmidae	57.14	Teloganodidae	35.9	Empididae	46.3	Caenidae	25.93
Philopotamidae	55.55**	Veliidae	35.56*	Aeshnidae	38.1	Leptophlebiidae	25.81
Tipulidae	53.33*	Ecnomidae	34.19	Athericidae	33.33	Ecnomidae	25
Chironomidae	52.24	Cladocera	33.33**	Hydrobiosidae	33.33	Oligochaeta	25
Blephariceridae	49.99*	Helodidae	32.56	Leptoceridae	27.16		
Empididae	48.48	Baetidae	31.41	Baetidae	25		
Hydracarina	48.28	Ceratopogonidae	30.77				
Oligochaeta	44.64	Petrothrincidae	27.78				
Leptoceridae	41.32	Paramelitidae	26.75				
Glossosomatidae	40.74						
Hydropsychidae	39.99*						
Ceratopogonidae	35.9						
Corydalidae	33.33						
Limnichidae	33.33						
Potamonautidae	33.33**						
Paramelitidae	28.81						

Only taxa with an indicator value higher or equal to 25 (IV) are presented.
*$P < 0.05$; **$P < 0.01$ by Monte Carlo permutation test (9999 runs).

of taxa (Lytle & Poff, 2004), macroinvertebrates of MCRs are presumed to be highly adapted to alternating permanent and temporary conditions. Indeed, comparisons of taxonomic and trait composition between rivers in temperate and mediterranean climates show that those of the Mediterranean Basin are more variable in composition than those of temperate Europe, where most rivers are permanent (Bonada, Dolédec & Statzner, 2007a). On the other hand, Delucchi & Peckarsky (1989) found overlapping communities in P and T reaches of a non-Mediterranean, North American river just before the drought season. As our study showed, however, the ways that regional evolutionary history and environmental characteristics constrain macroinvertebrate richness and composition in each MCR overrides this general vision of the similar response of MCRs at different scales of study. Northern hemisphere MCRs, having similar historical and environmental conditions, are thus the most similar regions at all scales in terms of macroinvertebrate structure.

Acknowledgments

We thank the following colleagues for field and laboratory assistance: M. McGuire (Murdoch University, Australia), B. Day (University of Cape Town, South Africa), P. Mendez, D. Rudnick, L. Bêche, F. Kerans, R. Mazor (all at the University of California, Berkeley). We also thank C. Madden at the Australian Water Quality Centre for providing regional composition of macroinvertebrates in the MCR of southern Australia, and two anonymous referees for helpful comments to improve the manuscript. This research was supported by the GUADALMED Project (HID98-0323-C05 and REN2001-3438-C07) and a grant to NB from the Ministerio de Ciencia y Tecnología (Spain).

References

Armesto J.J., Villagrán C. & Arroyo M.K. (1997) *Ecología de los Bosques Nativos de Chile*. Editorial Universitaria, Santiago de Chile.

Aschmann H. (1973) Distribution and peculiarity of mediterranean ecosystems. In: *Mediterranean Type Ecosystems. Origin and Structure* (Eds F. Di Castri & H.A. Mooney), pp. 11–19. Springer-Verlag, NY-Heidelberg-Berlin.

Bailey R.G. (1995) *Description of the Ecoregions of the United States*. Forest Service of the US Department of Agriculture, Washington, D.C.

Banarescu P. (1990) *Zoogeography of Fresh Waters. General Distribution and Dispersal of Freshwater Animals*. AULA-Verlag, Wiesbaden.

Bayly I.A.E. (1993) The fauna of athalassic saline waters in Australia and the Altiplano of South America: comparisons and historical perspectives. *Hydrobiologia*, **267**, 225–231.

Bonada N., Dolédec S. & Statzner B. (2007a) Taxonomic and biological trait differences of stream macroinvertebrate communities between mediterranean and temperate regions: implications for future climatic scenarios. *Global Change Biology*, **13**, 1658–1671.

Bonada N., Rieradevall M. & Prat N. (2007b) Macroinvertebrate community structure and biological traits related to flow permanence in a Mediterranean river network. *Hydrobiologia*, **589**, 91–106.

Bonada N., Rieradevall M., Prat N. & Resh V.H. (2006) Benthic macroinvertebrate assemblages and macrohabitat connectivity in Mediterranean-climate streams of northern California. *Journal of the North American Benthological Society*, **25**, 32–43.

Boulton A.J. & Lake P.S. (1992) The ecology of two intermittent streams in Victoria, Australia. II. Comparisons of faunal composition between habitats, rivers and years. *Freshwater Biology*, **27**, 99–121.

Boulton A.J. & Suter P.J. (1986) Ecology of temporary streams – an Australian perspective. In: *Limnology in Australia* (Eds P. De Deckker & W.D. Williams), pp. 313–327. CSIRO/Dr W. Junk, Melbourne.

Brown C.A. (1978) Freshwater molluscs. In: *Biogeography and Ecology of Southern Africa* (Ed. M.J.A. Werger), pp. 1153–1180. Dr. Junk Publishers, The Hague.

Brundin L. (1965) On the real nature of transanteartic relationships. *Evolution*, **19**, 496–505.

Bunn S.E. & Davies P.M. (1990) Why is the stream fauna of south-western Australia so impoverished? *Hydrobiologia*, **194**, 169–176.

Clarke K.R. (1993) Non-parametric multivariate analysis of changes in community structure. *Australian Journal of Ecology*, **18**, 117–143.

Cody M.L. & Mooney H.A. (1978) Convergence versus nonconvergence in Mediterranean-climate ecosystems. *Annual Review of Ecology and Systematics*, **9**, 265–321.

Cowling R.M. & Witkowski E.T.F. (1994) Convergence and non-convergence of plant traits in climatically and edaphically matched sites in Mediterranean Australia and South Africa. *Australian Journal of Ecology*, **19**, 220–232.

Cowling R.M., Ojeda F., Lamont B.B., Rundel P.W. & Lechmere-Oertel R. (2005) Rainfall reliability, a neglected factor in explaining convergence and divergence of plant traits in fire-prone mediterranean-climate ecosystems. *Global Ecology and Biogeography*, **14**, 509–519.

Dallas H.F. (2002) *Spatial and Temporal Heterogeneity in Lotic Systems: Implications for Defining Reference Conditions for Macroinvertebrates*. PhD Thesis, University of Cape Town, Rondebosch.

Deacon H.J. (1983) Comparative evolution of Mediterranean-type ecosystems: a southern perspective. In: *Mediterranean-Type Ecosystems: The Role of Nutrients* (Eds F.J. Kruger, D.T. Mitchell & J.U.M. Jarvis), pp. 3–40. Springer-Verlag, Berlin.

DeDeckker P. (1986) What happened to the Australian aquatic biota 18000 years ago? In: *Limnology in Australia* (Eds P. De Deckker & W.D. Williams), pp. 487–496. CSIRO, Melbourne.

Del Rosario R.B. & Resh V.H. (2000) Invertebrates in intermittent and perennial streams: is the hyporheic zone a refuge from drying? *Journal of the North American Benthological Society*, **19**, 680–696.

Delucchi C.M. & Peckarsky B.L. (1989) Life history patterns of insects in an intermittent and a permanent stream. *Journal of the North American Benthological Society*, **8**, 308–321.

Di Castri F. (1991) An ecological overview of the five regions of the world with a mediterranean climate. In: *Biogeography of Mediterranean Invasions* (Eds R.H. Groves & F. Di Castri), pp. 3–16. Cambridge University Press, Cambridge.

Dufrêne M. & Legendre P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, **67**, 345–366.

Dynesius M., Jansson R., Johansson M.E. & Nilsson C. (2004) Intercontinental similarities in riparian-plant diversity and sensitivity to river regulation. *Ecological Monographs*, **14**, 173–191.

Edmunds G.F.J. (1972) Biogeography and evolution of Ephemeroptera. *Annual Review of Entomology*, **17**, 21–42.

Endler J.A. (1982) Problems in distinguishing historical from ecological factors in biogeography. *American Zoologist*, **22**, 441–452.

Erman N. & Erman D.C. (1995) Spring permanence, Trichoptera species richness, and the role of drought. *Journal of the Kansas Entomological Society*, **68**, 50–64.

Figueroa R., Palma A., Ruiz V. & Niell X. (2007) Análisis comparativo de índices bióticos utilizados en la evaluación de la calidad de las aguas en un río mediterráneo de Chile: río Chillán, VIII Región. *Revista Chilena de Historia Natural*, **80**, 225–242.

Francis A.P. & Currie D.J. (2003) A globally consistent richness–climate relationship for angiosperms. *The American Naturalist*, **161**, 523–536.

Fuentes E.R. (1976) Ecological convergence of lizard communities in Chile and California. *Ecology*, **57**, 3–17.

Gasith A. & Resh V.H. (1999) Streams in mediterranean climate regions: abiotic influences and biotic responses to predictable seasonal events. *Annual Review of Ecology and Systematics*, **30**, 51–81.

Harrison A.D. (1978) Freshwater invertebrates (except molluscs). In: *Biogeography and Ecology of Southern Africa* (Ed. M.J.A. Werger), pp. 1139–1180. Dr. W. Junk Publishers, The Hague.

Hewitt G.M. (2004) The structure of biodiversity – insights from molecular phylogeography. *Frontiers in Zoology*, **1**, 1–16.

Lake P.S. (2000) Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society*, **19**, 573–592.

Lake P.S. (2003) Ecological effects of perturbation by drought in flowing waters. *Freshwater Biology*, **48**, 1161–1172.

Lake P.S., Barmuta L.A., Boulton A.J., Campbell I.C. & St Clair R.M. (1985) Australian streams and northern Hemisphere stream ecology: comparisons and problems. *Proceedings of the Ecological Society of Australia*, **14**, 61–82.

Lamouroux N., Poff N.L. & Argermeier P. (2002) Intercontinental convergence of stream fish community traits along geomorphic and hydraulic gradients. *Ecology*, **83**, 1792–1807.

Legendre P. & Legendre L. (1998) *Numerical Ecology*. Elsevier, Amsterdam.

Lein M.R. (1972) A trophic comparison of avifaunas. *Systematic Zoology*, **21**, 135–150.

Lobo J.M. & Davis A.L.V. (1999) An intercontinental comparison of dung beetle diversity between two mediterranean-climatic regions: local versus regional and historical influences. *Diversity and Distributions*, **5**, 91–103.

Logan P. & Brooker M.P. (1983) The macroinvertebrate faunas of riffles and pools. *Water Research*, **17**, 263–270.

Lytle D.A. & Poff N.L. (2004) Adaptation to natural flow regimes. *Trends in Ecology and Evolution*, **19**, 94–100.

McCulloch D.L. (1986) Benthic macroinvertebrate distributions in the riffle-pool communities of two east Texas streams. *Hydrobiologia*, **135**, 61–70.

Miller A.M. & Golladay S.W. (1996) Effects of spates and drying on macroinvertebrate assemblages of an intermittent and a perennial prairie stream. *Journal of the North American Benthological Society*, **15**, 670–689.

Mooney H.A. & Lloyd Dunn E. (1970) Convergent evolution of mediterranean-climate evergreen sclerophyll shrubs. *Evolution*, **24**, 292–303.

Morris D.W. (1987) Ecological scale and habitat use. *Ecology*, **68**, 362–369.

Munné A., Prat N., Solà C., Bonada N. & Rieradevall M. (2003) A simple field method for assessing the ecological quality of riparian habitat in rivers and streams: QBR index. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **13**, 147–163.

Pardo I., Álvarez M., Casas J. *et al.* (2004) El hábitat de los ríos mediterráneos. Diseño de un índice de diversidad de hábitat. *Limnetica*, **21**, 115–133.

Paruelo J.M., Jobbágy E.-G., Sala O.E., Lauenroth W.K. & Burke I.C. (1998) Functional and structural convergence of temperate grassland and shrubland ecosystems. *Ecological Applications*, **8**, 194–206.

Poff N.L. (1997) Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society*, **16**, 391–409.

Quinn G.P. & Keough M.J. (2002) *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge.

R Development Core Team (2007) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.

Robles S., Toro M., Nuño C. *et al.* (2004) Descripción de las cuencas mediterráneas seleccionadas en el proyecto GUADALMED. *Limnetica*, **21**, 35–61.

Sandin L. & Johnson R.K. (2004) Local, landscape and regional factors structuring benthic macroinvertebrate assemblages in Swedish streams. *Landscape Ecology*, **19**, 501–514.

Scullion J., Parish C.A., Morgan N. & Edwards R.W. (1982) Comparison of benthic macroinvertebrate fauna and substratum composition in riffles and pools in the impounded River Elan and the unregulated River Wye, mid-Wales. *Freshwater Biology*, **12**, 579–595.

Specht R.L. (1979) Heathlands and related shrublands of the world. In: *Heathlands and Related Shrublands* (Ed. R.L. Specht), pp. 1–18. Elsevier, Amsterdam.

Stamou G.P. (1998) *Arthropods of Mediterranean-Type Ecosystems*. Springer-Verlag, Berlin.

Statzner B., Gore J.A. & Resh V.H. (1988) Hydraulic stream ecology: observed patterns and potential applications. *Journal of the North American Benthological Society*, **7**, 307–360.

Storey A.W., Bunn S.E., Davies P.M. & Edward D.H. (1990) Classification of the macroinvertebrate fauna of two river systems in southwestern Australia in relation to physical and chemical parameters. *Regulated Rivers: Research and Management*, **5**, 217–232.

Suc J.-P. (1984) Origin and evolution of the Mediterranean vegetation and climate in Europe. *Nature*, **307**, 429–432.

Tonn W.M., Magnusson J.J., Rask M. & Toivonen J. (1990) Intercontinental comparison of small-lake fish assemblages: the balance between local and regional processes. *American Naturalist*, **136**, 345–375.

Vinson M.R. & Hawkins C.P. (2003) Broad-scale geographical patterns in local stream insect genera richness. *Ecography*, **26**, 751–767.

Williams D.D. (2006) *The Biology of Temporary Waters*. Oxford University Press, New York.

Wishart M.J. (1998) *Temporal Variations in a Temporary Sandbed Stream*. University of Cape Town, Cape Town.

Wright J.F., Hiley P.D., Cooling D.A., Cameron A.C., Wigham M.E. & Berrie A.D. (1984) The invertebrate fauna of a small chalk stream in Berkshire, England, and the effect of intermittent flow. *Archiv für Hydrobiologie*, **99**, 176–199.

(Manuscript accepted 28 November 2007)