RECENT PERSPECTIVES ON TEMPORARY RIVER ECOLOGY

Do seasonal changes in habitat features influence aquatic macroinvertebrate assemblages in perennial versus temporary Mediterranean streams?

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Abstract In this study we examined the importance of seasonal changes in habitat features and aquatic macroinvertebrate responses in temporary and perennial streams from two different catchments in the Western Mediterranean region in Spain. Macroinvertebrate sampling was spatially intensive to account for the relative frequency of meso- (i.e., riffles and pools) and micro-habitats (i.e., different mineral and organic-based substrata) at each site. Samples were collected at two distinctly different phases of the hydrograph: (1) during the flowing period, when pool-riffle sequences were well-established, and (2) during the dry phase, when only isolated pools were expected to occur in the temporary streams. During the dry season, both a reduction in the available total habitat and in microhabitat diversity in all sites studied was observed. As a result, taxon richness decreased in all streams, but more dramatically at temporary stream sites and particularly so in the infrequently remaining discontinuous riffles. Macroinvertebrate assemblages differed among catchments (i.e.,

geographical identity) and sites (perennial vs. temporary). Invertebrate differences were also strong within and among meso- and micro-habitats, particularly mineral and organic microhabitat patches, and differences were due to both loss of taxa from some habitats and some taxa exhibiting certain habitat affinities.

Keywords Aquatic macroinvertebrates · Habitat features · Mediterranean climate · Temporary streams · Undisturbed conditions

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Introduction

Although not always an available habitat for aquatic organisms, temporary streams constitute one of the most common fluvial ecosystems on Earth (Jacobson et al. 2004). Contrary to the preconception, temporary streams are not only restricted to arid and semiarid regions in the planet, where these watercourses are certainly abundant, but they occur in most terrestrial biomes between latitude 84°N and S (Larned et al. 2010). Despite this commonness, their ecology is still poorly known, especially compared to perennial streams. Due to climatic conditions and/or anthropogenic impacts, many streams in the Mediterranean region exhibit spatial and temporal discontinuities of surface water flow during the summer dry period (July–September). Typically, peak discharges occur in these streams from late fall to early spring (October–April; Gasith and Resh 1999). Interruption of surface water flow in summer is a semi-predictable natural constraint that leads to stagnant pools or the complete drying of the stream channel and requires aquatic organisms respond to these dramatic hydrologic changes (Williams 1985, 1996). Uys and O'Keefe (1997) classified these types of hydrologic

regimes in temporary rivers as "temporary seasonal". Despite this classification, temporary seasonal streams exhibit considerable intrinsic variability in the timing, duration and extent of the dry period (Boulton 2003; Lake 2003). This variability makes the study of the biology in these types of streams very difficult to study (Poff 1997).

Despite the long history of ecological studies on temporary streams (Stehr and Branson 1938; Hynes 1958), there is still a paucity of knowledge on factors influencing the structure and composition of aquatic macroinvertebrate communities in "temporary seasonal" streams. Past studies have typically been restricted to single temporary streams (Hynes 1958; Bunn and Davies 1992; Closs and Lake 1994) or, if several, to single catchments (Williams and Hynes 1976; Delucchi 1989; Feminella 1996; Miller and Golladay 1996; Pires et al. 2000; Bonada et al. 2007). As a consequence, it has been difficult to differentiate between the natural spatial variability of macroinvertebrate communities among these stream types and the effects of stream drying (Flinders and Magoulick 2002; Puntí et al. 2007).

Multiple spatial scales, varying from the catchment- to the microhabitat-level, have been showed to influence aquatic macroinvertebrate assemblages in lotic systems (Poff 1997; Townsend et al. 2003; Allan 2004). As the scale of resolution broadens, more abiotic and biotic filters (or factors) influence the occurrence and abundance of organisms and ultimately shape the local community assemblage (Poff 1997). In this manner, catchment-scale factors introduce regional and climatic constraints for the fauna (McCreadie and Adler 2006), whereas single streams within a catchment may filter (restrict or favor) organisms through bedrock properties and water chemistry (Huryn and Wallace 1987). In addition, environmental conditions at the mesohabitat level, such as fast (i.e., riffles) and slow (i.e., pools) water velocity conditions, further restricts the distribution of aquatic macroinvertebrates (McCulloch 1986; Statzner et al. 1988; Brown and Brussock 1991; Chaves et al. 2008). Finally, the microhabitat level contains a mosaic of substrata and food resources that are crucial for the development of life of stream macroinvertebrate communities (Armitage and Cannan 2000). All of these spatial scales are affected by seasonal heterogeneity of temporary streams, hence it is likely that seasonal heterogeneity constrains the distribution and abundance patterns of aquatic macroinvertebrates (Ward 1989; Williams 1996). Differences in the aquatic macroinvertebrate assemblages between perennial and temporary streams have been reported to be due to hydroperiod length (Feminella 1996; Sánchez-Montoya et al. 2007) or season (Williams and Hynes 1976, 1977; Delucchi 1988; Delucchi and Peckarsky 1989; Del Rosario and Resh 2000). Further, there is often a marked biological difference between ephemeral and intermittent temporary streams. Ephemeral streams (temporary streams that flow only during periods of significant runoff) have been shown to be more impoverished than intermittent streams (temporary streams that flow when groundwater levels are elevated) and both temporary stream types are impoverished compared to perennial streams (Bonada et al. 2007).

The length and frequency of the dry season may also be important factors in determining the occurrence of specific taxa (Flinders and Magoulick 2002; Fritz and Dodds 2005). For example, Delucchi (1988) observed a greater similarity in fauna between a temporary and a perennial stream after the temporary stream was flowing for a considerable time period compared to when flows were declining (entering drought periods) or the period immediately following rewetting after drought. This naturally leads us to the hypothesis that as the natural seasonal change leads to the disappearance of riffles during the dry season, organisms adapted to flowing water or lotic conditions will disappear and taxa better adapted to lentic conditions will appear in the pools that remain.

These studies have demonstrated that in order to understand biological structure and perhaps function of temporary streams, the hydrological conditions during drying, rewetting, and stable flow must be quantified and related to biotic responses. In this study, we stress the importance of identifying and accounting for specific hydrological conditions at the time of sample collection. We also propose a sampling procedure for macroinvertebrate assemblages in temporary streams that designed to support comparison between stable flow periods and drying or rewetting periods. We define the stable flow period in our study rivers to occur when the flow of water is relatively constant, usually after winter or spring flooding, and the entire stream section being studied is connected by surface flow (i.e., continuity of surface water flow among all stream reaches). Once the riverbed contains a series of disconnected pools, which typically occurs during the summer in the Mediterranean region, we initiated a second sampling period that we refer to as the drought period.

The goal of this study was to characterize seasonal changes in habitat features in some of the least anthropogenically disturbed temporary and perennial streams in the Western Mediterranean region in Spain, as well as to characterize the primary influencing factors structuring aquatic macroinvertebrate communities during these two hydrological periods (i.e., flowing and drought conditions). This approach is embedded in Habitat Templet Theory, which states that the presence and abundance of organisms is determined by habitat features operating at different scales and these habitat template components are spatially and temporally variable (Southwood 1977; Townsend and Hildrew 1994; Poff 1997). This may be especially

important in Mediterranean temporary streams subjected to inter-annual variation in seasonal shifts that have a profound effect on spatial scales of the aquatic habitat.

Methods

Study sites

We surveyed two nearly undisturbed catchments located in NE and SE Spain (Western Mediterranean), named Vallcebre and Taibilla (Fig. 1). We selected one perennial and one temporary stream from each catchment. The Vallcebre catchment area is 19 km^2 and is located in a moderate altitude mountain area (1,000–2,200 m a.s.l. in the Pyrenees range) in the headwaters of the Llobregat River, which is the primary drinking water source for the Barcelona metropolitan area (NE Spain). The basin is dominated by sedimentary rocks and silty-loamy soils (Gallart et al. 2002). Long-term annual precipitation is about 860 mm and annual potential evapotranspiration is 820 mm (Latron et al. 2009). During the summer, however, evapotranspiration largely exceeds precipitation, inducing a water deficit and the interruption of flow in many headwater streams. Within the Vallcebre catchment, we studied a temporary stream, Can Vila, and a perennial stream, Cal Rodó. The other study area, the Taibilla catchment, is approximately 600 km^2 and is a tributary of the Segura

River, which flows to the Mediterranean Sea from the SE Iberian Peninsula. Elevations of our study areas ranged from 800 to 2,100 m a.s.l. The dominant lithology consists of marls, limestones and sandstones. The climate is transitional between a sub-humid Mediterranean and a semiarid environment with an average annual rainfall of around 500 mm. Within the Taibilla catchment, we studied a temporary stream, Rambla de la Rogativa, and a perennial stream, Arroyo Blanco. These two sub-catchments together covered a total surface of 70 km^2. Distance between these two streams was ca. 6 km, so they were under similar climatic and geologic conditions. In both catchments, the study sites fulfilled most of the criteria for reference conditions proposed by Sánchez-Montoya et al. (2009), which allowed us to study the influence of a natural hydrological regime (i.e., flow interruption and channel drying) on the biological communities under nearly undisturbed environmental conditions. Table 1 lists several hydrological features of the streams studied.

Aquatic macroinvertebrate sampling

Aquatic macroinvertebrates were collected from the streams during the two selected hydrological periods in 2009: (1) during the flowing period, when pool-riffle sequences were well-established, and (2) during the dry phase, when only pools were expected to be present in the temporary streams. However, when sampling during the

Fig. 1 Location of the catchments and streams studied in the Iberian Peninsula
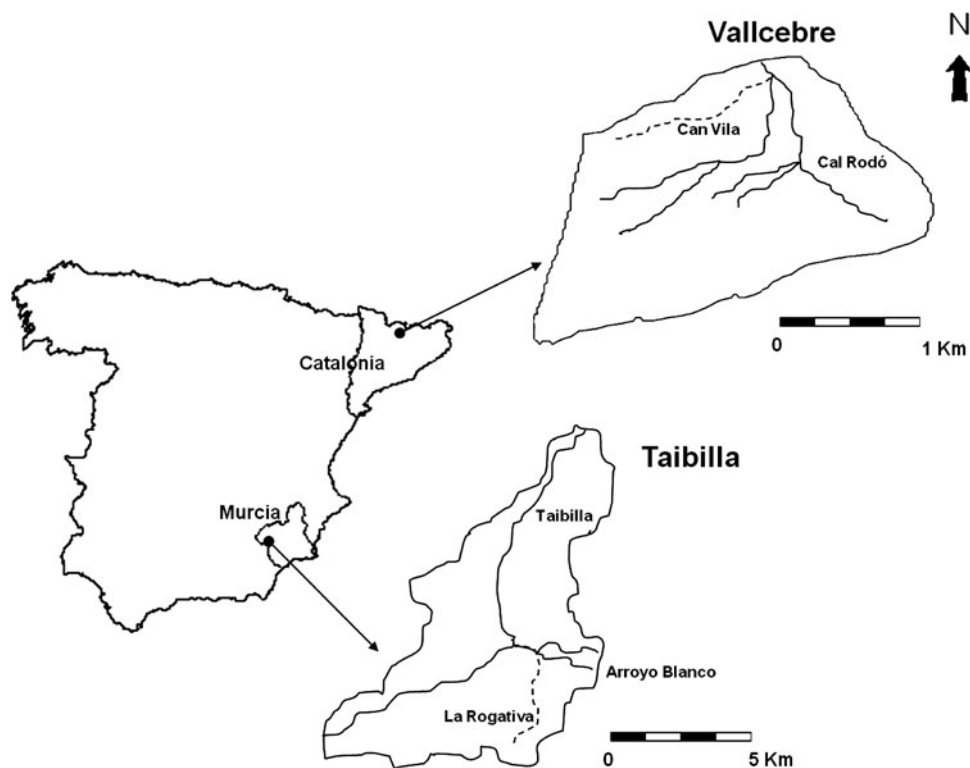
Table 1 Environmental characteristics of the streams studied

Variables	Streams			
	Cal Rodó	Can Vila	Arroyo Blanco	La Rogativa
Hydrology	Perennial	Temporary	Perennial	Temporary
Latitude	42°11′57″N	42°11′54″N	38°09′58″N	38°07′39″N
Longitude	1°49′26″E	1°49′26″E	2°11′01″W	2°13′31″W
Altitude (m a.s.l.)	1,058	1,064	1,149	1,146
Distance from source (km)	2.5	1.1	7	17.3
Drainage basin (km^2)	4.2	0.6	23	47.2
Order	2	1	1	1
Channel width (m)[a]	2.4; 1.9	1.4; 0.9	2.4; 1.5	0.7; 0.6
Average depth (m)[a]	0.24; 0.15	0.14; 0.11	0.03; 0.02	0.02; 0.01
Water discharge (L s^{-1})[a]	6.5; 0.3	2.2; 0.0	10.2; 1.5	1.9; 0.1
Water temperature (°C)[a]	15.2; 14.2	13.1; 16.3	19.7; 26.1	21.4; 21.9
pH[a]	7.1; 7.4	6.8; 7.4	8.4; 8.3	8.1; 8.4
Conductivity (µS cm^{-1})[a]	2,900; 2,300	1,735; 1,900	616; 658	923; 881
Dissolved O$_2$ (mg L^{-1})[a]	8.6; 8.3	8.8; 6.7	8.2; 8.5	11.6; 8.75
% O$_2$ saturation[a]	88.8; 85.4	85.8; 68.0	102.5; 119.2	149.6; 116.1
Nitrate (mg NO$_3^-$ L^{-1})[a]	1.73; 1.93	1.27; 2.08	1.15; 1.19	3.07; 5.83
Nitrite (mg NO$_2^-$ L^{-1})[a]	0.00; 0.00	0.00; 0.00	0.00; 0.09	0.00; 0.00
Ammonium (mg NH$_4^+$ L^{-1})[a]	0.1; 0.1	0.1; 0.2	0.1; 0.2	0.1; 0.2
Phosphate (mg L^{-1})[a]	0.01; 0.12	0.01; 0.06	0.01; 0.02	0.01; 0.03
IHF[a]	76; 70	71; 56	61; 49	56; 38
QBR	90	90	90	90

Wet (first value) and dry (second value) season values are separated with a semicolon (;)

[a] Values changed from the wet (first data) to the dry season (second data)

dry phase, there were several small runs still present in the temporary streams and were sampled as riffles for comparative purposes. Although both of the hydrological periods selected were expected to occur during spring and summer, respectively, the actual occurrence of these periods is like to be variable among years. For this reason, our sampling dates were determined after examining hydrological conditions in each stream. In both study catchments, observations of stream flow were available (from stage height recorders in the Vallcebre and from repetitive visits to the Taibilla, see below) to determine the points in time when the hydrological conditions were as described above. Samples were taken from representative stream reaches (20–35 m length) from each selected study streams. All stream reaches studied had at least two pool-riffle sequences during the wet-season sampling event. Surber samples (15 × 15 cm, 250 μm mesh) were collected from 20 different locations within each stream reach and were distributed within the reach based on the relative percentage of pool and riffle area (mesohabitat) and the relative proportion of substrate type (i.e., microhabitats defined as various mineral or organic substrata; see Table 2). The substrate types were similar to those described in the AQEM project protocols (Hering et al. 2004), which defines a level of detail not typically reported in macroinvertebrate monitoring surveys. In this study, samples were not pooled but were treated individually.

Mesohabitat (i.e., riffle vs. pool) and microhabitat (i.e., substrate), depth (cm), and flow velocity (m s^{-1}) were recorded for each sample and each sample was fixed in the field with formaldehyde (4% final concentration) and returned to the lab for sorting, counting and identification. Macroinvertebrate samples were examined using a stereoscope at 10× magnification in the laboratory. All individuals in each sample were picked and identified to the family level, except for Ostracoda, Oligochaeta and Hydracarina, according to Tachet et al. (2000).

Environmental variables

Several physico-chemical variables were measured at each stream reach using portable probes (WTW) on each sampling occasion: temperature (°C), conductivity (µS cm^{-1}), pH, ammonia (mg NH$_4^+$ L^{-1}) and dissolved oxygen (% and mg L^{-1}). Additionally, water samples (250 mL) were collected from each site, placed in a cooler for transport and returned to the lab for processing. In the lab, samples were filtered through 0.45 µm membrane filters and frozen for storage. Water samples were analyzed to determine the concentrations of nitrates (mg NO$_3^-$ L^{-1}) and nitrites (mg NO$_2^{2-}$ L^{-1}) using HPLC, and phosphates (mg PO$_4^{3-}$ L^{-1}), which were measured according to the method described by Murphy and Riley (1962) using a Shimadzu (UV-1201) spectrophotometer at 890 nm. Discharge (L s^{-1}) in the

Table 2 List of microhabitats (From AQEM protocol; Hering et al. 2004)

Microhabitat	Code
Mineral	
Argyllal < 6 μm	ARG
Psammal > 6 μm–2 mm	PSA
Akal > 2 mm–2 cm	AKA
Microlithal > 2–6 cm	MIL
Mesolithal > 6–20 cm	MEL
Macrolithal > 20–40 cm	MAL
Megalithal > 40 cm	MGL
Artificial	ART
Hygropetric—water layer on solid substrate	HYG
Organic	
Algae—filamentous algae, algal tufts	AL
Submerged macrophytes (including bryophytes)	SM
Living part of terrestrial plants—fine roots, floating riparian vegetation	TP
Xylal—tree trunks, dead wood, branches, roots	XY
CPOM—deposits of coarse particulate organic matter	CP
FPOM—deposits of fine particulate organic matter	FP
Sewage and sulphur bacteria, fungi and sapropel	SW

streams from the Taibilla catchment was determined in the narrowest section of the reach by measuring channel width and measuring velocity (at $0.6\times$ depth) at a minimum of five equal intervals across the channel. Daily average discharge was available from automatic gauging stations maintained by the Spanish Council of Scientific Research (CSIC; Latron and Gallart 2008) for Cal Rodó and Can Vila in the Vallcebre catchment.

Habitat quality at the four sites was evaluated by using the Fluvial Habitat Index (IHF; Pardo et al. 2004) and the Riparian Corridor Quality Index (QBR; Munné et al. 2003) on each sampling occasion. The IHF is derived from substrate composition, embeddedness, velocity regimes, riffle frequency, light exposure on the stream channel, presence of heterogeneity elements and aquatic vegetation, and was designed to evaluate the ability of the stream's physical habitat to support a rich fauna. The QBR index is derived from of the degree of vegetation cover, structure and quality of the vegetation, and the degree of alteration in the channel, and was developed to assess the integrity of the riparian corridor.

Data analysis

Macroinvertebrate abundance data were reported as density values (individuals m^{-2}), and environmental data were standardized in order to properly deal with variables of different magnitudes. All statistical analyses described below were carried out using R 2.10.1 statistical software (Ihaka and Gentleman 1996) using functions included in the following packages: stats (used for PCA and Fisher's exact tests), ecodist (for nMDS), vegan (for ADONIS) and labdsv (for IndVal).

A Principal Components Analysis (PCA) was performed to examine similarities of environmental features within and among streams. Highly correlated environmental variables were removed prior to analysis (e.g., QBR, IHF, concentrations of nitrates and nitrites, and oxygen saturation were removed after applying the criteria of $r > 0.8$ as cut-off threshold). Fisher's exact test of independence for $R \times C$ cross-tables was performed to statistically evaluate shifts in meso and microhabitat frequencies among seasons on each stream studied.

Family richness (S) accumulation curves for each stream were derived by randomly ordering samples in a species-by-sample spreadsheet and searching for asymptotical behavior (i.e., to confirm that sampling was exhaustive enough and that proper sample size and Surber dimensions were used). A total of 100 random permutations of sampling units order were performed for each site following a subsampling without replacement procedure as suggested by Gotellli and Colwell (2001).

To determine similarities among samples in macroinvertebrate data, non-metric multidimensional scaling (nMDS; Kruskal 1964) was performed on a Bray–Curtis distance matrix. Macroinvertebrate data were log-transformed prior to ordination to downweight the contributions of abundant taxa. The minimum stress level of the ordination (a measure of goodness of fit) and r^2 values (a measure of the total variance explained by each configuration) was noted after determining the minimum number of dimensions necessary to complete the ordination after 20 random starting configurations and then running 100 iterations of the final solution. Separate nMDS ordinations were completed for each sampling period. Individual samples were labeled within each ordination solution to help visually assess differences among streams, mesohabitats and microhabitats. Next, permutational multivariate analysis of variance using distance matrices (ADONIS; equivalent to Anderson's (2001) non-parametric multivariate ANOVA) were used to test for differences in macroinvertebrate assemblages in a nested hierarchical design accounting for (1) microhabitats (substrate type) within (2) mesohabitats (pools vs. riffles) within (3) streams within (4) catchments, all crossed against (5) season (wet vs. dry) and (6) temporality (temporary vs. perennial), and including their interactions. Note that levels of the nested stream, mesohabitat and microhabitat factors were deliberately arranged by the experimenters and did not represent a random sample of all possible levels of interactions in nature. Thus these factors were treated as

fixed and their effects analyzed following Quinn and Keough (2002). Finally, a total of 999 permutations were performed on the Bray–Curtis distance matrix obtained from log-transformed data (see above).

Indicator Value (IndVal) analysis (Dufrêne and Legendre 1997) was used to determine the most representative macroinvertebrate family taxa (based on an abundance data matrix) for each of the following groups: temporality (temporary vs. perennial streams), mesohabitat (pools vs. riffles), and microhabitat (substrate type). The IndVal is at a maximum (probability equals 100%) when all individuals of a taxon are found in just one group of samples and when the taxon is present in all samples of that group. We followed the criteria by Dufrêne and Legendre (1997) of considering a threshold level of 25 for the index to be accepted as relevant, which means that individuals of a given taxa are present in more than 50% of the samples of a group and with a relative abundance in that same group of more than 50%. For the assessment of the significance of a given taxon being characteristic of a single group, IndVal was tested by randomization (999 permutations of samples among sample groups). The importance of microhabitat was examined by considering the relative abundance of the most abundant families in each of the different substrate types.

Results

Seasonal changes in habitat features

Study sites had substantial seasonal shifts in water temperature, current speed, average depth, water discharge and dissolved oxygen concentration (Table 1). Although there was some seasonal variation in nutrient concentration, all sites studied were oligotrophic (<0.2 mg NH_4^+ L^{-1}, <10 mg NO_3^- L^{-1}, <0.1 mg PO_4^{3-} L^{-1}). Furthermore, QBR values were very high in general (90 in all streams), indicating that all four study streams were in areas without significant human disturbances (Sánchez-Montoya et al. 2009). The first two PCA factors explained 72.1% of the spatial variance in environmental variables measured (Fig. 2). The first factor explained 49.3% of total variance and was positively related to temperature and pH and negatively related to specific conductivity. PCA factor 1 primarily separated sites located in different catchments (NE Spain and SE Spain). The second factor explained 22.8% of total variance and was positively related to nutrient concentration and negatively related to dissolved oxygen concentration and water velocity. PCA factor 2 was interpreted as a gradient of environmental conditions related to seasonality.

At the mesohabitat (riffle and pool) and microhabitat (substrate) scale, differences related to seasonal flow
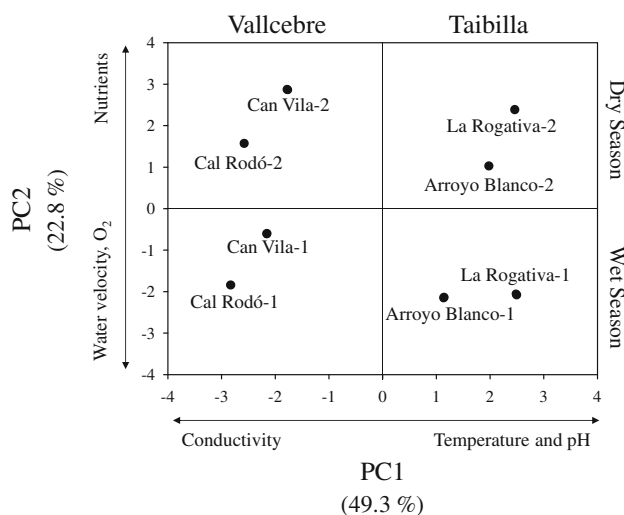
Fig. 2 Distribution of the streams studied at both sampling seasons (1 Wet season, 2 Dry season) in the space defined by the first two factors of the Principal Component Analysis. Correlation coefficients of variables on first axis: Temperature = 0.90, pH = 0.88, Conductivity = -0.88, Depth = -0.94. Correlation coefficients of variables on second axis: $NH_4^+ = 0.80$, $PO_4^{3-} = 0.65$, $O_2 = -0.65$, water velocity = -0.90

conditions were noticeable (Fig. 3). During the wet season, the relative frequency of pools and riffles was nearly even in streams from both catchments. As long as riffles nearly disappeared during the dry season, there was an observed reduction of the available habitat in three out of the four study sites, with the exception of the perennial stream of Arroyo Blanco in the Taibilla catchment. Fisher's exact tests did not reveal a significant change in mesohabitat frequencies among seasons at any stream, although p values ranged accordingly to the shift observed (Fig. 3). Total reduction in the area covered by water varied from ca. 75% in the perennial Cal Rodó to 55% in the temporary Can Vila in the Vallcebre catchment. Compared to riffles, pools had only a slight reduction in inundated area (Fig. 3). The dry season in the Taibilla catchment did not lead to a substantial reduction in total inundated habitat area and in the temporary La Rogativa, the partial disappearance of the riffle also lead to an increase in lentic conditions (i.e., riffles changed to pools due to flow cessation). However, even in the perennial Arroyo Blanco, water velocity and water depth were substantially reduced (Table 1). Both catchments differed in their microhabitat composition. While organic microhabitats (i.e., mainly fine and coarse deposits of organic matter) were dominant in Taibilla, a mixed mineral and organic composition of microhabitats was observed in the Vallcebre catchment streams. We found statistically significant differences in microhabitat composition among seasons in three out of the four streams studied, again with the exception of Arroyo Blanco (see Fisher's exact tests at Fig. 3). We observed an increase in

wood debris (i.e., xylal substrate) in both pools and riffles in La Rogativa during the dry season, which was likely to be a consequence of the shift from erosional to depositional conditions. In the Vallcebre catchment, the diversity of microhabitats declined with the general reduction in available inundated habitat. This was primarily related to a general loss in organic substrata (Fig. 3).

Aquatic macroinvertebrate community structure

A total of 163 Surber samples were collected and processed from these four study sites, and more than 58,000 specimens belonging to 56 different families of aquatic macroinvertebrates were identified. Densities ranged from 0 to 41,733 individuals m^{-2} with the family Chironomidae (Diptera) being the most abundant and ubiquitous taxon at all sites and all seasons, averaging $42.1 \pm 2.1\%$ (SE) of total density in samples.

Family richness (S) accumulation curves reached an asymptote after ca. 20 samples in all locations (Fig. 4). S differed among sites and among seasons and, in general, values were lower during the dry season with the exception of the perennial Arroyo Blanco. S was always higher in the perennial streams ($S_w = 34$ and $S_d = 31$ in Cal Rodó; $S_w = 30$ and $S_d = 33$ in Arroyo Blanco, where sub-indexes $_w$ and $_d$ refer to the wet and dry season, respectively) than in the temporary streams ($S_w = 28$ and $S_d = 26$ in Can Vila; $S_w = 18$ and $S_d = 14$ in La

Rogativa). Mean abundance of aquatic macroinvertebrates was also higher in perennial streams and decreased in the dry season in nearly all streams (from $7,055 \pm 1,058$ to $2,553 \pm 710$ individuals m^2 in Cal Rodó, $6,537 \pm 2,065$ to $1,006 \pm 169$ individuals m^2 in Can Vila, and $2,452 \pm 511$ to $1,900 \pm 613$ individuals m^2 in La Rogativa), except in the perennial stream of Arroyo Blanco (from $3,160 \pm 412$ growing up to $3,703 \pm 376$ individuals m^2).

In order to reveal underlying patterns in the community structure among sites, mesohabitats and microhabitats, we computed two separate 3D nMDS solutions based on samples collected during the wet or dry seasons (Fig. 5). Stress values of the ordinations were acceptable in both cases (Stress$_w$ = 0.178; Stress$_d$ = 0.156; Clarke and Warwick 2001) and the explained variances were high for both ordinations (>75%). The wet-season ordination revealed differences between catchments along the first axis (nMDS1) and between hydrological regimes in the second one (nMDS2). Samples from the same stream were also clustered tightly and highlighted consistent invertebrate assemblage differences among sites. However, during the dry season the ordination highlighted a greater differentiation between the perennial and the temporary stream from the Taibilla catchment, whereas samples from either perennial or temporary streams in the Vallcebre catchment streams were undifferentiated. In addition, pools and riffles were easily differentiated in the wet season ordination, as there was a positive and significant relationship between
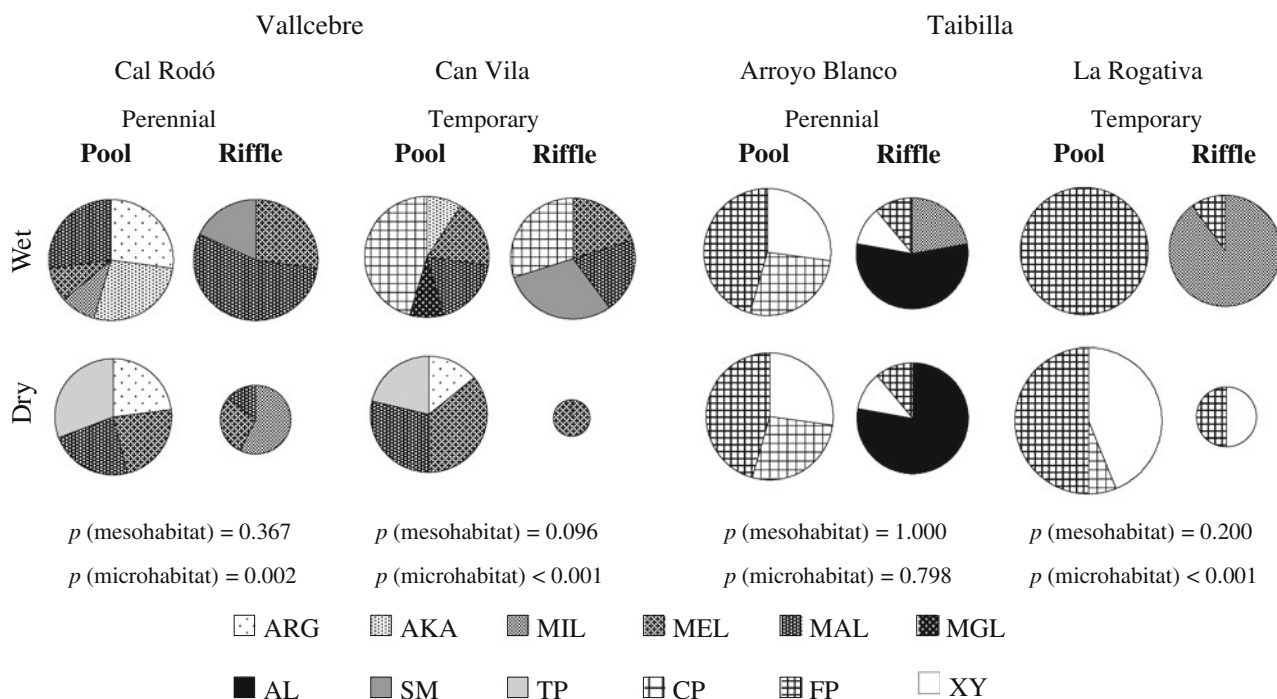
Fig. 3 Meso- and microhabitat relative frequency in the wet and dry season in the streams studied. p values at the bottom of the pie charts indicate Fisher's exact test significance in mesohabitat and microhabitat frequency change among seasons for each stream

Fig. 4 Cumulative family taxa richness of the studied streams at both sampling seasons. *Bars* represent SE of the estimates
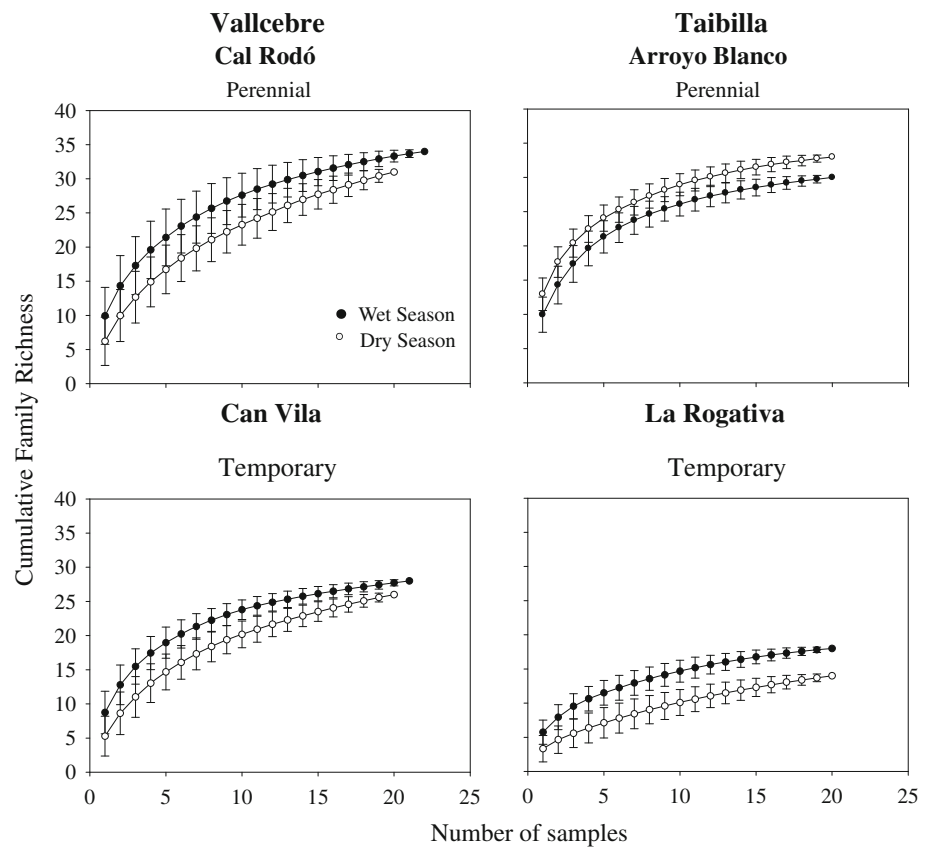
water velocity and site scores on nMDS axis 3 for the wet-season ordination ($r^2 = 0.160$, $t = 3.989$, $df = 81$, $p < 0.001$). This distinction was not apparent in the dry season ordination, as the invertebrate taxa in the riffle had transitioned to taxa more indicative of the pool habitat. At the microhabitat scale, there was a strong differentiation between invertebrate communities collected from organic and mineral microhabitats, especially in the dry season. This distinction was related to differences in microhabitat composition among catchments. In contrast, during the wet season we were able to identify some macroinvertebrate aggregations associated with algae, submerged macrophytes, or deposits of fine-particulate organic matter despite some degree of site overlap in the nMDS.

A summary of the significance of the various nested (catchment, stream, mesohabitat and microhabitat) and crossed (season and temporality) effects analyzed using ADONIS on the taxonomic structure of aquatic macroinvertebrate communities is shown in Table 3. This hierarchical-crossed model explained 67.8% of total variance and included as many interaction effects as allowed by the degrees of freedom. Our results showed that macroinvertebrate assemblages were affected by all of the spatially nested factors (i.e., from catchment- to microhabitat-level), as well as by season (wet vs. dry) and temporality (temporary vs. perennial streams). The highest

percentage of variance (14%) was explained by the microhabitat level (i.e., microhabitat within mesohabitat, within stream, within catchment). Interaction effects related to seasonality and temporality were generally significant, with the only exception being that involving microhabitat and season.

IndVal analyses revealed which taxa were the most indicative of perennial and temporary stream assemblages of mesohabitats and microhabitats (Tables 4, 5, 6, 7). Three families (Baetidae, Leuctridae and Simuliidae) that were characteristic of perennial streams (Table 4) were also indicative of the riffle mesohabitat (Table 5). Only one family (Hydrophilidae) was found to be characteristic of pools (Table 5).

As described in the "Methods", we explored the relative abundance dataset of dominant aquatic macroinvertebrates in the different microhabitats (Table 6). Aquatic macroinvertebrates were not equally distributed among the available substrata. As it was expected, the most ubiquitous taxa were also among the most abundant (e.g., Chironomidae, Leuctridae, Baetidae and Ceratopogonidae). In general, the organic substrate microhabitats had higher richness and higher relative abundances of aquatic macroinvertebrates than mineral substrata. The majority (60%) of the top-20 most abundant taxa had higher abundances in aquatic mosses (SM) with up to 42% of total individuals.
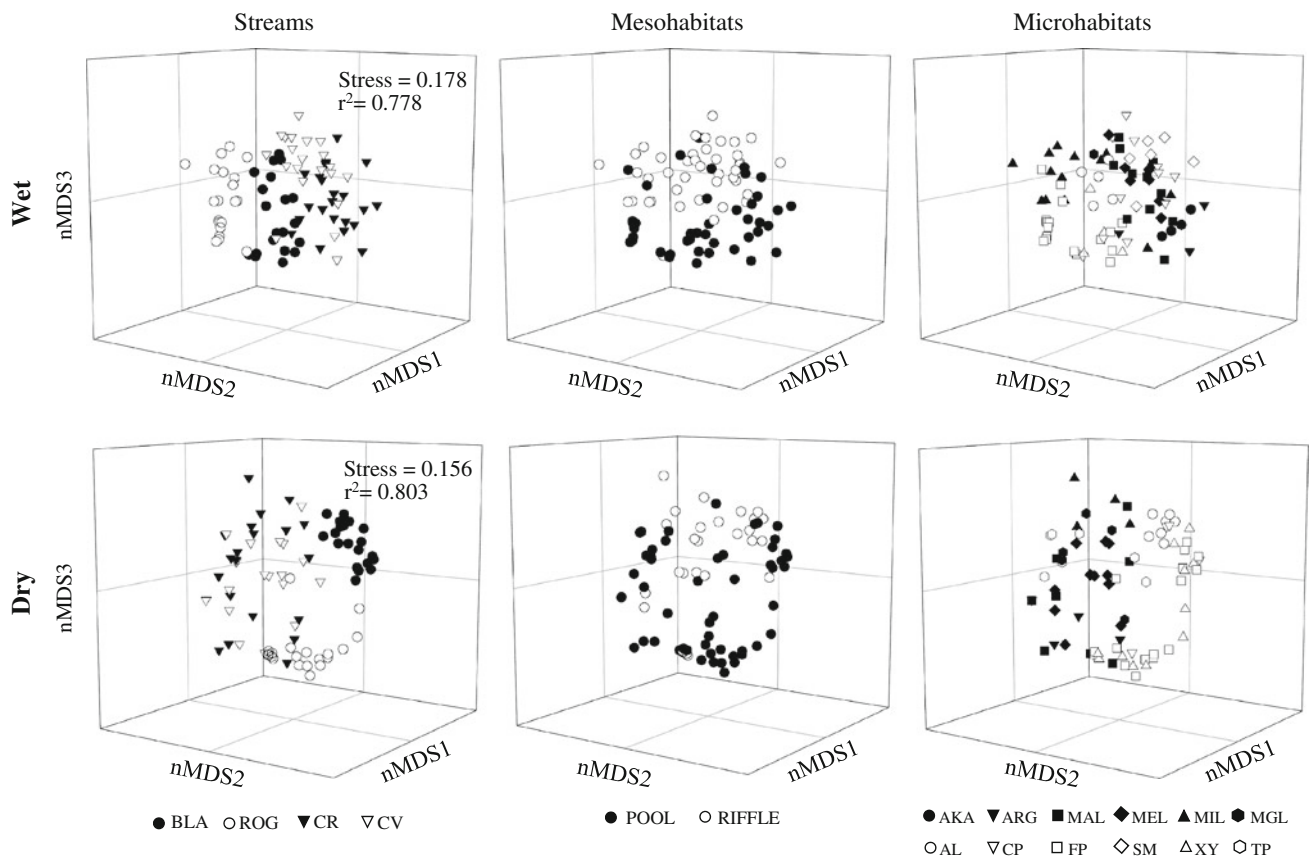
Fig. 5 Non-Metric Dimensional Scaling ordination of the aquatic macroinvertebrate community during both sampling seasons. Each *point* represents the aggregation of macroinvertebrates from individual Surber samples. These have been labeled according to their stream, mesohabitat and microhabitat features in three separate plots

Table 3 Summary of the nested-crossed ADONIS analysis performed on family level macroinvertebrate abundance data

Source of variation	df	r^2	p
Catchment	1	0.09	0.01
Stream (catchment)	1	0.08	0.01
Mesohabitat [stream (catchment)]	4	0.09	0.01
Microhabitat [mesohabitat (stream (catchment))]	28	0.14	0.01
Season	1	0.04	0.01
Temporality	1	0.08	0.01
Season × temporality	1	0.04	0.01
Season × catchment	1	0.05	0.01
Season × stream (catchment)	1	0.03	0.01
Season × mesohabitat [stream (catchment)]	4	0.02	0.05
Season × microhabitat [mesohabitat (stream (catchment))]	6	0.01	0.90
Residuals	113	0.32	

Table 4 Indicator value (IndVal) and associated significance level (p) for macroinvertebrate family taxa in perennial and temporary streams

Perennial			Temporary		
Family	IndVal	p	Family	IndVal	p
Baetidae	57.6	0.001	Nemouridae	25.5	0.002
Leuctridae	56.3	0.001	Limnephilidae	25.0	0.001
Gomphidae	41.7	0.001	Hydrophilidae	20.0	0.026
Caenidae	35.5	0.001			
Heptageniidae	33.3	0.001			
Simuliidae	29.5	0.005			
Elmidae	29.1	0.001			
Hydroptilidae	27.8	0.001			

We did not find any the top-20 most abundant taxa residing exclusively on a single microhabitat. Heptageniidae exhibited the highest microhabitat fidelity (72%) where it preferred algal substrata (AL). Note that Simuliidae was one of the few dominant taxa that were more abundant on mineral substrata (MIL). However, it is worth noting that the algal microhabitat typically covered mineral substrate (MAL or MEL). Caenidae were absent from mineral substrata and abundant on xylal substrata (XY), and Nemouridae and Hydropsychidae were predominantly found in CPOM and on mineral substrata, respectively.

Table 5 Indicator value (IndVal) and associated significance value (*p*) for macroinvertebrate family taxa in either mesohabitat

Pool			Riffle		
Family	IndVal	*p*	Family	IndVal	*p*
Hydrophilidae	25.8	0.003	Simuliidae	58.1	0.001
			Baetidae	56.9	0.001
			Leuctridae	48.8	0.001
			Hydropsychidae	47.7	0.001
			Nemouridae	27.5	0.002

Among the less abundant taxa (data not shown), those that were present in only one or two different microhabitats, always had very low densities (<1 individual m^{-2}) and appeared only in one or two Surber samples. Hence, those taxa were not considered to be indicative of any conditions we tested. We then constrained our interpretation of the microhabitat IndVal analysis to only the most frequently sampled microhabitats (*n* > 5) and Table 7 presents those results for the only substrata from which we obtained significant indicator taxa: algae and submerged macrophytes. In fact, these two substrata were taxon rich microhabitats. This result was consistent with that obtained from the nMDS ordination analyses (see above).

Discussion

Temporary streams are difficult to compare among themselves and with perennial streams because the time relative to significant hydrological events when biological samples are collected has a significant impact on taxonomic assemblages present. As a consequence, different community assemblages may propagate that are independent of regional or climatic constraints (Acuña et al. 2005; Sánchez-Montoya et al. 2007). In this study, we used a sampling design that accounted for seasonal changes affecting Mediterranean temporary streams and we examined invertebrate community patterns at multiple spatial scales.

During the wet season, well established pool-riffle sequences were observed at all study sites. By contrast, dry season differences in flow conditions among temporary and perennial streams were observed as water flow subsided and riffles were reduced to pools with differing degrees of connection between the two temporary streams. Throughout the study period, water flow was uninterrupted in perennial streams. Observations of environmental factors and habitat features revealed differences between perennial and temporary streams within catchments (Fig. 3). While environmental variables in the perennial streams studied

Table 6 Top 20 most abundant taxa and their relative abundance per microhabitat

Family	Mean ± SE (individuals m^{-2})	Relative abundance											
		Mineral						Organic					
		ARG	AKA	MIL	MEL	MAL	MGL	AL	SM	CPOM	FPOM	XY	TP
Chironomidae	1,653.13 ± 511.18	0.04	0.03	0.05	0.08	0.10	0.09	0.01	0.35	0.11	0.05	0.03	0.06
Leuctridae	803.55 ± 363.88	<0.01	0.05	0.02	0.07	0.07	<0.01	0.12	0.48	0.08	0.02	0.07	<0.01
Baetidae	644.61 ± 144.79	<0.01	<0.01	0.14	0.05	0.12	0.03	0.09	0.24	0.10	0.07	0.06	0.09
Simuliidae	175.49 ± 75.25	<0.01	–	0.37	<0.01	0.02	0.02	0.28	0.11	0.15	<0.01	0.04	–
Ceratopogonidae	173.41 ± 54.03	0.05	0.06	0.01	0.02	0.04	0.02	<0.01	0.25	0.11	0.14	0.26	0.02
Nemouridae	109.62 ± 51.45	–	–	0.06	0.08	0.07	0.05	–	0.42	0.30	–	–	0.02
Hydropsychidae	63.70 ± 24.81	–	–	0.05	0.20	0.03	0.01	0.15	0.37	0.05	–	0.14	–
Ostracoda	60.89 ± 17.49	0.18	0.20	0.06	0.02	0.02	0.17	<0.01	0.20	0.12	0.01	<0.01	0.02
Caenidae	60.32 ± 31.54	–	–	–	–	–	–	0.05	0.07	0.15	0.22	0.51	0.01
Heptageniidae	59.23 ± 42.13	–	–	0.05	–	<0.01	–	0.72	–	0.08	0.01	0.14	–
Oligochaeta	31.75 ± 15.15	0.04	0.03	0.04	0.02	0.14	–	–	0.49	0.17	<0.01	–	0.07
Hydracariba	24.75 ± 8.96	0.11	0.15	0.02	0.07	0.09	0.10	<0.01	0.37	–	–	0.01	0.06
Elmidae	22.46 ± 10.70	0.06	0.04	0.03	0.08	0.17	0.03	0.02	0.49	–	0.02	<0.01	0.05
Gomphidae	22.13 ± 9.83	–	–	0.01	–	–	–	0.41	–	0.17	0.17	0.19	0.05
Copepoda	21.13 ± 6.70	0.20	0.26	0.03	0.03	0.10	0.06	–	0.15	–	–	–	0.18
Scirtidae	18.55 ± 9.16	–	–	0.05	0.01	–	–	0.28	0.20	0.03	–	0.43	–
Hydroptilidae	15.54 ± 6.56	–	–	0.02	0.06	0.03	–	0.15	0.40	0.24	0.06	0.02	0.03
Dytiscidae	14.55 ± 4.95	–	–	0.19	0.03	0.05	–	0.02	0.08	0.11	0.25	0.26	–
Leptophlebiidae	13.75 ± 5.06	0.03	0.20	–	0.14	0.01	–	–	0.31	0.20	0.01	0.08	–
Empididae	13.44 ± 4.75	–	0.07	0.08	0.12	0.04	–	–	0.32	0.11	0.01	0.02	0.24

Table 7 Indicator value (IndVal) and associated significance (*p*) of macroinvertebrate taxa in the richest microhabitats (see text for details)

Algal			Submerged macrophytes		
Family	IndVal	*p*	Family	IndVal	*p*
Heptageniidae	50.3	0.001	OLIGOCHAETA	32.1	0.002
Gomphidae	26.8	0.003	HYDRACARINA	31.9	0.002
Simuliidae	26.5	0.002	Elmidae	31.7	0.001
Leptoceridae	25.0	0.009	Hydropsychidae	30.9	0.001
			Scirtidae	25.4	0.005
			Nemouridae	25.1	0.006

were more constant between wet and dry periods, a higher variability was observed among the temporary streams. The combination of habitat contraction and fragmentation over time in temporary streams and the greater variation in environmental conditions within temporary streams, lead us to expect aquatic macroinvertebrate community structure to shift seasonally to a greater degree in temporary compared to perennial streams (Bonada et al. 2006).

Seasonal changes in aquatic macroinvertebrate assemblages accompanied changes in habitat features and environmental conditions resulting from stream flow reducation or cessation (Table 3). In general, macroinvertebrate abundance and richness was higher during the wet compared to the dry season, with the exception of the perennial Arroyo Blanco in the Taibilla catchment (discharge was never <1 L s^{-1} in this stream). In the other three study streams, we observed a reduction of habitat area and a decline in microhabitat diversity (substrate types) during the dry season. In Arroyo Blanco during the dry season, a higher incidence of pool habitats may have resulted in a greater variety of environments and refuges for macroinvertebrates that could explain the increase in the above-cited metrics.

Spatial variability in macroinvertebrate community structure was examined at multiple scales, from substrate type to catchment differences (Table 3). We found differences in macroinvertebrate assemblages among both catchments, streams within catchments, mesohabitats within streams, and microhabitats within mesohabitats. Overall, the most important factor in the assemblage of macroinvertebrate communities, accounting for 14% of total variance, was microhabitat (substrate type). Different assemblages were found among the different microhabitats studied within higher inclusive levels of spatial organization. Hence, it was revealed that the importance of substrate affinity was strong enough to arise over major geographical constrains. Since the composition of microhabitats varies among catchments and streams, it is likely that an important part of the spatial variation in aquatic macroinvertebrate

communities at higher spatial scales may be due this finer scale effect. Variability in microhabitats provides a diversity of sites for resting, food acquisition, reproduction, and development, as well as refuge from predators and inhospitable physical conditions (Armitage and Cannan 2000). Our results stress that the nature of substrata is of prime importance for macroinvertebrates.

Despite the existence of regional differences and unique faunal properties of each stream, we observed differences in the comparison of streams according to their temporality (temporary vs. perennial) with these patterns being accentuated in the dry season (Table 3, Fig. 5). Indeed, Indicator Value analysis revealed that several macroinvertebrate families were characteristic of perennial streams (Table 4). Many of the families associated with perennial streams were also characteristic of riffles rather than pools, most of them being EPT taxa (Ephemeroptera, Plecoptera and Trichoptera). This was in agreement with previous results by Bonada et al. (2007), who proposed that the relationship between EPT and OCH may be an easy and appropriate indicator for river temporariness. At the mesohabitat level, a striking distinction was observed between aquatic macroinvertebrate assemblages from pools and riffles (Table 3), especially during the wet season (also see the nMDS ordination analysis in Fig. 5) where there was a significant relationship between the nMDS3 axis and current velocity. Previous studies have revealed how hydraulic conditions, especially current velocity, are among the features that best explain the distribution of aquatic macroinvertebrates (Statzner and Higler 1986; Statzner et al. 1988). Differences were not as strong during the dry season because of the shift towards more lentic conditions in the remaining riffles in both temporary and perennial streams. During the early stages of the dry period, reduced flow and decreased water velocity favors a shift from rheophilic (EPT) to lentic (OCH) taxa (Feminella 1996; Rieradevall et al. 1999; Boulton 2003; Lake 2003; Bonada et al. 2007). This was confirmed also by Indicator Value analysis through the finding of significant indicator taxa associated with either riffles or pools (Table 6). Scarce intermittent riffle areas between some pools still supported some lotic taxa during the dry period in temporary streams in both study catchments. The presence of perennial streams in the area may serve as a source of lotic taxa for re-colonization of temporary stream riffles during the wet season.

Spatial and temporal heterogeneity affect organisms independently, however, knowledge about their interaction could help to refine our understanding of the factors affecting the structure of aquatic macroinvertebrate communities (Keddy 1991; Bonada et al. 2007). Nearly all the interaction effects related to seasonality and temporality examined in this study were significant. This indicated that

the macroinvertebrate communities, whatever their spatial scale of structure, were affected differentially by seasons. Similarly, the temporality interaction meant that these assemblages, both spatial and temporal scales, depended on whether they inhabited a temporary or a perennial stream. Their mutual interaction (Season × Temporality) highlighted that macroinvertebrate assemblages from perennial and temporary streams had to face different conditions in the change of season, as also found by Delucchi (1988). Also, the lack of significance among seasonal change and microhabitat on macroinvertebrate community structure suggested that when microhabitats persisted they harbored specific assemblages. To conclude, our observation on the affinity of certain families of invertebrates for certain microhabitats underscored the idea that fine-scale physical structure played a major role in organizing stream macroinvertebrate assemblages.

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