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The influence of natural flow regimes on macroinvertebrate assemblages in a semiarid Mediterranean basin.

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1　**Abstract**

2　The investigation of flow-ecology relationships constitutes the basis for the

3　development of environmental flow criteria. The need to understand hydrology-ecology

4　linkages in natural systems has increased due to the prospect of climate change and flow

5　regime management, especially in water-scarce areas such as Mediterranean basins. Our

6　research quantified the macroinvertebrate community response at family, genus and

7　species level to natural flow regime dynamics in freshwater streams of a Mediterranean

8　semiarid basin (Segura River, SE Spain), and identified the flow components that

9　influence the composition and richness of biotic assemblages. Flow stability and

10　minimum flows were the principal hydrological drivers of macroinvertebrate

11　assemblages, whereas the magnitude of average and maximum flows had a limited

12　effect. Perennial stable streams were characterised by flow sensitive lotic taxa

13　(Ephemeroptera, Plecoptera, Tricoptera) and intermittent streams by predominately

14　lentic taxa (Odonata, Coleoptera, Heteroptera and Diptera). Relatively minor biological

15　changes were recorded for intermediate flow regime classes along a gradient of flow

16　stability. Seasonal variation and minimum flows are key hydrological components that

17　need to be considered for river management and environmental flows in the Segura

18　River Basin and other Mediterranean basins. The anthropogenic modification of these

19　parameters, due to both human activities and climate change, would probably lead to

20　significant changes in the structure and composition of communities in perennial stable

21　streams. This would be characterised by a reduction of flow sensitive EPT taxa and an

22　increase in more resilient OCHD taxa.

23

24　**Key words: natural flow regime, flow stability, minimum flows, macroinvertebrate**

25　**composition, richness, Segura River Basin, semiarid Mediterranean streams**

26

27　**Introduction**

28

29　The search for links between instream ecology and hydrology has become one of the

30　fundamental issues in contemporary river science (Vaughan *et al*., 2009). Empirical

31　investigation of regional flow-ecology relationships constitutes the basis for the

32　development of environmental flow (e-flow) criteria (Arthington *et al*., 2006; Poff *et*

33　*al*., 2010). In addition, the need to understand ecology-hydrology linkages in natural

34　systems has been highlighted by the need to define reference conditions against which

1   modified dynamics can be compared (Tockner *et al*., 2003). These needs are

2   particularly pressing in the light of predicted climate change (European Environment

3   Agency, 2008) and anthropogenic modification of natural flow regimes, especially in

4   water-scarce areas such as Mediterranean basins.

5

6   Instream hydrological variability, encapsulating elements of the entire flow regime such

7   as the daily, seasonal and annual patterns of discharge, the frequency, timing,

8   predictability and duration of extreme flows (high and low), rates of change in

9   discharge, and the magnitude of flows, are widely recognised as key ecological

10   organizers in fluvial ecosystems (Richter *et al*., 1996; Poff *et al*., 1997; Hart and Finelli,

11   1999; Bunn and Arthington, 2002). Spatial variation of these characteristics is

12   determined by variations in climate and mediated by basin geology, topography and

13   vegetation (Winter, 2001). These hydrological and environmental factors influence the

14   physical habitat for aquatic and riparian biota determining the conditions for

15   reproduction and recruitment and affecting the availability of trophic resources, refuges

16   during adverse situations and opportunities for dispersal (Naiman *et al*., 2008).

17   Consequently, flow variability has strong ecological implications which shape the

18   structure and function of riverine ecosystems from the local to regional scales, and from

19   days (ecological effects) to millennia (evolutionary effects) (Lytle and Poff, 2004). It

20   has been hypothesised that sites with similar hydrological characteristics should share

21   similar faunal community composition, traits and ecosystem functioning (Poff and

22   Ward, 1989). Therefore, as Arthington *et al*. (2006) and Poff *et al*. (2010) suggested,

23   ecological responses of flow regimes to a given anthropogenic change should be

24   broadly similar in rivers with similar natural flow regimes.

25

26   This hypothesis provides a powerful foundation to predict ecological responses to future

27   flow regime changes, constituting the key element of a new holistic framework for

28   developing scientifically-credible regional environmental flows: the ''Ecological Limits

29   of Hydrologic Alteration'' (ELOHA) (Arthington *et al*., 2006; Kennard *et al*., 2010;

30   Poff *et al*., 2010). Therefore, identifying and quantifying specific relationships between

31   flow regimes and biological communities in undisturbed river ecosystems are essential

32   steps to ensure sustainable river management (Arthington *et al*., 2006; Jowett and

33   Biggs, 2009). Such relationships have been studied in general at the regional scale,

34   using macroinvertebrates (e.g. Monk *et al*., 2006; Konrad *et al*., 2008; Kennen *et al*.,

2

1   2010, Armanini *et al.*, 2011), fisheries (e.g Poff and Allan, 1995; Pegg and Pierce,

2   2002; Kennard *et al*., 2007; Snelder *et al*., 2009) or multiple taxonomic groups (e. g.

3   Jowett and Duncan, 1990; Clausen and Biggs, 1997). However, the strength and nature

4   of relationships between the flow regime and the biological assemblage vary depending

5   on the geographical region, the floral or faunal group considered and the taxonomic

6   resolution analysed.

7

8   In some areas, such as Mediterranean-climate regions, organisms have to withstand high

9   intra and interannual hydrological variability, together with frequent natural flow

10 extremes (floods and droughts) (Gasith and Resh, 1999). Species may respond over

11 evolutionary time scales by developing morphological, physiological and/or life-history

12 traits to bear such stresses (Poff *et al*., 1997; Bonada *et al*., 2007a; Bonada *et al*.,

13 2007b). Previous studies of Mediterranean streams (e. g. Bonada *et al*., 2002; Jáimez-

14 Cuéllar *et al*., 2002; Vivas *et al*., 2002; Bonada *et al*., 2004; Mellado, 2005; Sanchez-

15 Montoya *et al*., 2007; Argyroudi *et al*., 2009) as well as other semiarid areas (e. g.

16 Boulton and Lake, 2008) have highlighted the importance of flow permanence on the

17 composition and structure of macroinvertebrate communities. A progressive

18 replacement of Ephemeroptera, Plecoptera and Trichoptera (EPT) taxa by Odonata,

19 Coleoptera and Heteroptera (OCH) taxa has been reported as flow permanence

20 decreases (Sánchez-Montoya *et al*., 2007; Argyroudi *et al*., 2009) or hydrological

21 connectivity is reduced (Bonada *et al*., 2006); although Diptera have also been

22 associated with river sections with low or no flows and dominate lentic habitats in

23 Southeast Spain (Vivas *et al*. 2002). Consequently, flow stability and hydrological

24 extremes (especially low flows) are expected to be the most important components of

25 Mediterranean flow regimes shaping instream assemblages, although its relative

26 importance is still unclear.

27

28 The aim of this study was to quantify the effect of different flow regimes on

29 macroinvertebrate communities. We utilised a dataset containing stream

30 macroinvertebrate records at family, genus and species level across a semiarid

31 Mediterranean region that encompasses a wide gradient of hydrological regimes

32 (Belmar et al 2011) to test these predictions: (1) Flow stability and minimum flows

33 should be the principal hydrological drivers of macroinvertebrate assemblage

34 composition and richness; (2) an increase in the explanatory power of hydrology should

1 occur as taxonomic resolution increases; and (3) a replacement of taxa should take place

2 along a hydrological gradient from permanent streams with stable discharges to streams

3 with high flow intermittence and flow variability. In general, a decrease in the

4 percentage of flow sensitive Ephemeroptera, Plecoptera and Trichoptera families should

5 occur as an increase in the percentage of more resilient Odonata, Coleoptera,

6 Heteroptera and Diptera families takes place.

7

8 **Methods**

9 *Study area*

10 Located in the Southeast of Spain, the Segura River Basin drainage network, including

11 coastal watercourses draining to the Mediterranean Sea, was selected as the study area.

12 The management area of the Segura River Basin, one of the most arid zones of the

13 Mediterranean region, includes watercourses with highly heterogeneous flow regimes.

14 These water-bodies range from perennial rivers, with low seasonal and interannual flow

15 variability, to highly seasonal ephemeral streams (Belmar *et al*., 2011). This variability

16 is due to a strong climatic and altitudinal gradient from NW to SE, despite its relatively

17 small size (18 870 km^2). Climate ranges from wet (>1 000 mm mean annual

18 precipitation) and cold in the high elevation mountains of the NW (>1 000 m.a.s.l.) to

19 semiarid and hot in the SE lowlands (< 350 mm mean annual precipitation). Mean

20 annual temperatures range between 10 and 18 ºC (CHS, 2007). The lithology of the

21 plains is characterised by limestone (karst) and Miocene and Triassic marls, with some

22 small influences of volcanic strata. In contrast, calcites and dolomites dominate the

23 mountainous headwaters. The vegetation is varied and ranges from Mediterranean

24 conifer forests in the NW mountains to arid and semi-arid shrublands in the SE

25 lowlands. This gradient in altitude and climate is coupled with an anthropogenic

26 population density gradient. The river network has low population densities in the

27 forested headwaters, intermediate densities in the agricultural midlands (with major

28 flow regulation) and highly populated cities in the lowlands (Mellado, 2005).

29 Agricultural (52.1%), forest and semi natural (45.2%), and artificial (2.1%) are the

30 dominant landuses in the Segura basin (estimated from Corine Land Cover 2000),

31 making the Segura River Basin one of the most regulated in Europe (Ministerio de

32 Medio Ambiente MMA, 2004). Water resource demands exceed 224% of that available

33 and only 4% of runoff reaches the mouth of the river (Zimmer, 2010). This has resulted

34 in over exploitation of the surface waters, an inter-basin transfer from the Tagus River

1 (a mean of 325 hm^3 yr^{-1}), a mean groundwater extraction of around 478 hm^3/year (over

2 80% of natural recharge) and a high regulatory capacity of 770 hm^3 (over 90% of the

3 natural input) due to 24 dams over 10 m in height (Grindlay *et al*., 2009; Grindlay *et al*.,

4 2011).

5

6 *Hydrological data*

7 A drainage network was derived from a 25 m digital elevation model (DEM) developed

8 by the *Instituto Geológico Nacional* (IGN) and layers available from the website of the

9 Spanish Ministry of Environment, using the ArcGIS software (v 9.2) and the ArcHydro

10 extension (v 1.2) (ESRI, Redlands, California, U.S.A.). The network comprises sections

11 that link each network junction or node, and each node was associated with its

12 corresponding watershed (derived from the DEM). The minimum watershed area to

13 define a river section was 10 km^2, resulting a hydrological network with 390 river

14 sections.

15

16 The hydrological classification developed for the Segura River Basin in Belmar *et al*.

17 (2011) was used to define distinct natural hydrological regimes. This classification was

18 developed using 73 indices based on the "Indicators of Hydrologic Alteration" (IHA)

19 (Mathews and Richter, 2007). These flow indices represent a wide range of

20 ecologically-relevant flow statistics (Richter *et al*., 1996; Olden and Poff, 2003; Monk

21 *et al*., 2006; Mathews and Richter, 2007; Monk *et al*., 2007) and comprise monthly and

22 annual flow statistics including measures of duration of droughts as well as the central

23 tendency and dispersion of flow magnitude (average, low and high flow conditions).

24 Indices related to the frequency, duration and rate of change of high flow events were

25 not used by Belmar *et al*. (2011) due to the absence of daily flow data. Natural flows

26 were derived from a monthly rainfall-runoff model developed by the Centre for

27 Hydrographic Studies (CEDEX, Ministry of Environment and Public Works, Spain), for

28 the period 1980/81 – 2005/06. The classification of the flow regimes recorded

29 comprised eight flow-regime classes (names are provided throughout to aid

30 interpretation) principally characterised by the magnitude of mean annual flow, the

31 duration of droughts and the interannual variation of flow (Table I). The resulting flow

32 regimes can be placed into four broad hydrological groups: (1) mainstem rivers, with

33 perennial flow thorough the year, low interannual variation and an average annual

34 discharge greater than 10 m^3/s (class 1, *large rivers*) or between 2 and 10 m^3/s (class 2,

1   *medium rivers*); (2) perennial stable streams, which only difference respect to mainstem

2   rivers is their reduced average discharge, between 0.3 and 2 m^3/s (class 3, *creeks*) or

3   lower than 0.3 m^3/s (class 4, *headwater streams*); (3) perennial seasonal streams, which

4   eventually cease flowing (although perennial surface water persists) and with peak

5   discharges in winter (class 5, *winter peak flow seasonal streams*) or spring (class 6,

6   *spring peak flow seasonal streams*); and (4) temporary streams, including *intermittent*

7   *streams* (class 7), which do not flow for between 20% and 50% of the time, and

8   *ephemeral streams*, that do not experience flow for more than 50% of the time (class 8).

9   Indices and classes were assigned to their corresponding river section.

10

11   *Macroinvertebrate data*

12   Macroinvertebrate abundance data at family, genus and species level were compiled

13   from the *Biodiversidad* database (*Ecología Acuática* research group, Department of

14   Ecology and Hydrology, University of Murcia, Spain). Species data were available for

15   beetles (Coleoptera), which have been recorded in all kinds of water bodies in the

16   region and have been shown to be good indicators of aquatic biodiversity (Bilton *et al.*,

17   2006; Sanchez-Fernandez *et al.*, 2006). Samples had been taken along 100 m stream

18   transects using a kick-net (500 – 1000 µm) and following the multi-habitat protocol

19   (Jáimez-Cuéllar *et al.*, 2002). Baseline macroinvertebrate samples were collected

20   between 1980 and 2006.

21

22   A minimum of 5 samples per hydrological class were selected, ensuring that they had

23   been collected in freshwater streams (conductivity $<$ 5 000 µS cm^{-1}), above water

24   regulation infrastructures (e.g., dams or weirs) and abstraction areas and in absence of

25   significant evidences of anthropogenic alteration. However, using the criteria above two

26   classes did not have any biological data: *large rivers* (class 1), due to the absence of

27   reference conditions, and *ephemeral streams* (class 8), where no sampling had been

28   undertaken due to their frequent dry status.

29

30   Every sample was collected during the spring or early summer from a different

31   sampling site (Figure 1). This time-period is considered the most representative of the

32   annual macroinvertebrate community composition in Mediterranean streams (Bonada *et*

33   *al.*, 2009). Each site was paired with the closest downstream node in the drainage

34   network. In order to avoid pseudoreplication, when there was more than one site (and

6

1   sample) available for the same node, only the closest to the hydrological node was

2   selected. The final dataset consisted of 35 samples associated with 83 macroinvertebrate

3   families, and 133 genera, and 43 samples associated with 110 Coleoptera species

4   (Appendix A).

5

6   *Environmental data*

7   Climatic, topographic and geologic variables that were assumed to control hydrological

8   processes (Snelder *et al*., 2005) were derived from different GIS layers available for the

9   watershed. Average annual precipitation and air temperature were derived from 1 km

10   grid maps created by the Spanish Ministry of Environment by means of interpolation

11   using data from the Spanish weather stations network (Estrela *et al*., 1999). Drainage

12   area, mean altitude and slope were calculated using the IGN's digital elevation model

13   (DEM). Geology was characterised by the percentage of karst area in each watershed

14   and derived from the "Spain's Map of Karst" 1:1 000 000 developed by the *Instituto*

15   *Geológico y Minero de España* (IGME) and, indirectly, through water conductivity

16   (recorded for every biological sample). We hypothesised that the karstic surface would

17   control groundwater storage and baseflow (Snelder and Biggs, 2002) and that higher

18   conductivities would reflect the predominance of sedimentary marls that result in flashy

19   hydrographs that reflect precipitation patterns (Bracken *et al*., 2008).

20

21   *Data analysis*

22   A Principal Component Factor Analysis (PCFA) (i.e. a Principal Components Analysis

23   (PCA) combined with a Varimax rotation) was used to examine dominant patterns of

24   intercorrelation among the hydrological indices (Belmar *et al*. 2011) and to identify

25   subsets of indices that describe the major sources of variation while minimizing

26   redundancy (i.e. multicollinearity). The Varimax rotation allows obtaining a clearer

27   pattern of loadings (indices clearly marked by high loadings for some axes and low

28   loadings for others) and, therefore, a better interpretation of the meaning of each axis.

29   The hydrological characteristics of each stream in the network were defined through the

30   corresponding PCFA scores (hydrological components) and hydrological class.

31

32   Rare taxa (those collected at fewer than 5% of sampling sites) were removed for

33   multivariate analyses. Abundance data were transformed by means of the Beals

34   smoothing function (Beals, 1984; McCune, 1994) to reduce noise by enhancing the

1   pattern of joint occurrences. This function is appropriate in the current investigation

2   because the data consist of a large number of small sample units (Peck *et al*., 1995) and

3   fulfill the requirements established by De Cáceres and Legendre (2008).

4

5   For each taxonomic level analysed, we performed a non-metric multidimensional

6   scaling (NMDS) ordination based on Bray-Curtis distances among the sampling sites.

7   The strength of the correlation between the NMDS axes and the environmental

8   variables, as well as the hydrological components, was plotted as vectors. In addition,

9   the individual variables and components were analyzed using Pearson coefficients.

10   Covarying (redundant) environmental variables were removed for subsequent model

11   development since the primary objective of the research was to determine the most

12   important flow components influencing macroinvertebrate assemblages and not to

13   distinguish the independent effect of hydrological and environmental drivers.

14

15   Distance based linear models (DistLM) were developed to assess the importance of

16   hydrological components driving taxonomical differences among sites. DistLM

17   calculates a multivariate multiple regression analysis between any symmetric distance

18   matrices, including a permutation test, as described by McArdle and Anderson (2001).

19   The final models were selected following a forward-stepwise procedure. For each

20   taxonomic level, marginal tests determined the variance explained by each flow

21   component and the sequential procedure discarded the variance shared by more than one

22   thereby avoiding the overestimation of their effect on the community.

23

24   Similarly, generalised linear models (GLM) were employed to determine how

25   hydrological components (independent variables) affected faunal richness patterns.

26   Models were constructed using log-transformed data following a forward-stepwise

27   procedure, assuming a Gaussian error distribution for the dependent variables. These

28   variables were the richness of Coleoptera species, number of macroinvertebrate genera,

29   number of macroinvertebrate families and the ratio EPT/EPTOCHD (defined by the

30   richness of Ephemeroptera, Plecoptera, Trichoptera, Odonata, Coleoptera, Heteroptera

31   and Diptera families). The latter is based on the EPT/EPTOCH ratio, which is used to

32   characterise temporary and lotic–lentic conditions in Mediterranean-climate regions

33   (Bonada *et al*., 2006).

34

1   A non-metric single-factor Analysis of Similarity (ANOSIM) was used to test whether

2   assemblage composition differed among hydrological classes and, therefore, if natural

3   regimes can be used to differentiate distinct groups of invertebrate communities. Global

4   R indicates if assemblages are randomly grouped (i.e., R=0) or not (usually $0 < R \leq 1$,

5   although negative values are possible *sensu* Clarke (1993)). R pairwise values were also

6   obtained for each pair of classes, indicating whether intra-class similarities were greater

7   than inter-class similarities (R value close to 1).

8

9   Indicator taxa were defined for each hydrological class using the Indicator Species

10   analysis (IndVal) of Dufrene & Legendre (1997). This analysis generates an indicator

11   value index (IV) for each taxon and class, calculated on the basis of the specifity

12   (maximum when a taxon only occurs in one class) and fidelity (maximum when all sites

13   in a class have the taxon) of each taxon to each class.

14

15   All permutation tests (DistLM, ANOSIM and IndVal) were undertaken using 999

16   permutations. PCFA was undertaken in STATISTICA v 6 (Statsoft, 2001). NMDS and

17   IndVal were conducted using PC-ORD software v 4.42 (McCune and Grace, 2002).

18   ANOSIM and DistLM were undertaken in PRIMER v6 (Clarke and Gorley, 2006).

19   GLM were performed using the R statistical software v 2.12.2 (R Development Core

20   Team, 2008).

21

22   **Results**

23   *Hydrological components*

24   The three first PCFA axes were selected to represent the set of hydrological indices

25   since all of them explained greater than 10% of the variance (46, 28 and 12%,

26   respectively) and the forth axis only explained an additional 4%. The first axis was

27   positively correlated with mean and maximum monthly flows (Table IIa), representing

28   the flow magnitude component of the IHA. The second axis was negatively correlated

29   with the inter-annual coefficients of variation in monthly flows, the intra-annual

30   coefficient of variation in maximum monthly flows and the percentage of time without

31   flows. These variables characterise the inter- and intra-annual variability of the flow

32   regime and as a result this axis was defined as the flow stability component (Table IIb).

33   The third axis, magnitude of minimum flows, was correlated with all the minimum

34   monthly flows and their average value (Table IIc).

1

2 These three hydrological components (PCFA axes) displayed significant positive

3 correlations with mean altitude and precipitation in the watershed, and negative

4 correlations with mean temperature (Table III). In addition, karst surface and slope were

5 positively correlated with flow stability and minimum flows, while drainage area was

6 associated with the magnitude of flow. As anticipated, conductivity displayed a negative

7 association with flow magnitude and stability.

8

9 *Hydrological components determining assemblage composition*

10 The macroinvertebrate NMDS ordinations for different taxonomic resolutions identified

11 similar patterns (Figure 2). Sites were structured along a flow stability gradient from

12 perennial headwater streams (left side, class 4) to intermittent streams (right side, class

13 7), although some classes were widely dispersed (particularly class 6 - spring peak flow

14 seasonal streams). This gradient was associated with several environmental variables

15 and hydrological components (PCFA axes). Perennial stable streams (classes 3 and 4)

16 were predominately located on karstic rocks and sites in higher altitude areas with

17 steeper slopes, higher flow stability and relatively high minimum flows. In contrast,

18 intermittent streams were associated to low slopes, reduced flow stability and low

19 minimum flows, but higher conductivity and air temperature.

20

21 DistLM models indicated that hydrological components accounted for a significant

22 proportion of the variance in the macroinvertebrate community that increased with

23 taxonomic resolution (Table IV): 28% for families, 30% for genus and 38% for

24 Coleoptera species. In all cases, flow stability and minimum flows were the dominant

25 hydrological drivers of taxonomical differences among sites.

26

27 *Response of taxonomic richness to hydrological components*

28 GLM results showed a moderate effect of hydrological variables on the richness of

29 macroinvertebrate families, genera and species (Table V). However, the model obtained

30 for the EPT/EPTOCHD ratio explained 36 % of the variance using flow magnitude and

31 flow stability as independent variables. Gradual changes to the relative richness of EPT

32 families were observed from perennial to intermittent hydrological classes, decreasing

33 along the flow magnitude gradient, whilst the OCHD families displayed the opposite

34 pattern (Figure 3).

1

Differences in assemblage composition among hydrological classes

3   The hydrological classes identified supported significantly different invertebrate

4   assemblages at the family (ANOSIM, R = 0.39; *P*-value < 0.05), genus (ANOSIM, R =

5   0.34; *P*-value < 0.05) and species taxonomic level (ANOSIM, R = 0.40; *P*-value < 0.05)

6   (Table VI). Pair-wise comparisons revealed significant assemblage differences at all

7   taxonomic resolutions between the extremes of the hydrological gradient, perennial

8   stable streams (creeks and headwaters, classes 3 and 4 respectively) and intermittent

9   streams (class 7). Differences between creek and medium river communities (class 2) as

10 well as between creeks and perennial seasonal streams with peak flows during the

11 winter (class 5) increased with the taxonomic resolution, except for the genus level.

12 However, intermittent streams and perennial seasonal streams, both with winter (class

13 5) and spring peak flows (class 6), differed at the genus or at the genus and species

14 levels, respectively. No significant differences were found both between creeks and

15 headwater streams or within seasonal streams (winter and spring peak flows) (Table

16 VI).

17

18 The IndVal analyses determined indicator families for medium rivers (class 2),

19 headwater streams (class 4), spring peak flow seasonal streams (class 6) and intermittent

20 streams (class 7) (Table VII). Medium rivers were characterised by Polycentropodidae

21 (Trichoptera) and Potamanthidae (Ephemeroptera). Headwater streams were defined by

22 one Ephemeroptera (Leptophlebiidae), five families of Trichoptera (Limnephilinae and

23 Beraeidae showed slightly higher Indicator Values) and one Crustacea (Astacidae).

24 Spring peak flow seasonal streams were characterised by Syrphidae (Diptera), which

25 presented the highest Indicator Value in the Segura Basin. Intermittent streams were

26 defined by the presence of Coenagrionidae and Libellulidae (Odonata), Pleidae

27 (Heteroptera) and Noteridae and Hydrophilidae (Coleoptera).

28

29 Indicator genera were found for all classes except creeks (class 3) and winter peak flow

30 seasonal streams (class 5). Medium rivers (class 2) and headwater streams (class 4)

31 were characterised by Ephemeroptera: *Habrophlebia* and *Potamanthus* for the former

32 and *Epeorus* and *Rhithrogena* for the latter. Headwaters were also characterised by

33 seven Coleoptera genera (*Oreodytes*, *Graptodytes*, *Esolus*, *Limnebius*, *Normandia*,

34 *Hydrocyphon* and *Oulimnius*), two Trichoptera (*Rhyacophila* and *Sericostoma*), one

1   Crustacea (*Austropotamobius*) and two Plecoptera (*Perla* and *Isoperla*). Spring peak

2   flow seasonal streams (Class 6) were characterised by one genus of Coleoptera

3   (*Dytiscus*), Hirudinea (*Helobdella*), Molusca (*Pseudamnicola*) and Odonata

4   (*Platycnemis*), with identical indicator values. Intermittent streams (class 7) highlighted

5   the highest number of indicator genera, with the highest Indicator Values for two

6   Diptera (*Dasyhelea* and *Anopheles*), two Heteroptera (*Heliocorisa* and *Anisops*), two

7   Odonata (*Anax* and *Sympetrum*) and two Coleoptera (*Enochrus* and *Berosus*).

8

9   Coleoptera indicator species were detected for all classes except spring peak flow

10   seasonal streams (class 6) (Table VII). Medium rivers (class 2) were primarily

11   characterised by *Hydraena manfredjaechi* and *Normandia nitens*; creeks (class 3) by

12   *Hydraena exasperata*; headwater streams (class 4) by *Helophorus alternans*; winter

13   peak flow seasonal streams (class 5) by *Eretes griseus* and *Ranthus suturalis;* and

14   intermittent streams (class 7) by *Ochthebius delgadoi*.

15

16   **Discussion**

17   *The importance of hydrological components on macroinvertebrate assemblages*

18   The research presented herein supports the general hypothesis that streams with similar

19   flow regimes express greater than random similarity in macroinvertebrate assemblages

20   composition (Resh *et al*., 1988; Poff, 1996). Our results demonstrate relatively strong

21   relationships between community composition and the flow regimes at different

22   taxonomic levels. The strength of these relationships increased with taxonomic

23   resolution suggesting that the species level data yields the strongest relationships and

24   that, where it is available, it should be used in ecohydrological investigations (Monk *et*

25   *al*., 2012). Flow stability and minimum flows were shown to be the principal

26   hydrological drivers/descriptors of the macroinvertebrate community assemblages in the

27   Segura River Basin. Similar results were reported by Chinnayakanehalli *et al*. (2011) in

28   western USA, where baseflows and seasonality were the main predictors of invertebrate

29   composition. However, these results contrast with studies performed in temperate-

30   maritime regions where the magnitudes of mean flows or high flows were reported to be

31   the best predictors of macroinvertebrate assemblages (Clausen and Biggs, 1997; Monk

32   *et al*., 2006; Monk *et al*., 2008).

33

1   Flow stability and minimum flows are major determinants of habitat availability and

2   connectivity that affect aquatic macroinvertebrate assemblages. Flow stability reflects

3   seasonal and interannual patterns of variation, associated with the predictability of flows

4   (Poff, 1996) and the stability of habitat conditions in terms of depth, flow velocity and

5   hydraulic forces (Suen and Herricks, 2009). The variation of stream flow velocity

6   configures stream morphology, water temperature, bed stability and consequently the

7   availability of aquatic habitats for instream organisms (Jowett and Duncan, 1990).

8   Minimum flows represent an extreme of the flow, particularly in the dry season, and

9   reflect the magnitude of seasonal droughts (Smakhtin, 2001). Habitat heterogeneity is

10 reduced under low flow conditions because wetted width, water depth and flow velocity

11 also diminishes (Walters and Post, 2011). In addition, extreme low flows can reduce

12 longitudinal connectivity and increase physical stresses transforming streams into series

13 of isolated pools with higher water temperature and elevated conductivity (Stanley *et*

14 *al.*, 1997). Consequently, droughts have been recognised as an important part of the

15 natural flow regime in intermittent streams (Boulton, 2003; Lake, 2003; Sheldon and

16 Thoms, 2006, Chase, 2007). Species inhabiting intermittent streams must have

17 physiological, behavioural or life-history adaptations to cope with higher conductivities,

18 predation pressures and habitat isolation, such as short life-histories, generalist feeding,

19 aerial respiration or active aerial dispersal (e.g. Bonada *et al.*, 2007b). Under these

20 conditions, dispersal abilities and distances between or along water bodies have been

21 found to be primary determinants of community composition (McAbendroth *et al.*,

22 2005), because active movement when the riverbed is dry is limited to a small number

23 of taxa such as dytiscid and hydrophilid beetles (Boulton *et al.*, 2006; Larned *et al.*,

24 2010).

25

26 Our results indicate a moderately strong relationship between flow regime and faunal

27 richness at the different taxonomic resolutions, weaker than that between flow regime

28 and community composition (especially at species level). Other studies have also

29 reported a moderate effect of minimum flows (Walters and Post, 2011), flow seasonality

30 or the number of days with zero flow (Chinnayakanahalli *et al.*, 2011).

31

32 In Mediterranean regions, ephemeral and intermittent streams are recognised to be

33 significantly less diverse than perennial streams (Bonada *et al.*, 2007b) and to differ in

34 community composition (e.g. Bonada *et al.*, 2006; Argyroudi *et al.*, 2009). Our results

1   found a strong relationship between flow magnitude, and stability, and the ratio of

2   EPT/EPTOCHD. This supports the findings of Bonada *et al*. (2006) and Sánchez-

3   Montoya *et al*. (2007), who reported a decrease in EPT richness as hydrological

4   isolation and the length of the dry period (temporality) increased. EPT taxa in particular

5   tend to occur in riffles, whereas pools support the majority of OCHD taxa (Vivas *et al*.,

6   2002; Oscoz *et al*., 2011). Therefore, riffle permanence has a strong effect on the

7   structure of benthic assemblages in streams (Feminella, 1996).

8

9   *Biological significance of hydrological classes*

10   The six hydrological classes examined in this study indicate distinct macroinvertebrate

11   assemblages at all of the taxonomic resolutions considered. Taxonomic differences were

12   greatest between the classes at both extremes of the flow stability gradient, and are

13   similar to results reported by other studies in the Iberian Peninsula (Sanchez-Montoya *et*

14   *al*., 2007) and in the Segura Basin (Millan *et al*., 2006; Diaz *et al*., 2008; Carbonell *et*

15   *al*., 2011). However, when the other classes were considered, only minor and gradual

16   biological changes along the gradient were detected. Consequently, a simpler

17   classification with four broad hydrological types (Belmar *et al*. 2011) is more

18   appropriate for management purposes in the Segura River Basin and other semi-arid

19   Mediterranean basins: (1) mainstream rivers (classes 1 and 2), (2) perennial stable

20   streams (classes 3 and 4), (3) perennial seasonal streams (classes 5 and 6) and (4)

21   temporary streams (classes 7 and 8).

22

23   We found a clear agreement between the selection of indicator taxa in this study and

24   those from other studies in the Mediterranean region in Spain (e.g., Bonada *et al*., 2004;

25   Mellado, 2005; Sanchez-Montoya *et al*., 2007). Headwater streams were characterised

26   by taxa that inhabit the upper reaches of rivers with colder and oxygen-rich waters, in

27   areas of cobbles and small boulders. These sites supported the greatest presence of

28   Ephemeroptera (Leptophlebiidae) and Trichoptera (e.g. Limnephilinae and Beraidae)

29   families and were also characterised by the presence of typically reophilic

30   Ephemeroptera (*Epeorus* and *Rhitrogena*) and Plecoptera (*Perla* and *Isoperla*) genera.

31   In general, these taxa are considered to have high oxygen requirements and their

32   presence is associated with good water quality (Jacobsen *et al*., 2003). Medium rivers

33   were characterised by Ephemeroptera genera, such as *Potamanthus* and *Habrophlebia,*

34   typical of reaches of large rivers where low to moderate flow velocities, associated with

14

1   gravel and sand substrates, predominate (Puig *et al*., 1984). Intermittent streams were

2   associated with taxa from shallow standing waters or those with reduced velocities, such

3   as numerous Coleoptera (e.g., *Enochrus, Berosus* and *Noterus*), Odonata (e.g., *Anax,*

4   *Sympetrum* and *Isnchnura*) and Heteroptera (e.g., *Heliocorisa*, *Anisops* and *Sigara*),

5   with highly mobile adults (Bilton *et al*., 2001) and short life-history development times

6   (Velasco *et al*., 1990; Barahona *et al*., 2005). The importance of Coleoptera in

7   temporary streams highlighted in this study has also been demonstrated in several

8   previous studies (Picazo *et al*., 2012).

9

10   *Implications to river restoration and conservation*

11   Based on the results presented, the magnitude of monthly minimum flows and the inter-

12   and intra-annual natural variation of flows are two key flow components for the

13   definition of environmental flows in Mediterranean basins. Currently, many historically

14   perennial streams have already become intermittent due to excessive abstraction and

15   impoundment, while others exhibit an inverse seasonal pattern due to water release from

16   reservoirs during the summer months (Belmar *et al*., 2010). Such hydrological

17   modifications could become more intense in the future as a result of climate change

18   (European Environment Agency, 2008), which is expected to intensify supra-seasonal

19   droughts and lead to more anthropogenic water withdrawals. This may lead to the

20   depletion of groundwater in local aquifers and, therefore, flow intermittency in

21   previously perennial streams. Such intermittency could result in significant changes to

22   the faunal community, increasing the risk of local extinctions of drought-sensitive taxa.

23   This effect has already been documented in desert streams (Bogan and Lytle, 2011),

24   where simplified pools composed of the most tolerant and resilient species have been

25   described (*sensu* Cote and Darling, 2010). Therefore, the conservation and, where

26   appropriate, restoration of natural hydrological variability is crucial for the maintenance

27   of riverine ecosystem integrity (i.e., ecosystem structure and function) (Thoms, 2006;

28   Vaughan *et al*., 2009).

29

30   Future research should focus on how the degree of hydrological alteration affects

31   aquatic communities and ecosystem functioning. Aquatic macroinvertebrates are ideal

32   candidates for the development of hydro-ecological models to quantify the effects of

33   flow reduction (Castella *et al*., 1995; Niu and Dudgeon, 2011a; Niu and Dudgeon,

34   2011b). Using the four broad hydrological types stated we will be able to provide a

1 reference framework in the near future to achieve a more sustainable management of

2 ecohydrological resources in the Segura River Basin and other Mediterranean basins,

3 fulfilling the objectives of ELOHA and EU Water Framework Directive criteria.

4

Table I. Mean and standard deviation of the mean annual flow (MADIS), time with zero flow (D_L) and coefficient of variation in annual flows (CV_{INTER}) for the natural flow regime classes defined in the Segura River Basin (Belmar *et al*. 2011).

Hydrological class	Number of stream sections	MADIS (m^3/s)	D_L (%)	CV_{INTER}
Class 1: Perennial large size rivers	17	11.30 (± 0.74)	0.00 (± 0.00)	0.52 (± 0.01)
Class 2: Perennial medium size rivers	31	3.76 (± 2.26)	0.00 (± 0.00)	0.50 (± 0.13)
Class 3: Perennial stable creeks	21	1.00 (± 0.45)	0.00 (± 0.00)	0.32 (± 0.09)
Class 4: Perennial stable headwater streams	43	0.18 (± 0.17)	0.00 (± 0.00)	0.26 (± 0.13)
Class 5: Perennial winter peak flow seasonal streams	26	0.37 (± 0.09)	2.31 (± 2.06)	1.39 (± 0.29)
Class 6: Perennial spring peak flow seasonal streams	110	0.06 (± 0.06)	4.46 (± 6.32)	0.81 (± 0.30)
Class 7: Temporary intermittent streams	101	0.04 (± 0.04)	24.88 (± 13.15)	1.71 (± 0.38)
Class 8: Temporary ephemeral streams	41	0.01 (± 0.01)	61.90 (± 20.21)	3.43 (± 0.84)

17

Table II. Pearson correlation coefficients between the three rotated PCFA axes and the 73 hydrological indices. Coefficients higher than |0.70| are in bold letter. Horizontal lines separate indices associated to the three flow components represented by the axes: (a) magnitude (average and maximum flows), 1st axis (46% of variance); (b) flow stability, 2nd axis (28% of variance); and (c) minimum flows, 3rd axis (12% of variance).

	Variable	Description	PCFA axis 1st	2nd	3rd
(a)	$M_A 1$	Mean monthly flow (October)	**0.98**	0.13	0.02
	$M_A 2$	Mean monthly flow (November)	**0.98**	0.13	0.02
	$M_A 3$	Mean monthly flow (December)	**0.99**	0.12	0.05
	$M_A 4$	Mean monthly flow (January)	**0.98**	0.14	0.04
	$M_A 5$	Mean monthly flow (February)	**0.98**	0.14	0.04
	$M_A 6$	Mean monthly flow (March)	**0.99**	0.12	0.03
	$M_A 7$	Mean monthly flow (April)	**0.98**	0.14	0.02
	$M_A 8$	Mean monthly flow (May)	**0.98**	0.15	0.04
	$M_A 9$	Mean monthly flow (June)	**0.98**	0.15	0.03
	$M_A 10$	Mean monthly flow (July)	**0.97**	0.16	0.04
	$M_A 11$	Mean monthly flow (August)	**0.97**	0.16	0.05
	$M_A 12$	Mean monthly flow (September)	**0.98**	0.13	0.02
	$M_A 16$	Mean annual flow divided by catchment area	0.18	0.50	0.35
	MEDDIS/A	Median annual discharge divided by catchment area	0.22	0.52	0.35
	$M_H 1$	Mean of the maximum monthly flows (October)	**0.96**	0.08	0.01
	$M_H 2$	Mean of the maximum monthly flows (November)	**0.96**	0.06	0.07
	$M_H 3$	Mean of the maximum monthly flows (December)	**0.91**	0.00	0.05
	$M_H 4$	Mean of the maximum monthly flows (January)	**0.97**	0.14	0.08
	$M_H 5$	Mean of the maximum monthly flows (February)	**0.97**	0.15	0.11
	$M_H 6$	Mean of the maximum monthly flows (March)	**0.94**	0.03	0.02
	$M_H 7$	Mean of the maximum monthly flows (April)	**0.98**	0.10	0.04
	$M_H 8$	Mean of the maximum monthly flows (May)	**0.98**	0.15	0.08
	$M_H 9$	Mean of the maximum monthly flows (June)	**0.98**	0.13	0.00
	$M_H 10$	Mean of the maximum monthly flows (July)	**0.98**	0.13	-0.03
	$M_H 11$	Mean of the maximum monthly flows (August)	**0.98**	0.13	-0.03
	$M_H 12$	Mean of the maximum monthly flows (September)	**0.95**	0.05	-0.04
	$M_H 13$	Mean of the mean maximum flows for all months	**0.98**	0.08	0.04
	MADIS	Mean annual flow for all years	**0.98**	0.14	0.03
	RANGE	Maximum annual discharge minus minimum annual discharge	**0.98**	0.06	-0.05
	Q1	Percentile flow with the annual discharge exceeded 1% of time	**0.99**	0.09	0.01
	Q50	Median annual flow for all years	**0.97**	0.14	0.03
(b)	$CV_A 1$	Coefficient of variation (October)	-0.08	**-0.83**	-0.30
	$CV_A 2$	Coefficient of variation (November)	-0.12	**-0.86**	-0.15
	$CV_A 3$	Coefficient of variation (December)	-0.09	**-0.84**	-0.19
	$CV_A 4$	Coefficient of variation (January)	-0.19	**-0.88**	-0.21
	$CV_A 5$	Coefficient of variation (February)	-0.21	**-0.89**	-0.17
	$CV_A 6$	Coefficient of variation (March)	-0.19	**-0.81**	-0.25
	$CV_A 7$	Coefficient of variation (April)	-0.26	**-0.90**	-0.20
	$CV_A 8$	Coefficient of variation (May)	-0.02	**-0.91**	-0.19
	$CV_A 9$	Coefficient of variation (June)	0.02	**-0.83**	-0.35
	$CV_A 10$	Coefficient of variation (July)	0.09	**-0.82**	-0.37
	$CV_A 11$	Coefficient of variation (August)	0.09	**-0.84**	-0.36
	$CV_A 12$	Coefficient of variation (September)	-0.03	**-0.81**	-0.34
	$M_A 13$	Range divided by median monthly flow	-0.06	**-0.90**	-0.03
	$M_A 14$	Interquartile divided by median monthly flow	0.09	**-0.80**	0.05
	CV_{INTRA}	Coefficient of variation in mean monthly flows	0.02	**-0.90**	-0.03
	$M_A 15$	Mean minus median monthly flow divided by median monthly flow	-0.15	**-0.73**	0.06
	$M_A 17$	Range divided by median annual flow	-0.22	**-0.93**	-0.10
	$M_A 18$	Interquartile divided by median annual flow	-0.17	**-0.83**	-0.05
	$M_A 19$	Mean minus median annual flow divided by median annual flow	-0.17	**-0.84**	0.03
	CV_H	Coefficient of variation in mean maximum monthly flows	-0.27	**-0.79**	-0.08
	D_L	Percentage of months with zero flow	-0.38	**-0.75**	-0.24
	CV_{INTER}	Coefficient of variation in annual flows for all years	-0.21	**-0.92**	-0.14
	Q5/Q50	Q5 divided median monthly flow	-0.23	**-0.88**	-0.08
	Q10/Q50	Q10 divided median monthly flow	-0.21	**-0.87**	-0.06
	STDEV	Standard deviation of annual discharge	**0.99**	0.07	-0.09
	AMAX/Q50	Maximum annual discharge divided by Q50	-0.23	**-0.92**	-0.08
	AMIN/Q50	Minimum annual discharge divided by Q50	-0.25	0.63	0.42
	I_H	Q5 divided mean monthly flow	0.08	-0.04	-0.27
	I_L	Q95 divided mean monthly flow	-0.26	0.60	0.48
(c)	$M_L 1$	Mean minimum monthly flow (October)	0.02	0.19	**0.92**
	$M_L 2$	Mean minimum monthly flow (November)	0.04	0.19	**0.92**
	$M_L 3$	Mean minimum monthly flow (December)	0.03	0.19	**0.92**
	$M_L 4$	Mean minimum monthly flow (January)	0.11	0.20	**0.77**
	$M_L 5$	Mean minimum monthly flow (February)	0.08	0.18	**0.88**
	$M_L 6$	Mean minimum monthly flow (March)	0.04	0.18	**0.93**
	$M_L 7$	Mean minimum monthly flow (April)	0.10	0.23	**0.78**
	$M_L 8$	Mean minimum monthly flow (May)	0.03	0.17	**0.93**
	$M_L 9$	Mean minimum monthly flow (June)	0.00	0.17	**0.90**
	$M_L 10$	Mean minimum monthly flow (July)	0.01	0.17	**0.90**
	$M_L 11$	Mean minimum monthly flow (August)	0.04	0.16	**0.89**
	$M_L 12$	Mean minimum monthly flow (September)	0.05	0.16	**0.88**
	$M_L 13$	Mean of the mean minimum flows for all months	0.06	0.20	**0.96**

Table III. Pearson correlation coefficients between environmental variables and hydrological components (PCFA axes). Significant correlations (p<0.05) are in bold letter.

Environmental variable	Flow magnitude	Flow stability	Minimum flows
Mean precipitation (mm)	**0.26**	**0.64**	**0.39**
Conductivity ($\mu S/cm^2$)	**-0.28**	**-0.54**	-0.21
Mean altitude (m)	**0.34**	**0.64**	**0.34**
Mean slope (º)	0.24	**0.37**	**0.27**
Karst surface (%)	0.21	**0.36**	**0.37**
Mean temperature (º C)	**-0.37**	**-0.57**	**-0.27**
Drainage area (km^2)	**0.83**	-0.16	-0.14

Table IV. Results of the DistLM analyses for each taxonomic level. Significance levels are indicated with asterisks (*: p≤0.05; **: p≤0.01; ***: p≤0.001).

Hydrological component	Macroinvertebrate families		Macroinvertebrate genera		Coleoptera species	
	Marginal (%)	Sequential (%)	Marginal (%)	Sequential (%)	Marginal (%)	Sequential (%)
Flow magnitude	7	6*	6	5	4	3*
Flow stability	12***	9**	24***	24***	27***	27***
Minimum flows	13**	13***	11**	6*	16***	8***
Total (%)		**28**		**30**		**38**

20

Table V. GLM analyses for the different dependent variables, based on richness. Significance levels are indicated with asterisks (*: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$).

Dependent variable	Variance explained (%)	Explanatory hydrological components
EPT/EPTOCHD	36	Flow magnitude**, flow stability*
Macroinvertebrate families	21	Minimum flows**
Macroinvertebrate genera	24	Minimum flows**
Coleoptera species	17	Minimum flows**

21

Table VI. Results of ANOSIM analyses. Significance levels are indicated with asterisks (*: p≤0.05; **: p≤0.01; ***: p≤0.001).

Classes	Macroinv. families	Macroinv. genera	Coleop. species
2, 5	0.22	0.15	0.50**
2, 7	0.59*	0.62*	0.49**
3, 2	0.26*	0.06	0.56**
3, 5	0.25*	0.20	0.76***
3, 6	0.49**	0.30*	0.05
3, 7	0.50**	0.53**	0.86***
4, 2	0.85**	0.67**	0.37**
4, 3	0.00	-0.02	-0.09
4, 5	0.81**	0.80**	0.66***
4, 6	0.53**	0.77**	0.09
4, 7	0.88**	0.86**	0.77***
5, 7	0.29	0.42*	0.17
6, 2	0.27**	0.33**	-0.01
6, 5	0.12	0.02	0.16
6, 7	0.09	0.44*	0.38**
Global R	0.39***	0.34***	0.40***

Class 2: Perennial medium rivers
Class 3: Perennial stable creeks
Class 4: Perennial stable headwater streams
Class 5: Perennial winter peak flow seasonal streams
Class 6: Perennial spring peak flow seasonal streams
Class 7: Temporary intermittent streams

Table VII. Indicator taxa (IV≥25 & p ≤ 0.05) for each hydrological class and taxonomic level.

Hydrological class	Macroinvertebrate families	IV (%)	Macroinvertebrate genera	IV	Coleoptera species	IV (%)
2. Perennial medium rivers	Polycentropodidae	31	Habrophlebia	28	Hydraena manfredjaechi	47
	Potamanthidae	27	Potamanthus	27	Normandia nitens	47
					Limnius intermedius	44
					Ochthebius difficilis	34
					Limnius opacus	28
					Pomatinus substriatus	25
3. Perennial stable creeks					Hydraena exasperata	55
					Ilybius meridionalis	50
					Ochthebius bellieri	46
					Limnius volckmari	34
					Agabus brunneus	32
					Hydroporus marginatus	30
					Ochthebius bonnairei	30
					Anacaena bipustulata	29
					Deronectes moestus	29
					Hydraena carbonaria	29
					Hydraena capta	27
					Hydraena rufipennis	26
					Stictonectes epipleuricus	26
					Agabus didymus	25
4. Perennial stable headwater streams	Leptophlebiidae	41	Oreodytes	45	Helophorus alternans	29
	Limnephilinae	29	Epeorus	35	Helophorus brevipalpis	28
	Beraeidae	29	Rhyacophila	31	Laccobius obscuratus	28
	Brachycentridae	28	Graptodytes	30	Hydroporus tessellatus	26
	Rhyacophilidae	27	Austropotamobius	30	Limnebius cordobanus	26
	Sericostomatidae	26	Esolus	29		
	Astacidae	26	Sericostoma	29		
			Limnebius	28		
			Normandia	27		
			Hydrocyphon	27		
			Rhithrogena	27		
			Oulimnius	25		
			Perla	25		
			Isoperla	25		
5. Perennial winter peak flow seasonal streams					Eretes griseus	76
					Rhantus suturalis	76
					Hydrochus nooreinus	52
					Stictotarsus duodecimpustulatus	52
					Berosus hispanicus	34
					Hydrophilus pistaceus	32
					Laccobius moraguesi	31
					Agabus ramblae	29
6. Perennial spring peak flow seasonal streams	Syrphidae	85	Dytiscus	35		
			Helobdella	35		
			Pseudamnicola	35		
			Platycnemis	35		
7. Temporary intermittent streams	Noteridae	35	Dasyhelea	63	Ochthebius delgadoi	42
	Pleidae	35	Anopheles	63	Enochrus politus	38
	Coenagrionidae	30	Heliocorisa	63	Helophorus fulgidicollis	38
	Libellulidae	28	Anisops	63	Laccophilus minutus	38
	Hydrophilidae	26	Anax	52	Ochthebius auropallens	38
			Enochrus	48	Ochthebius grandipennis	38
			Sympetrum	48	Ochthebius viridis fallaciosus	38
			Berosus	45	Ochthebius jaimei	35
			Sigara	45	Helochares lividus	27
			Plea	45		
			Ischnura	45		
			Noterus	42		
			Potamopyrgus	42		
			Cercion	42		
			Libellula	42		
			Helochares	41		
			Bidessus	40		
			Procambarus	40		
			Limnophora	40		
			Tipula	40		
			Microvelia	40		
			Agabus	36		
			Dryops	32		
			Laccobius	32		
			Orthetrum	32		
			Gerris	30		
			Nebrioporus	27		
			Cloeon	27		
			Micronecta	25		

Appendix A. Taxa collected in the Segura Basin grouped by taxonomic order.

Hirudinea
Erpobdellidae
Dina
Glossiphoniidae
Helobdella
Mollusca
Ancylidae
Ancylus
Ferrissia
Hydrobiidae
Mercuria
Potamopyrgus
Pseudamnicola
Lymnaeidae
Lymnaea
Melanopsidae
Melanopsis
Physidae
Physella
Planorbidae
Gyraulus
Planorbarius
Sphaeriidae
Pisidium
Crustacea
Astacidae
Austropotamobius
Atyiidae
Atyaephyra
Cambaridae
Procambarus
Gammaridae
Echinogammarus
Coleoptera
Dryopidae
Dryops
Dryops gracilis (Karsch, 1881)
Dryops sulcipennis (Costa, 1883)
Pomatinus
Pomatinus substriatus (Müller, 1806)
Dytiscidae
Eretes griseus Motschulsky 1849
Hygrotus confluens (Fabricius, 1787)
Hyphydrus aubei Ganglbauer, 1892
Ilybius meridionalis Aubé, 1836
Meladema coriacea Castelnau, 1834
Rhantus suturalis (McLeay, 1825)
Stictotarsus duodecimpustulatus (Fabricius, 1792)
Agabus
Agabus biguttatus (Olivier, 1795)
Agabus bipustulatus (Linnaeus, 1767)
Agabus brunneus (Fabricius, 1798)
Agabus didymus (Olivier, 1795)
Agabus nebulosus (Forster, 1771)
Agabus nitidus (Fabricius, 1801)
Agabus paludosus (Fabricius, 1801)
Agabus ramblae Millán & Ribera, 2001
Bidessus
Bidessus minutissimus (Germar, 1824)
Deronectes
Deronectes depressicollis (Rosenhauer, 1856)
Deronectes fairmairei (Leprieur, 1876)
Deronectes hispanicus (Rosenhauer, 1856)
Deronectes moestus Leprieur, 1876
Dytiscus
Graptodytes
Graptodytes fractus (Sharp, 1880-82)
Graptodytes ignotus (Mulsant, 1861)
Graptodytes varius (Aubé, 1836)
Hydroglyphus
Hydroglyphus geminus (Fabricius, 1792)
Hydroglyphus signatellus (Klug, 1834)
Hydroporus
Hydroporus discretus Fairmaire, 1859
Hydroporus lucasi Reiche, 1866
Hydroporus marginatus (Duftschmid, 1805)
Hydroporus nigrita (Fabricius, 1792)
Hydroporus pubescens (Gyllenhal, 1808)
Hydroporus tessellatus Drapiez, 1819
Laccophilus
Laccophilus hyalinus (De Geer, 1774)
Laccophilus minutus (Linnaeus, 1758)
Nebrioporus
Nebrioporus bucheti cazorlensis (Lagar, Fresneda & Hernando, 1987)
Nebrioporus clarki (Wollaston, 1862)

Oreodytes
Stictonectes
Stictonectes epipleuricus (Seidlitz, 1887)
Stictonectes optatus (Seidlitz, 1887)
Yola
Yola bicarinata (Latreille, 1804)
Elmidae
Elmis
Elmis aenea (Müller, 1806)
Elmis maugetii maugetii Latreille, 1798
Elmis rioloides (Kuwert, 1890)
Esolus
Esolus parallelepipedus (Müller, 1806)
Limnius
Limnius intermedius Fairmaire, 1881
Limnius opacus Müller, 1806
Limnius volckmari (Panzer, 1793)
Normandia
Normandia nitens (Müller, 1817)
Normandia sodalis (Erichson, 1847)
Oulimnius
Oulimnius troglodytes (Gyllenhal, 1827)
Oulimnius tuberculatus perezi Sharp, 1872
Potamophilus
Riolus
Riolus cupreus (Müller, 1806)
Riolus illiesi Steffan, 1958
Gyrinidae
Aulonogyrus
Aulonogyrus striatus (Fabricius, 1792)
Gyrinus
Gyrinus dejeani Brullé, 1832
Orectochilus
Orectochilus villosus (Müller, 1776)
Haliplidae
Peltodytes rotundatus (Aubé, 1836)
Haliplus
Haliplus lineatocollis (Marsham, 1802)
Haliplus mucronatus Stephens, 1832
Helophoridae
Helophorus
Helophorus alternans Gené, 1836
Helophorus brevipalpis Bedel, 1881
Helophorus fulgidicollis Motschuslky, 1860
Helophorus occidentalis Angus, 1983
Helophorus nubilus Fabricius, 1776
Helophorus seidlitzii Kuwert, 1885
Hydraenidae
Hydraena
Hydraena capta Orchymont, 1936
Hydraena carbonaria Kiesenwetter, 1849
Hydraena exasperata Orchymont, 1935
Hydraena hernandoi Fresneda & Lagar, 1990
Hydraena manfredjaechi Delgado & Soler, 1991
Hydraena pygmaea Waterhouse, 1833
Hydraena quilisi Lagar, Fresneda & Hernando, 1987
Hydraena rufipennis Boscá Berga, 1932
Hydraena servilia Orchymont, 1936
Limnebius
Limnebius cordobanus Orchymont, 1938
Limnebius maurus Balfour-Browne, 1978
Limnebius oblongus Rey, 1883
Ochthebius
Ochthebius auropallens Fairmaire, 1879
Ochthebius bellieri Kuwert, 1887
Ochthebius bonnairei Guillebau, 1896
Ochthebius delgadoi Jäch, 1994
Ochthebius difficilis Mulsant, 1844
Ochthebius dilatatus Stephens, 1829
Ochthebius (Enicocerus) exsculptus Germar, 1824
Ochthebius grandipennis Fairmaire, 1879
Ochthebius jaimei Delgado & Jäch, 2007
Ochthebius quadrifoveolatus Wollaston, 1854
Ochthebius tudmirensis Jäch, 1997
Ochthebius viridis fallaciosus Ganglbauer, 1901
Hydrochidae
Hydrochus
Hydrochus grandicollis Kiesenwetter, 1870
Hydrochus nooreinus Henegouven & Sáinz-Cantero, 1992
Hydrophilidae
Anacaena bipustulata (Marsham, 1802)
Anacaena globulus (Paykull, 1798)
Anacaena lutescens (Stephens, 1829)
Coelostoma hispanicum (Küster, 1848)
Hydrophilus pistaceus (Castelnau, 1840)

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Appendix A (cont.).

Berosus
Berosus hispanicus Küster, 1847
Enochrus
Enochrus ater (Kuwert, 1888)
Enochrus politus Küster, 1849
Helochares
Helochares lividus (Forster, 1771)
Laccobius
Laccobius bipunctatus (Fabricius, 1775)
Laccobius hispanicus Gentili, 1974
Laccobius gracillis gracillis Motschulsky, 1849
Laccobius moraguesi Régimbart, 1898
Laccobius neapolitanus Rottenberg, 1874
Laccobius obscuratus Rottenberg, 1874
Laccobius sinuatus Motschulsky, 1849
Laccobius ytenensis Sharp, 1910
Noteridae
Noterus
Noterus laevis Sturm, 1834
Scirtidae
Cyphon
Elodes
Hydrocyphon
Diptera
Anthomyiidae
Limnophora
Athericidae
Atrichops
Ibisia
Ceratopogonidae
Dasyhelea
Chironomidae
Chironomini
Corynoneura
Tanytarsini
Culicidae
Anopheles
Diamesinae
Dixidae
Empididae
Ephydridae
Hemerodromiinae
Limoniidae
Eloeophyla
Pseudolimnophila
Orthocladiinae
Simuliidae
Stratiomyidae
Oxycera
Syrphidae
Tabanidae
Tabanus
Tanypodinae
Tipulidae
Tipula
Ephemeroptera
Baetidae
Baetis
Centroptilum
Cloeon
Procloeon
Caenidae
Caenis
Ephemerellidae
Ephemerella
Serratella
Torleya
Ephemeridae
Ephemera
Heptageniidae
Ecdyonurus
Epeorus
Rhithrogena
Leptophlebiidae
Habroleptoides
Habrophlebia
Paraleptophlebia
Polymirtacidae
Ephoron
Potamantidae
Potamanthus
Hemiptera
Aphelocheiridae
Aphelocheirus

Corixidae
Heliocorisa
Micronecta
Sigara
Gerridae
Aquarius
Gerris
Hydrometridae
Hydrometra
Naucoridae
Naucoris
Nepidae
Nepa
Notonectidae
Anisops
Notonecta
Pleidae
Plea
Veliidae
Microvelia
Velia
Odonata
Aeshnidae
Anax
Boyeria
Calopterigydae
Calopteryx
Coenagrionidae
Cercion
Ischnura
Pyrrhosoma
Cordulegastridae
Cordulegaster
Gomphidae
Gomphus
Onychogomphus
Libellulidae
Libellula
Orthetrum
Sympetrum
Platycnemididae
Platycnemis
Plecoptera
Leuctridae
Leuctra
Nemouridae
Nemoura
Protonemura
Perlidae
Dinocras
Eoperla
Perla
Perlodidae
Isoperla
Trichoptera
Beraeidae
Brachycentridae
Micrasema
Drusinae
Hydropsychidae
Cheumatopsyche
Hydropsyche
Hydroptilidae
Agraylea
Hydroptila
Lepidostomatidae
Lasiocephala
Leptoceridae
Athripsodes
Limnephilidae
Allogamus
Halesus
Stenophylax
Limnephilinae
Polycentropodidae
Psychomyiidae
Metalype
Tinodes
Rhyacophilidae
Rhyacophila
Sericostomatidae
Sericostoma

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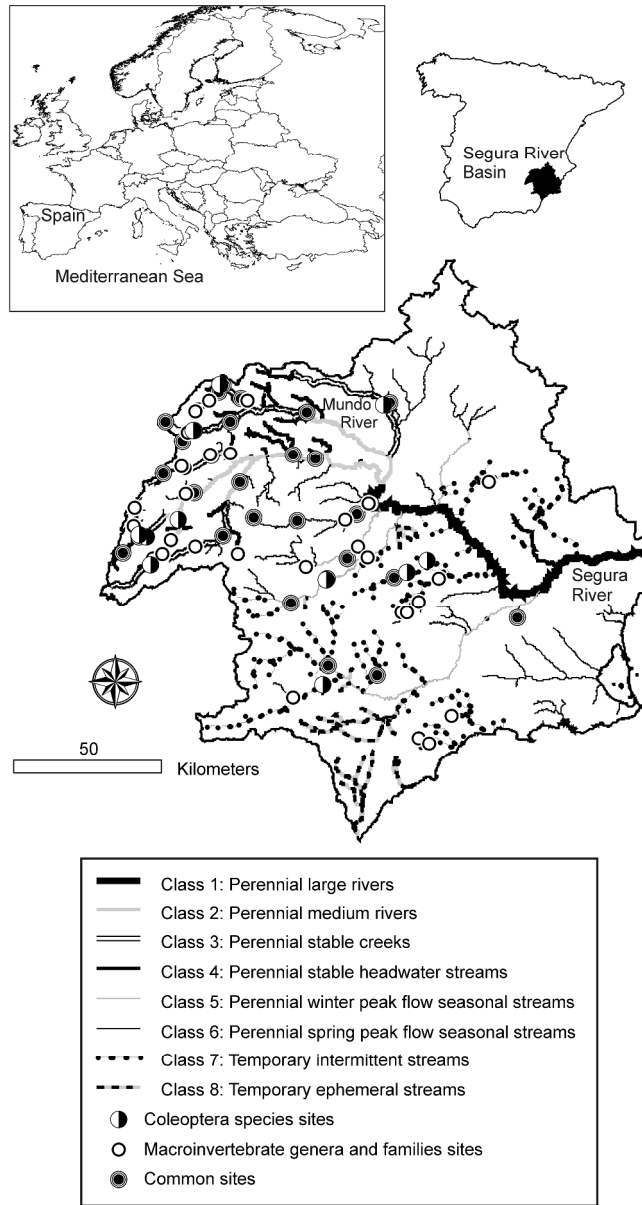41
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Figure 1. Location of the study area, hydrological classes in the river network and sampling sites.
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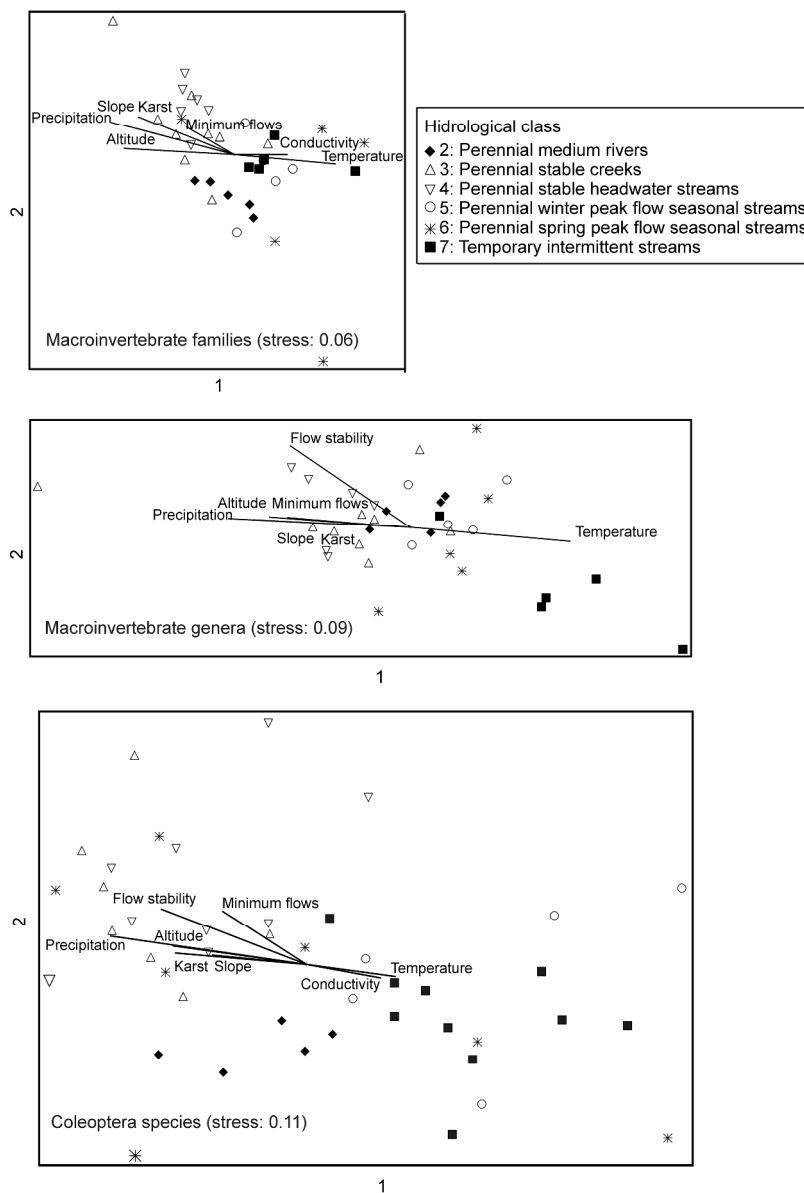51
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Figure 2. NMDS plots of sites for each taxonomic level. The magnitudes of the correlations between the NDMS axes and the hydrological components as well as the environmental variables are shown as vectors.
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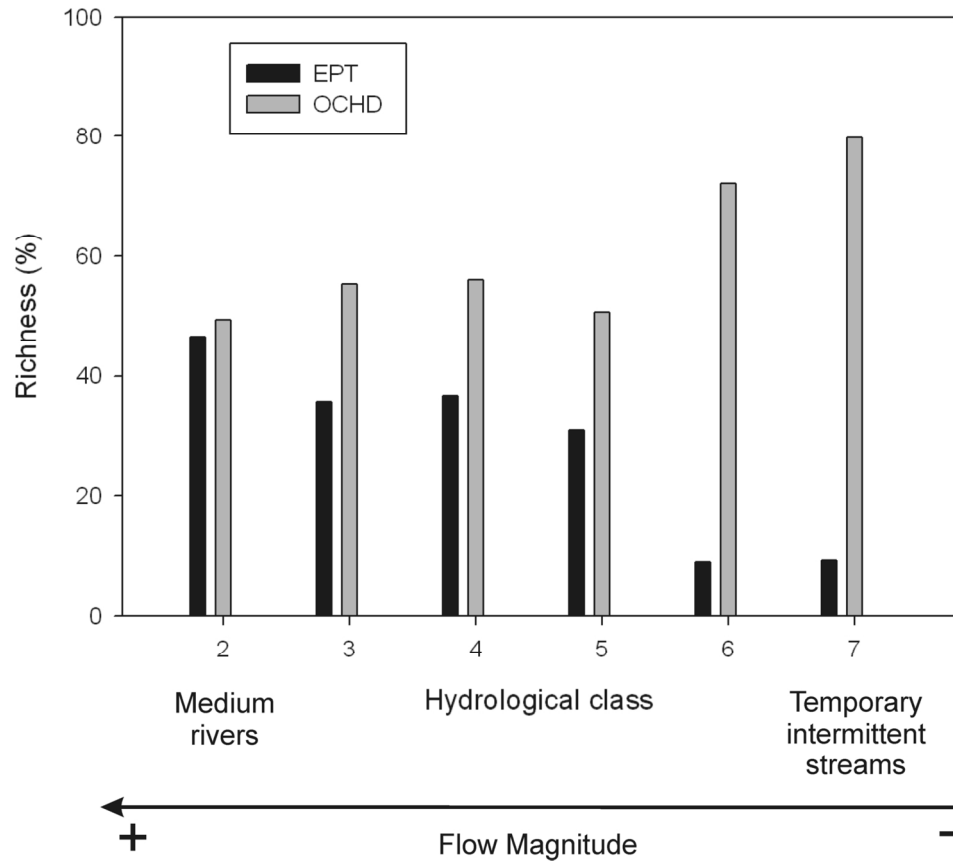51
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Figure 3. Variation of the percentage of families of the EPT and OCDH groups in the different hydrological classes along the flow magnitude gradient.
140x130mm (300 x 300 DPI)